FACTORS AFFECTING APHID POPULATIONS ON BROAD BEANS

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ABSTRACT

Exclusion techniques were used to study the effect of predators on aphid populations on broad beans (*Vicia faba*) in the field. Birds caused high mortality among populations of *Megoura viciae* and both biotypes of *Acyrthosiphon pisum* but *Aphis fabae* was apparently unaffected by birds.

The continued build-up of aphids in cages covered with Terylene net was mainly due to the fact that emigration was prevented. Invertebrate predators had no obvious impact on the aphid populations.

Studies on seasonal variation in abundance of invertebrate predators and parasites in 1970 indicated that predators are active early enough to suppress the build-up of aphid populations but that their effectiveness is limited by the restricted height range for oviposition of species occurring in spring and by the marked preference of ovipositing adults (particularly syrphids) for plants with high aphid densities.

The decline in populations of green and pink *A. pisum* and *M. viciae* on potted bean seedlings in 1970 appeared to be due mainly to dispersal of the aphids occasioned by harassment of the aphids by adult hymenopterous parasites.

Rate of development and fecundity were determined for each species/biotype at three constant temperatures. Temperature significantly affected the rate of development and the reproductive rate, and hence the intrinsic and finite rates of increase.

The theoretical threshold temperature of development was calculated for each species/biotype and the feasibility of using temperature summation to predict rate of population growth was tested in field experiments.

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GENERAL INTRODUCTION

Broad beans (*Vicia faba*) are subject to attack by several aphid species, including *Aphis fabae* Scop (Sub-family : Aphidinae), *Megoura viciae* Bckt. and *Acyrthosiphon pisum* (Harris) (Sub-family : Dactynotinae). Despite the suitability of *V. faba* as a host plant for all three species, only one - *A. fabae* - is regarded as a serious pest of broad beans in the field. Apart from direct injury to the host plant, which may result in a considerable reduction in yield, *A. fabae* excretes large quantities of honeydew which provide a suitable substrate for sooty moulds. These lower the photosynthetic efficiency of the plants.

The pea aphid, *Acyrthosiphon pisum*, is a common pest of lucerne and peas, and is widespread in the United States and Europe. It frequently forms dense infestations on the growing parts of the plant, particularly young leaves at the apex and consequently retards the development of the host plants. Frohlich (1962) found that *A. pisum* showed a marked preference for *Vicia* spp., particularly *V. faba* and *V. sativa* and that lucerne and peas were less suitable hosts.

The vetch aphid, *Megoura viciae*, is sometimes a pest of fodder crops in Europe but is not normally considered to be of economic importance in Britain.

This thesis represents a comparative study of *A. fabae*, *M. viciae* and two biotypes of *A. pisum* (the green and the pink) on broad beans and field beans in order to determine:-

(i) Their relative susceptibility to various biotic and abiotic factors operating in the field;

(ii) The effect of temperature on rate of development, fecundity and longevity;

(iii) Population growth statistics for each species at constant temperatures.

SECTION I : FIELD EXPERIMENTS TO DETERMINE THE MAJOR FACTORS CONCERNED IN THE REGULATION OF APHID POPULATIONS ON BROAD BEANS

A. INTRODUCTION

In spite of the extensive literature concerning aphids, comparatively little is known about the impact of individual biotic or abiotic factors on populations in the field. In most cases, the relative importance of various factors has been inferred by correlating fluctuations in an aphid population with the appearance and abundance of natural enemies and with prevailing weather conditions.

Van Emden (1966) has pointed out that the efficiency of a predator depends not only on its synchronization with the aphid prey, but also on its voracity and on the fecundity of the aphids.

An analysis of the effect of individual factors is difficult because many of the factors interact and the aphid populations generally consist of widely overlapping generations. Hafez (1961) mentioned the additional problem of obtaining systematic observations on reproduction and migration as affected by field conditions.

Hughes (1962, 1963) overcame these difficulties to a large extent by analyzing the instar-distribution of the population. This method enabled him to estimate the potential rate of increase, the overall mortality rate and the reproductive rate of the adults. Since the incidence of parasitism and disease in a population can be determined, it is also possible to determine the mortality rate due to these factors.

Mortality due to invertebrate predators can seldom be measured directly in the field because many predators consume the entire aphid. Others, such as syrphids, imbibe the contents of the aphids and van Emden (1963) was able to compare the intensity of syrphid predation in different parts of a field by recording the number of 'sucked' aphids in labelled colonies. This method would not always give a reliable quantitative

estimate of predation because the aphid remains are liable to be lost, particularly if the colonies are exposed to wind and rain.

Feeding rates have been determined for a number of invertebrate predators under experimental conditions (Fluke, 1929; Knowlton et al, 1938; Dunn, 1949; Hill, 1957; Smith, 1957; Simpson & Burkhardt, 1960; Hagen and Sluss, 1966; Sundby, 1966; Hodek, 1967). Smith used his data in an attempt to analyse mortality in a population of Acyrthosiphon spartii on broom. He pointed out, however, that the feeding rate of predators was likely to be lower under field conditions where the area of search was large and the aphids scattered.

The potential voracity of predators is only likely to be realised in the field when the aphid density is high. At low densities, the efficiency of a predator will largely depend on its searching behaviour. Dunn (1952) and Skuhravy and Novak (1966) found that the efficiency of predators is also affected by temperature.

Because of the many factors governing both the feeding rate of predators and the reproductive rate of the aphids, the ratio of predators to aphids in the field will give only an indication of whether invertebrate predation is likely to have a significant effect on the aphid population. An alternative approach is to compare the behaviour of aphid populations which are subjected to predation with others which are protected from predators.

Three main methods have been devised to minimise the effect of invertebrate predators.

(i) The insecticidal check method (De Bach, 1955; Manglitz and Hill, 1964) involves the use of selective insecticides which are toxic to predators but apparently harmless to their prey.

(ii) Manual removal of predators from experimental plants. Fleschner (1958) preferred this method to the other two methods but it is very time-consuming and smaller predators are sometimes overlooked. Way et al (1969) reported that it disturbed the aphids and damaged their host plants.

(iii) Mechanical exclusion of predators by means of cages or sleeves (Way & Banks, 1968; Eldin, 1970). The disadvantages of this method are its effect on the microenvironment and its interference with the free movement of the prey. It has, however, an important advantage over the other methods in that the cages can be modified to determine the effect not only of invertebrate predators but also of birds and rain (Smith, 1957; Eldin, loc. cit.).

Very little is known about the importance of birds in the regulation of aphid populations. Folsom (1923), Dudley (1924) and Fluke (1929) believed birds to be important natural enemies of the pea aphid, Illinoia pisi in North America. Way et al (1969) observed greenfinches underneath brussels sprout plants jumping up and scraping colonies of Brevicoryne brassicae from the lower leaves.

Exclusion techniques were used by Smith (1957) and Eldin (1970) to determine the effect of bird predation on aphids. In both investigations, mortality was lower in the caged populations then in those exposed to birds. Smith considered birds, particularly blue tits and chaffinches, to be of major importance in controlling populations of Acyrthosiphon spartii on broom.

Many aphid species appear to be adversely affected by rain (Wadley, 1931; Dunn & Wright, 1955; Manglitz and Hill, 1964; Otake, 1966). Wadley, and Manglitz and Hill found that aphids on small plants suffered a higher mortality than those on large plants. Wadley also observed that the

intensity of the rainfall was important, heavy rain being more effective than a fine drizzle.

Smith (1957) counted populations of A. spartii on broom before and after rain. His results showed that the aphids were apparently unaffected by rain.

The primary objective of the work described in this section was to determine the relative importance of some of the major factors affecting aphid populations on broad beans in the field.

B. MATERIALS AND METHODS

Field beans (*Vicia faba*) were planted in Drive Field at Silwood Park in rows alternately three feet and one foot apart. Plant spacing within rows was approximately six inches after thinning.

Caged plants were artificially infested with aphids from clones maintained under greenhouse conditions.

Field cages used in the experiments were 5 ft. high x 4 ft. x 3 ft. All cages were initially covered with white Terylene netting to enable the populations in the different treatments to have an equal chance of becoming established on the plants before being exposed to predators and/or physical factors. The cages were sunk into the ground to a depth of about three inches and anchored by means of guy ropes.

Counting

Weekly counts were made of the number of aphids on each plant, and the geometric mean per plant was then calculated for each treatment after the log (n + 1) transformation had been applied to the data. A dental mirror was used to facilitate counting.

Detailed counts were only possible when the number of aphids was relatively low and the plants small. When accurate counting became impracticable, the populations had to be estimated.

Sampling

In order to check the accuracy of field estimates and to obtain information about invertebrate predators and parasites attacking the aphids, sample plants were removed at intervals for detailed examination in the laboratory. One plant was removed from each

treatment on each sampling occasion. The plant selected was the one having an estimated population size closest to the calculated average for the treatment. In the case of sample plants which were heavily infested with Megoura viciae, it was impossible to cut through the stem without dislodging some of the aphids. Overlapping semi-cicular plates of cellulose acetate coated with 'Ostico' tree-banding grease were therefore placed on the ground around the plant prior to its removal to catch any aphids which fell from the plant.

The stem was cut just above ground level with a pair of sharp secateurs; long stems were cut into two or more convenient lengths. The plant was then placed in a polythene bag which was closed by means of a rubber band, or directly into the aphid extractor (See below).

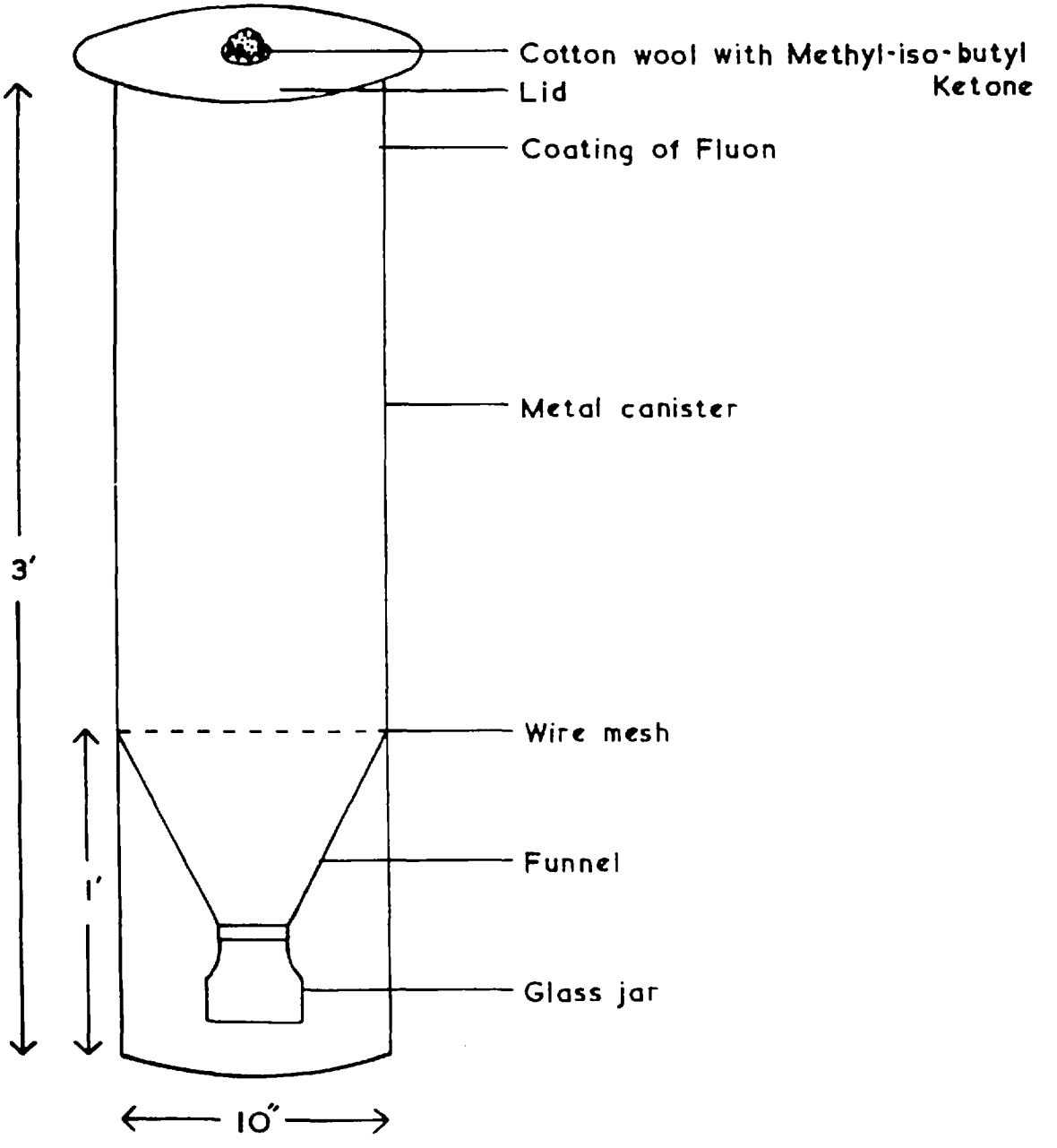
In the laboratory, the aphids were either counted immediately or preserved in 80% alcohol containing 10% glycerol until they were subsequently counted and, in some cases, sorted into instars. The number of predators and of parsitised and diseased aphids on each plant was recorded.

When no aphids were found in a particular treatment in the field, the remaining plants were removed and examined in the laboratory.

Aphid Extractor

Certain of the aphid species investigated were very active and it was impossible to count large numbers on the sample plants in the laboratory without first anaesthetising or killing the aphids. This problem was overcome by using an aphid 'extractor' into which the sample plant was placed directly after its removal from a treatment in the field. The plant was then transported to the laboratory in the extractor.

Figure 1 : Aphid extractor


Cotton wool with Methyl-iso-butyl Ketone
Lid
Coating of Fluon
Metal canister
Wire mesh
Funnel
Glass jar
3'
1'
10"

The extractor was a modified version of the sampling can described by Gray and Schuh (1941). It consisted of a galvanized zinc cylinder 3 feet long and 10 inches in diameter, with a metal funnel soldered to the inner surface 1 foot above the base. The upper end of the funnel was covered by chicken wire (½ inch mesh) to prevent large pieces of vegetation from falling down into the glass preserving jar, which was screwed to the neck of the funnel.

The top of the cylinder was closed by means of a tightly-fitting lid with a central hole. Cotton wool dampened with methyl iso-butyl ketone was inserted into the hole. The fumes anaesthetised the aphids which consequently dropped from the plant and into the jar below. The inner surface of the cylinder just below the lid was coated with Fluon to prevent the aphids from escaping before the lid was in position.

The extractor was used for sample plants infested with large numbers of M. viciae. Up to 93% of the population could be removed from the plant using this method. The relatively small numbers remaining on the plant after extraction could easily be counted.

Attempts to use the extractor to remove Aphis fabae from sample plants proved unsuccessful because of the tenacity with which the aphids cling to the plant. They nearly always died with their mouthparts still inserted in the plant.

1) 1967

A preliminary study was made to compare the effect of various factors on populations of Aphis fabae Scop., Megoura viciae Buckton and the pink and green biotypes of Acyrthosiphon pisum Harris. Except in the 'competition' treatments, only one species was introduced into each treatment.

The experimental area measured 42 ft. x 33 ft. and the beans were planted on 1st June. The cages were placed in position before the bean seedlings had emerged to prevent natural infestation. There were 12 plants in each cage.

The gauge of the Terylene netting covering the cages was 8 meshes/cm. Although this permitted the entry of smaller predators, it was used in preference to a finer gauge to reduce the effect on the microclimate within the cage.

Treatments

I Roof and sides of Terylene net.

II Roof and sides of chicken wire ($\frac{1}{2}$" mesh).

III Cage removed

IV Roof of Terylene net, covered by a double layer of Polythene; no sides.

V Sides of Terylene net; no roof.

VI As treatment I, but roof covered by a double layer of Polythene.

A. fabae and M. viciae were each subjected to all six treatments. Only treatments I, II and III were used in the study of the two biotypes of A. pisum, and to determine the effect of interspecific competition.

The caged plants were infested on 6th and 7th July; 10 apterous adults taken at random from the relevant greenhouse culture were placed on each plant. In the competition cages, the species were placed on separate plants. The sequence of infestation in the competition cages was as follows:-

Plant No.	Aphid Species	Plant No.	Aphid Species
(1)	A.f.	((7)	A.p. (i)
(2)	M.v.	(8)	A.p. (ii)
(3)	A.p. (i)	(9)	A.f.
(4)	A.p. (ii)	(10)	M.v.
(5)	A.f.	(11)	A.p. (i)
(6)	M.v.	(12)	A.p. (ii)

A.f. = A. fabae
M.v. = M. Viciae
A.p. (i) = A. pisum - pink biotype
A.p. (ii) = A. pisum - green biotype

Plants 6 and 12 were nearest the door of the cage. This system of numbering the plants was adopted in all treatments.

The population in the cages was allowed to build-up for two weeks before the experiment commenced. The relevant parts of the cages were removed on 21st July.

Sample plants were removed once a fortnight, commencing at the end of July.

A check was kept on the natural aphid population in the plot by counting the aphids on a number of uncaged plants at fortnightly intervals from the 13th July.

M. viciae from sample plants were sorted into instars. 4th instar nymphs were classified as alate or apterous, apterous adults as viviparous or oviparous, and alate adults as male or female.

2) 1968

Studies in 1968 were confined to one species - the pink biotype of A. pisum.

The beans were planted towards the end of March in an area measuring 90 ft. x 50 ft. The cages were placed in position on 17th May, and the number of plants was reduced to six in each cage.

The gauge of the Terylene netting used on the sides of the cages was the same as that used in 1967 i.e. 8 meshes/cm. The roofs of the cages were covered with a slightly larger gauge (5 meshes/cm) to allow alate adults to escape.

Treatments

I : Roof and sides of Terylene net.

II Terylene net sides; wire mesh roof.

III Terylene net sides; no roof.

IV Wire mesh sides; Terylene net roof.

V Wire mesh sides; wire mesh roof.

VI Wire mesh sides; no roof.

VII No sides; Terylene net roof.

VIII No sides; wire mesh roof.

IX Cage removed.

The cages were positioned in the field to conform with a randomised block design with two replicates.

Each of the caged plants was infested on 5th June with five alate adults, all of which had entered the adult stage within the previous five days.

The first field count on the 10th June revealed that the aphids had suffered a high mortality. This was probably due to heat injury caused

by high temperatures in the greenhouse in late May and early June. On the 10th June, the numbers of aphids in some of the cages were extremely low and there was considerable variation between cages. In order to have a comparable number of aphids in all cages at the start of the experiment, it was necessary to boost the populations in some of the cages. The greenhouse culture had almost completely died out by this time, and it was therefore necessary to transfer some of the aphids from cages with relatively high populations to those with low populations. By the following week, there were still six cages with low numbers so the procedure was repeated.

By early July, the populations had become satisfactorily established and the relevant parts of the cages were removed on 3rd and 4th July.

The aphids in each treatment were counted at weekly intervals until the end of July. The final count was made four weeks later when the experiment was terminated. At the first three counts in July, all the plants in each treatment were examined. On the last two occasions, however, the aphids were counted on only two plants in each treatment.

In addition to the number of healthy aphids on the plants, records were kept of the incidence of diseased aphids, mummified aphids - both 'hatched' and 'unhatched' -, and the numbers of predators seen on the plants. Any predators found in treatment I were removed from the plants.

Because of the low number of plants in the treatments, only one plant was removed from each treatment for detailed examination in the laboratory. The remaining plants were only removed after the experiment was terminated on the 22nd August.

The aphids found on sample plants were stored in 80% alcohol containing 10% glycerol, and subsequently sorted into instars.

Pull-out appendices

Treatment numbers used in 1968 differed from those used in 1967. To avoid confusion and to obviate the necessity of frequent reference to the section on Materials and Methods, pull-out appendices are provided in which the various treatments and their probable effects are summarised. Treatments used in 1967 may be found in Appendix 9 and those used in 1968 in Appendix 10.

Determination of the Potential Rate of Increase

When an insect population is increasing (or decreasing) at a steady rate, the frequency of individuals in successive instars should form a geometric progression (Williams, 1961). Hughes (1962) demonstrated that stable-instar distributions of this type frequently occur in aphid populations.

The stability of the instar distribution of M. viciae on sample plants in 1967 and of pink A. pisum in 1968 was tested on the basis of Hughes' method.

The potential rate of increase (λ) was calculated for each sample as

$$e^{\lambda} = \frac{a_1 + a_2}{a_2 + a_3}$$

where a_1 , a_2 and a_3 represent the number of individuals in instars 1, 2 and 3 respectively. As the first three instars are of approximately equal duration (See section III) the proportion (r) of aphids in each instar in relation to the first instar is as follows:-

$$\text{1st instar } (r_1) = 1$$

$$\text{2nd instar } (r_2) = e^{-\lambda}$$

$$\text{3rd instar } (r_3) = e^{-2\lambda}$$

The expected number of individuals in each instar is then equal to

$$\frac{Nr_i}{\sum_{i=1}^{3} r_i}$$

where N is the total number of individuals in instars 1, 2 and 3.

The concordance between observed and expected frequencies was tested by X^2. If the value of X^2 was less than 3.84 (1 d.f.; $P > 0.05$) it was assumed that the population had developed a stable-instar distribution and that the calculated value of λ gave a realistic estimate of the potential rate of increase of the population.

C. RESULTS

1. Preliminary Studies on Populations of Aphis fabae, Megoura viciae and Acyrthosiphon pisum in 1967

Daily records of mean temperature, mean relative humidity and rainfall for July, August and September are given in Appendix 1.

(a) Aphis fabae

Weekly estimates of the number of aphids on individual plants in each treatment are given in Appendix 2. The results are summarised in Figure 2.

The heavy rain which fell on the 22nd and 23rd July, immediately after the experiment commenced, had no direct effect on the aphids. Although the populations in treatments II, III and V received no protection from the rain, they either continued to increase or remained at approximately the same level as before the start of the experiment.

Birds had access to the populations in treatments III, IV and V, but there was no evidence of bird predation in any of these treatments.

After the count on the 25th July, the populations declined fairly rapidly and had completely died out by the end of August. This downward trend was reflected by the natural population of A. fabae on uncaged plants in the plot (Table I). At the first count on the 13th July, the level of infestation was relatively high, particularly on the plants in the guard rows (the outer two rows on each side of the plot). Two weeks later, the numbers had dropped considerably and, by the end of August, there were no living aphids on any of the plants.

Figure 2 : Weekly estimates of the number of A. fabae in each treatment

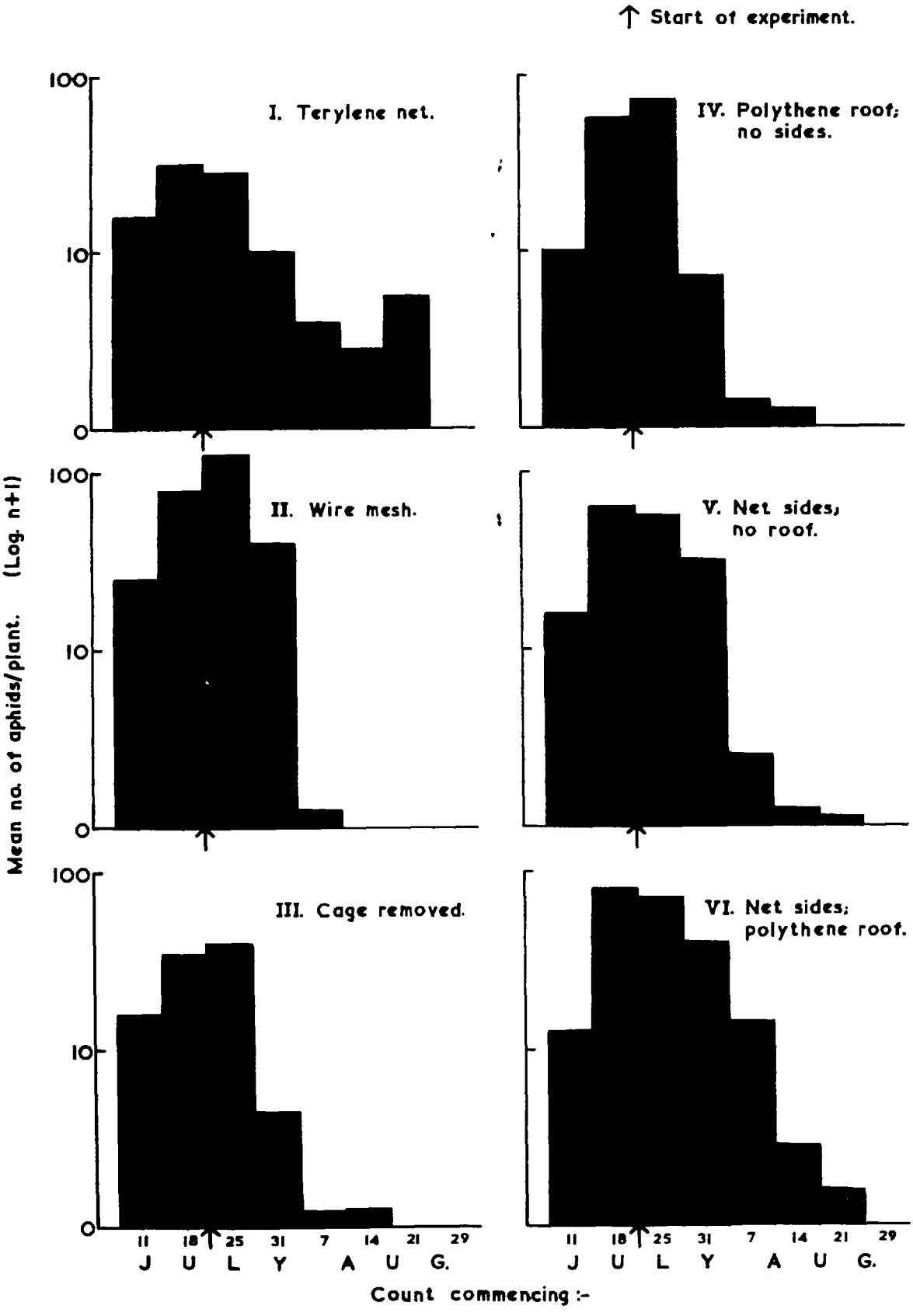

↑ Start of experiment.
I. Terylene net.
II. Wire mesh.
III. Cage removed.
IV. Polythene roof; no sides.
V. Net sides; no roof.
VI. Net sides; polythene roof.
Mean no. of aphids/plant. (Log. n+1)
100
10
0
11 18 25 31 7 14 21 29
J U L Y A U G.
Count commencing :-

Table I : Average number of A. fabae on uncaged bean plants in 1967.

Date	Mean No. of aphids per plant	
	Guard Rows	Inner Rows
13/7	175.0	67.6
27-28/7	2.4	4.7
11/8	0.1	0.1
24/8	0.0	0.0

Guard rows - 40 plants examined

Inner rows - 70 plants examined

The major factor responsible for the mortality in this species was an epizootic caused by Entomophthora sp.

Wilding (1969, 1970) studied the effect of humidity on species of Entomophthora, particularly E. aphidis and E. thaxteriana. He found that sporulation would only occur when the relative humidity of the microhabitat exceeded 90%, although that of the general environment was sometimes lower. Thus epizootics caused by species of Entomophthora are usually associated with damp weather.

Rain fell at Silwood Park on several occasions during the last two weeks of July and the first three weeks of August. This resulted in a high humidity in the microenvironment of the bean plants which provided ideal conditions for the Entomophthora sp. to become established.

More recent work on E. aphidis and E. thaxteriana has shown that the optimum temperature for the development of the epizootic is 20°C (Wilding, in press). At 15° and 25°C, the mean incubation period was only slightly longer - up to 6.2 days, including the infection period.

The average daily temperature recorded at the meteorological site at Silwood Park during the last two weeks of July was usually over 17°C

(Appendix 1), and the minimum temperature seldom fell below 15°C. Thus the disease, once established was able to spread rapidly through the population. The lower temperatures recorded in August did not appear to impede the progress of the infestation to any appreciable extent.

Details of the number of predators found on sample plants are given in Table II.

Table II : Numbers of aphids and predators on sample plants removed from treatments infested with A. fabae.

Sampling Date	Treatment	No. of Aphids	PREDATORS			
			A. nemorum	Syrphids	Coccinellids	Neuroptera
31/7	I	35				
	II	40		2 (L.)	2 (L.)	
	III	0			2 (L.)	
	IV	2		6 (L.)		
	V	85				1 (L.)
	VI	225			1 (L.)	
14-16/8	I	2	8			
	* II	0	2			
	III	0	7	1 (P.)	1 (P.)	
	IV	0	5			
	V	0	3			
	VI	1	0			

(L.) = Larvae ; (P.) = Pupae

* These figures for treatment II represent the average number per plant on the remaining 11 plants in the treatment, all of which were removed on 14th August.

The most common predators on the sample plants at the end of July were Syrphids and Coccinellids. These had virtually disappeared two weeks later, possibly because lack of food had induced them to leave the plants.

Anthocorids were found only on the second sampling occasion. They appeared too late in the season to have had much effect on the aphid

populations. There were no aphids on most of the plants on which anthocorids were found but psocids were frequently seen and these may have provided an alternative source of food.

The aphid populations never attained a high level - even in mid-July, the average number per plant seldom exceeded 100. Predators could, therefore, have contributed to the decline of the populations.

No predators were found on the sample plant removed from treatment I at the end of July, and there was only one on that from treatment VI. The virtual absence of predators may account for the more gradual decline of the populations in these two treatments.

Field counts were fairly accurate at low levels of infestation but were invariably too low when the populations were relatively high. This was because large numbers of aphids were concealed among the young furled leaves at the tip of the plant and it was impossible to count them accurately without damaging the plant and killing some of the aphids.

(b) Megoura viciae

The population trends in the six treatments are shown in Figures 3 and 4. Details of the weekly counts are given in Appendix 3.

There were considerable differences between treatments in this species. Removal of the entire cage (Treatment III) or of the sides of the cage (Treatment IV) had an adverse effect on the aphid populations which was already apparent on 25th July, only four days after the experiment started. By mid-August, the aphids had virtually disappeared from both treatments.

Mortality in this instance was due mainly to bird predation. The rate of decline was too rapid for invertebrate predators to have been a major factor; nor could the mortality in treatment III be attributed to the effect of rain. Heavy rain fell on the 22nd and 23rd July, but the

Figure 3 : Weekly estimates of the number of M. viciae in Treatments I - III

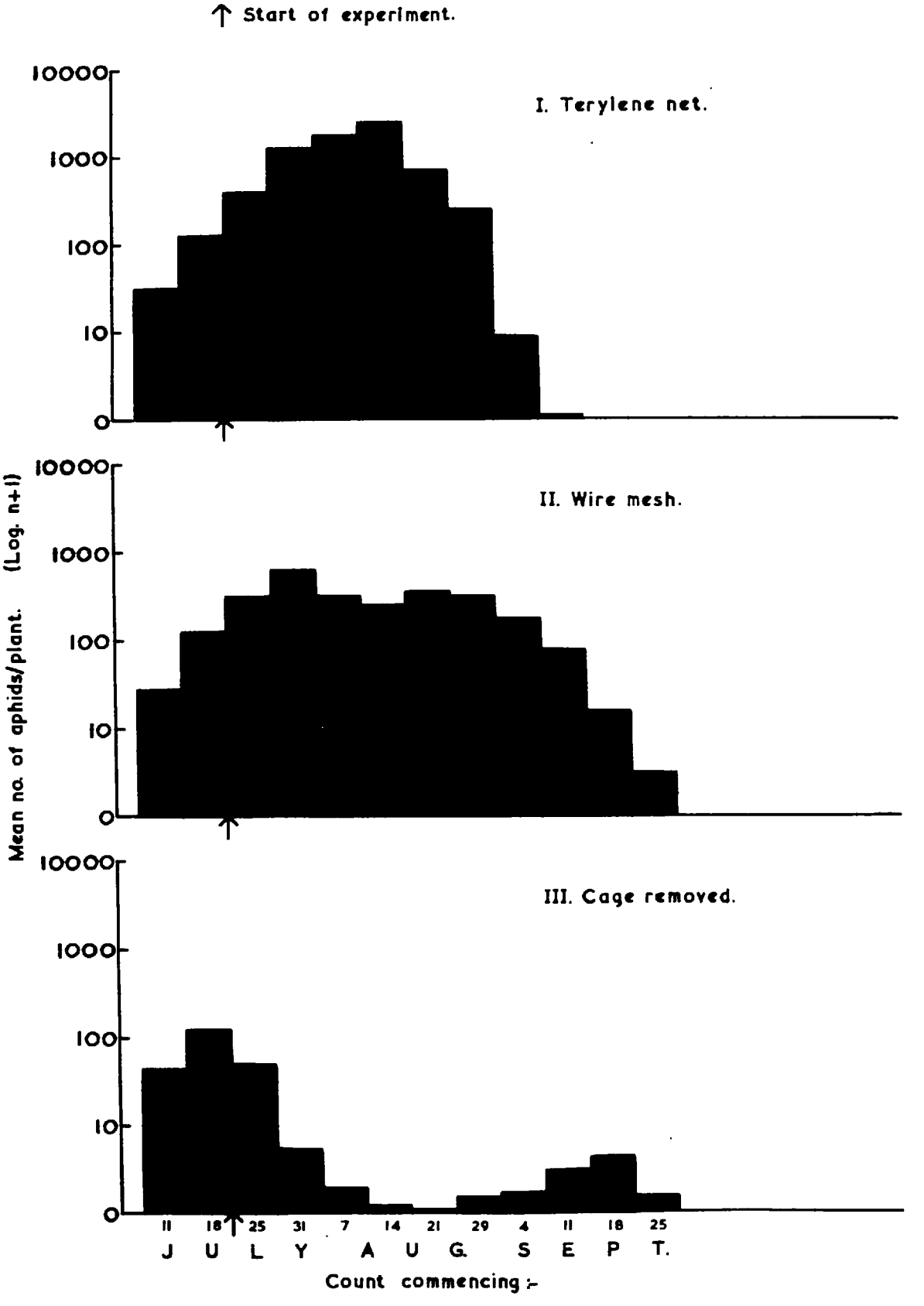
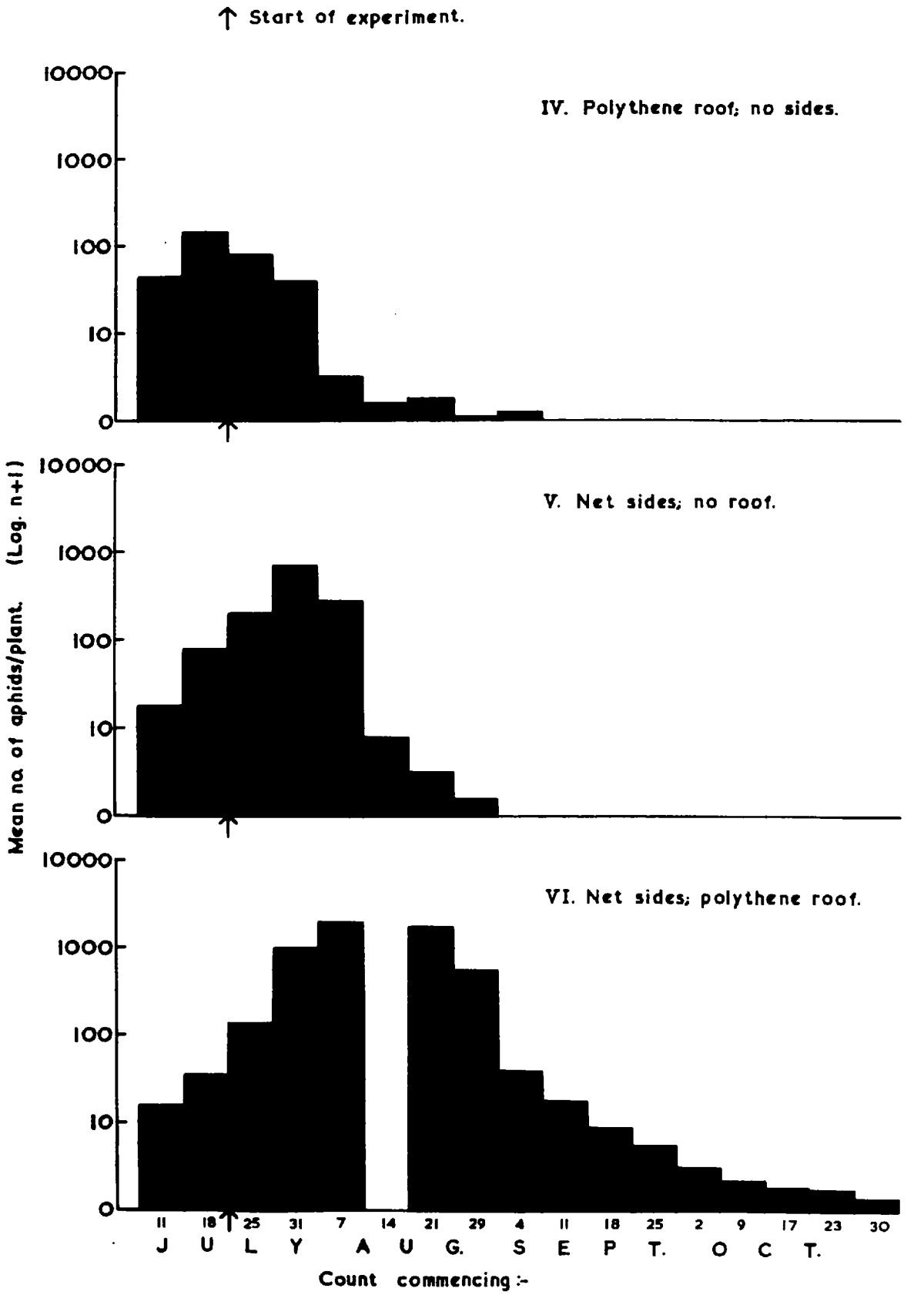

↑ Start of experiment.
10000
1000
100
10
0
I. Terylene net.
II. Wire mesh.
III. Cage removed.
Mean no. of aphids/plant. (Log. n+1)
11 18 25 31 7 14 21 29 4 11 18 25
J U L Y A U G. S E P T.
Count commencing :-

Figure 4 : Weekly estimates of the number of M. viciae in treatments IV - VI


↑ Start of experiment.
IV. Polythene roof; no sides.
V. Net sides; no roof.
VI. Net sides; polythene roof.
Mean no. of aphids/plant. (Log. n+1)
10000
1000
100
10
0
11 18 25 31 7 14 21 29 4 11 18 25 2 9 17 23 30
J U L Y A U G. S E P T. O C T.
Count commencing :-

populations in treatments II and V were apparently unaffected by it.

Bird predation was also the major mortality factor operating in treatment V, but it occurred only two to three weeks after the start of the experiment. About that time, birds were observed perching on the plants within the cage, pecking at the aphids. The response of the birds was probably delayed by the relative inaccessibility of the plants, as compared to those in treatments III and IV. Another possible reason was that the aphids congregated mainly on the stems of their host-plants and were therefore not readily seen from above.

The populations in the remaining three treatments were protected - either by wire mesh (Treatment II) or by Terylene netting (Treatments I and VI) - against bird predation and remained at a high level throughout the summer. Only towards the end of August did the numbers begin to decline.

The population curve for treatment II differed significantly from those for treatments I and VI; the former flattened out into a plateau after the 31st July, whereas the latter two both exhibited distinct peaks approximately two weeks later. These differences were caused by the effect of the treatments on the behaviour of the alatae. After the removal of the Terylene netting from treatment II, alate adults were able to leave the cage and the population became self-regulatory. In treatments I and VI, however, the alatae were confined to the plants within the treatments and contributed to the build-up of the populations.

The incidence of alatae on sample plants from the three treatments is given in Table III.

Alate production in M. viciae is known to be induced primarily by crowding (Lees, 1967). Up until the end of August, there was an obvious

Table III : The incidence of alatae in the fourth instar and adult stages of Megoura viciae, expressed as a percentage of total fourth instar nymphs and total yiviparous adults, respectively.

Date	TREATMENT								
	I			II			VI		
	No. of aphids on plant	% Alate		No. of aphids on plant	% Alate		No. of aphids on plant	% Alate	
		4th Instar	Adults		4th Instar	Adults		4th Instar	Adults
1/8	3,114	21.8	13.3	1,252	29.3	1.8	2,595	34.2	8.9
17/8	≈ 7,000	36.1	34.5	2,002	15.8	7.5	5,206	30.5	50.7
30/8	3,910	6.0	8.0	688	8.1	4.6	4,698	2.6	4.9
12/9	-	-	-	531	43.4	21.4	544	69.7	23.1
25/9	-	-	-	19	0.0	100.0	106	21.3	80.0

correlation between the size of the population and the incidence of alatae. The relatively high percentage of alate fourth instar nymphs on the plant taken from treatment II on 1st August was probably the result of the build-up of the population before the start of the experiment 11 days earlier. Until that time the cage was covered with Terylene netting and alate adults were unable to escape.

Despite the progressive decline in the aphid population, alate production increased again during September. This probably resulted indirectly from the deterioration of the host plants. Lees (1967) found that nutrition alone had no direct effect on alate production, but that aphids confined on mature and senescent leaves were more restless than those feeding on young bean plants. The increased restlessness resulted in more frequent contacts between individuals and produced a crowding effect. Under these circumstances, even two aphids constituted a 'crowd'.

The main factor responsible for the eventual decline of the populations in treatments I, II and VI was the decreasing day-length which resulted in the production of oviparae. Peak populations in treatments I and VI occurred in mid-August. On the 17th August, sample plants were removed from the treatments and all the adults were examined to determine whether any oviparae were present on the plants. There were none on the plants removed from treatments II and VI and only one on the plant from treatment I. By the end of August, however, over 20% of all the adult females in the three treatments were oviparous (Table IV). The relatively higher proportion of oviparae in treatments I and VI may have resulted from the reduced light intensity within these cages. Way and Banks (1967) found that the light intensity in field cages having Terylene netting sides and roofs of thin Polythene sheet was 20% lower than in the open.

Table IV : Proportion of oviparous adults in aphid samples, expressed as a percentage of total adult females.

Date	TREATMENT		
	I	II	VI
1/8	0.0	0.0	0.0
17/8	0.2	0.0	0.0
30/8	24.0	20.7	34.1
12/9	-	24.4	15.6
25/9	-	33.3	89.5

Apart from the low figure for treatment VI on the 12th September, there was a progressive increase in the incidence of oviparous females on successive sampling dates, and a corresponding decrease in aphid numbers. The lower ambient temperatures in the field during September slowed down the rate of reproduction of viviparous adults and the rate of development of nymphs and thus contributed to the fall in numbers. Most of the plants in treatment I had died by the 11th September, resulting in a more rapid decline in numbers in this treatment than in treatments II and VI. The high aphid population in treatment I probably contributed to the death of the host plants.

The aphid populations on only five of the sample plants (from treatment VI on the 2nd, 18th and 31st ~~July~~ August, and from treatments I and II on the 30th ~~July~~ August) were found to have developed a stable-instar distribution. Instar distribution analysis could not therefore be used to compare the potential and intrinsic rates of increase and the overall mortality rate per instar period in different treatments.

Invertebrate predators were not recorded for the first sample plants

examined at the beginning of August. The numbers of predators on each of the plants sampled subsequently are given in Table V.

Table V : Numbers of aphids and predators on sample plants removed from treatments infested with M. viciae.

Sampling Date	Treatment	No. of Aphids	PREDATORS			
			A. nemorum	Syrphids	Coccinellids	Neuroptera
17/8	I	≈ 7,000	1	3 (L.)		
	II	2,002	8	4 (L.)		
	III	0	3			
	IV	1	3		1 (P.)	
	V	23	2	2 (L.)	1 (P.)	
	VI	5,206	2			
30/8	I	3,910	11			
	II	688	8			
	III	1	6			
	IV	0	1			
	V	1	10			
	VI	4,698	7	10 (L.) 4 (P.)		
12/9	II	531	15	1 (P.)	1 (L.)	
	III	9	7			
	VI	544	14			
25/9	II	19	5	2 (L.), 1 (P.)		
	III	0	3			
	VI	106	9	3 (L.), 5 (P.)		1
9/10	VI	23		2 (L.), 1 (P.)		
30/10	VI	6	2			

(L.) = Larvae ; (P.) = Pupae

Anthocoris nemorum was the most common predator, followed by syrphids. Coccinellids and Neuroptera were relatively scarce; they constituted only 3% and 0.6% respectively of all the predators found on the plants. The Terylene netting was apparently completely ineffective at excluding invertebrate predators except, perhaps, coccinellids.

During most of the season, the number of predators per plant in treatments I, II and VI was very low compared to the number of aphids on

the plants and it is unlikely that they could have played a significant part in controlling the populations. They were probably responsible for the mortality of aphids which escaped bird predation in treatments III, IV and V, and may have accelerated the decline of the populations in the other treatments towards the end of the season.

Estimates of populations in the field were invariably too low - sometimes by as much as 75%. The large number of plants in each cage made it difficult to approach close enough to the aphids for detailed counts to be made, particularly as the aphids readily fell from the plants if they were disturbed. Furthermore, the aphids were so closely packed together on the stems of the plants at high densities that the smaller aphids tended to be concealed by the bodies of the larger ones.

Bean plants are apparently able to support large numbers of M. viciae but the effect on the yield was not determined.

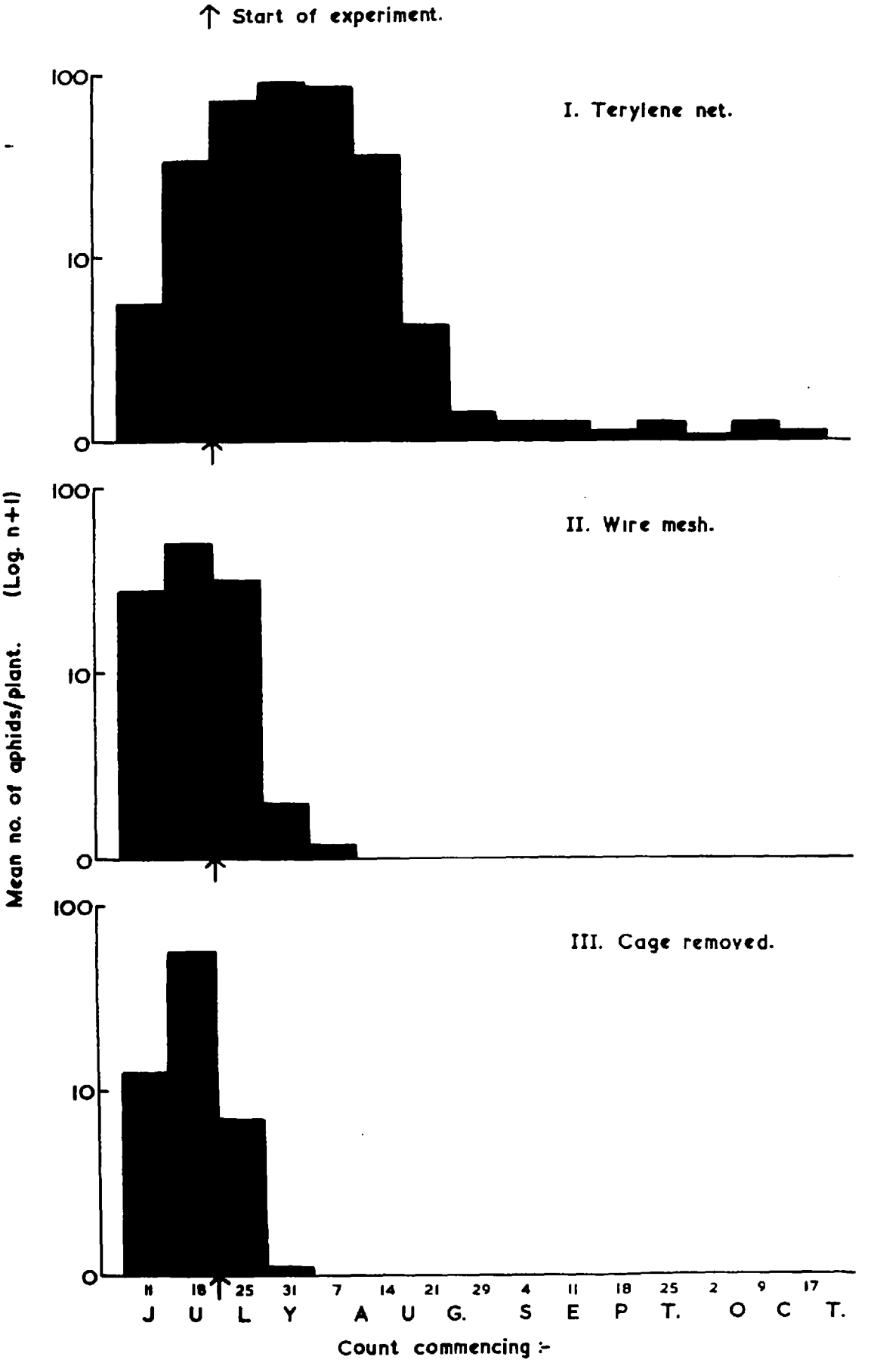
(c) Acyrthosiphon pisum - Pink Biotype

Between the 11th and 18th July, the rate of increase of the populations in all three treatments was comparable to that shown by the other species, although the number of aphids was generally much lower.

In treatment III, removal of the entire cage on 21st July resulted in a rapid decline in the population (Figure 5), primarily as a result of bird predation. (The numbers of aphids on individual plants are given in Appendix 5).

Although the heavy rain which fell on 22nd and 23rd July apparently had an adverse effect on the population in treatment II, the decline of the population during the following three weeks was mainly due to the combined effect of invertebrate predation and parasitism.

Figure 5 : Weekly estimates of the number of pink A. pisum in each treatment


↑ Start of experiment.
100
10
0
I. Terylene net.
II. Wire mesh.
III. Cage removed.
Mean no. of aphids/plant. (Log. n+1)
11 18 25 31 7 14 21 29 4 11 18 25 2 9 17
J U L Y A U G. S E P T. O C T.
Count commencing :-

In treatment I, the population continued to increase until early August. The subsequent decline was again the result of predation and parasitism. Although the Terylene netting did not exclude invertebrate predators or parasites, it apparently delayed the ingress of certain species. Syrphids and coccinellids seemed to be particularly affected in that the former appeared much later in treatment I than in the other treatments, and no coccinellids were found on any of the plants taken from treatment I (Table VI).

Anthocorids were apparently undeterred by the Terylene netting as several were found on each of the sample plants removed from treatment I. The relatively low numbers of predators in treatments II and III at the time of sampling were probably due to the fact that the aphid populations had died out by then. Many of the predators had probably left the plants in search of food or resorted to cannibalism.

Spiders were found on several plants but it is not known whether they actually preyed upon the aphids. Aphids were sometimes seen trapped in webs. Because of its characteristic restlessness and its tendency to fall from the plant when disturbed, this biotype runs a greater risk of being caught in spiders' webs than a relatively more sessile species such as A. fabae.

Adult parasites had started to emerge from mummified aphids by the 9th August. Assuming a generation time of approximately two weeks under field conditions, parasitism probably commenced about mid-July. The percentage parasitism was not determined but appeared to be quite high, particularly later in the season.

The mummies recovered from sample plants were characteristic of those produced by Aphidius spp. and Aphelinus sp. The primary parasites could not be positively identified, however, as only hyperparasites emerged from

Table VI : Numbers of aphids and predators on sample plants removed from treatments infested with the pink biotype of A. pisum.

Date	Treat	Aphids	MUMMIES		PREDATORS			
			'A' - Type	'E' - Type	A. nem.	Syrph.	Cocc.	Neur.
9/8	I	185	4 (1 h.)		several			
	II	0	1		0	1 (L.)		
16/8	III*	0	0.6		4	0.1 (L.)	0.2 (L.)	
23/8	I	18	2	7	25			
	II*	0	1.0		4.4	0.2 (L.)	0.1 (P.)	0.1 (L.)
4/9	I	0	2 (1 h.)		13			
18/9	I	1	3					
2/10	I	1	1 (h.)		1	1 (L.)		1 (L.)

(L.) = Larvae ; (P.) = Pupae

* These figures are the average per plant, based on all the remaining plants in the treatment.

'A' - type and 'E' - type mummies are those characteristic of Aphidius spp. and Aphelinus spp. respectively.

(h.) = number of hatched mummies. The first figure includes both unhatched and hatched mummies.

A. nem. = Anthocoris nemorum

Syrph. = Syrphidae

Cocc. = Coccinellidae

Neur. = Neuroptera - Chrysopidae

the 'unhatched' mummies in the laboratory.

Field counts of the number of aphids on young bean plants were reasonably accurate because the aphids were very conspicuous against the

green background of their host plants and were distinctly non-gregarious, tending to spread out over most of the plant. As the plants grew bigger, however, it became increasingly difficult to approach a particular plant without disturbing the aphids on other plants and causing them to fall to the ground. Another factor responsible for the relative inaccurany of field counts of aphids on mature plants was the marked preference shown by the aphids for buds and flowers. Aphids feeding on the flowers were often hidden from view by the overlapping petals and were therefore not included in the counts. Under these conditions, approximately one-third of the population was missed during field estimates.

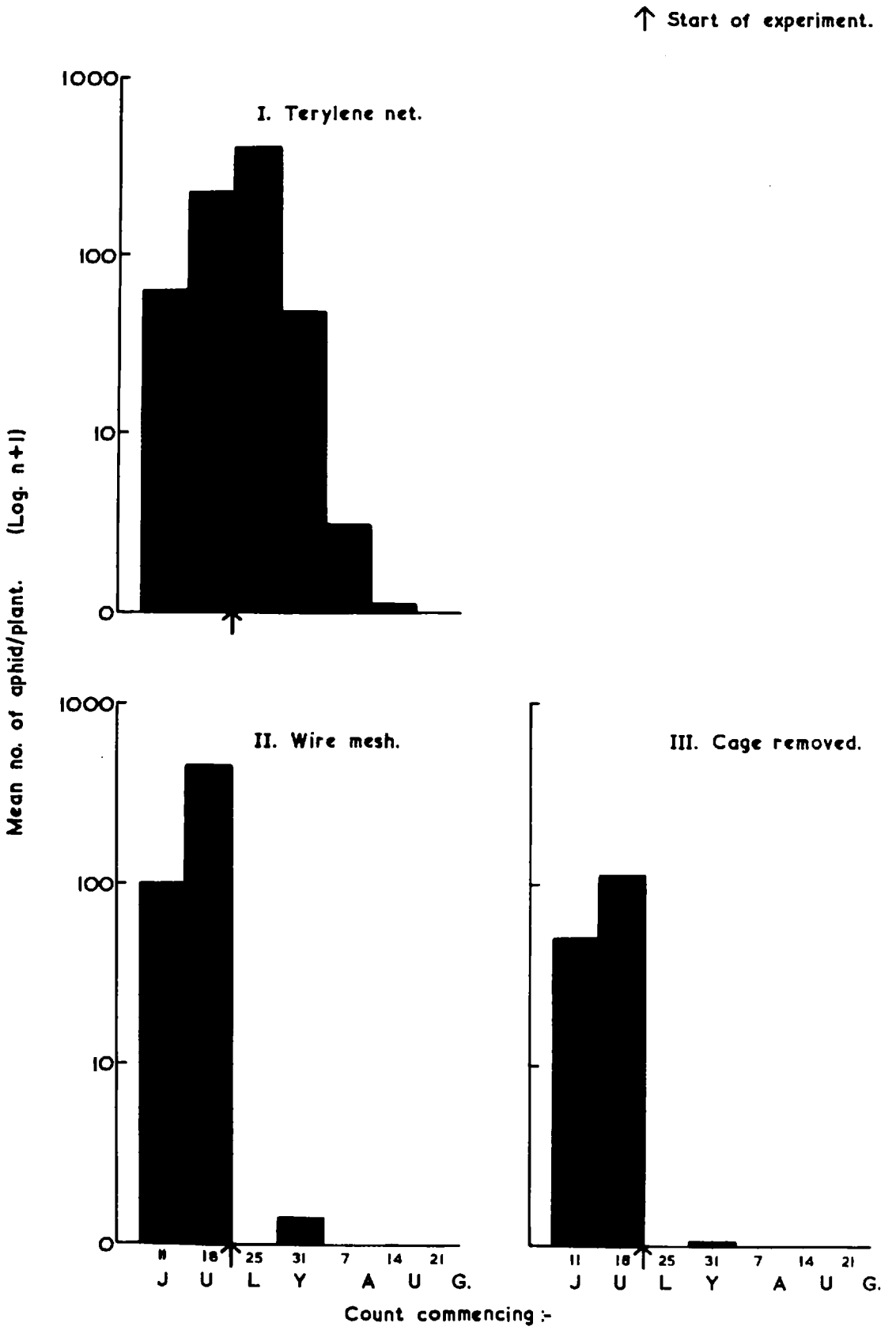
(d) Acyrthosiphon pisum - Green Biotype

The green biotype of A. pisum was initially more successful than any of the other species investigated in 1967. Conditions apparently favoured the rapid growth of the populations and, by the 18th July, the average number of aphids per plant was estimated at between 100 and 500 in each of the three treatments (Figure 6). (Details of the number of aphids on individual plants are given in Appendix 6). In fact, the actual numbers were probably very much higher as field counts invariably underestimated the size of the population.

The immediate effect on the aphids of the removal of the Terylene netting from treatment II or of the entire cage (treatment III) could not be assessed because the population estimates for these treatments on the 25th July were unfortunately lost. The heavy rain which fell on the 22nd and 23rd July may have caused some mortality. The aphids tend to feed mainly on the young leaves at the tip of the plant and would therefore receive little protection from rain.

Bird predation was probably primarily responsible for the decline of the population in treatment III. Nevertheless, the population in treatment

Figure 6 : Weekly estimates of the number of green A. pisum in each treatment


↑ Start of experiment.
1000
100
10
0
I. Terylene net.
II. Wire mesh.
III. Cage removed.
Mean no. of aphid/plant. (Log. n+1)
11 18 25 31 7 14 21
J U L Y A U G.
Count commencing :-

II declined almost as rapidly. In the latter treatment, the decrease in numbers was apparently due largely to emigration. By feeding on the young leaves, green A. pisum causes considerable damage to the host plant at high densities. While the Terylene net was in position, the population increased rapidly and the young leaves soon became overcrowded. As crowding became more intense, the production of alatae increased. The alate adults were unable to leave the cage until the Terylene net was removed and their continued presence aggravated the already crowded conditions. The host plants were still relatively small and were unable to survive the high populations. As their condition deteriorated, the increased restlessness of the aphids resulted in an increase in the production of alatae. It probably also stimulated large numbers of apterae to leave the plants. Removal of the Terylene net was followed by a rapid decline of the population, presumably due to a mass exodus from the plants.

By the beginning of August, the aphids had completely disappeared from treatments II and III and all the plants were taken to the laboratory. The incidence of mummified aphids on the plants (Table VII) suggested that parasitism contributed to the decline of the population in treatment II and was partly responsible for the mortality of the few aphids which escaped bird predation in treatment III. There were very few predators on the plants but, as the aphids had all disappeared by then, the number of predators had probably decreased. Some may have left the plants in search of food or the numbers may have been reduced by cannabalism.

In treatment I, the population continued to increase until the end of July. The rapid decline which followed was due to the combined effect of parasitism, predation and the deterioration of the host plants. The latter factor probably resulted in the aphids becoming increasingly restless and would therefore have had an adverse effect on their rate of development and fecundity. The Terylene netting may have delayed the advent of parasites

Table VII : Numbers of aphids and predators on sample plants removed from treatments infested with the green biotype of A. pisum.

Date	Treat	Aphids	MUMMIES			PREDATORS				
			'A' - Type	'E' - Type	'P' - Type	A. nem.	Syrph.	Cocc.	Neur.	Staph.
9/8	I	5	18 (2 h.)			3	1 (L.)	1 (A.)		1 (A.)
10/8	II*	0	8.8 (0.6 h.)	1.8	0.6		0.3 (L.); 0.1 (P.)			
16/8	III*	0	0.9		0.2	3.8		0.2 (L.); 0.2 (P.); 0.1 (A.)	0.1((L.)	
31/8	I*	0	11.5 (3.5 h.)	3.0 (0.1 h.)		6.8		0.1 (A.)	0.2 (A.)	

* These figures represent the average per plant and are based on all the remaining plants in each treatment.

Mummies

'A' - Type = Aphidius type
'E' - Type = Aphelinus type
'P' - Type = Praon type

Figures outside brackets represent the total number of mummies found, both 'unhatched' and 'hatched'. Figures in brackets represent the number of 'hatched' mummies

Predators

A. nem. = Anthocoris nemorum
Syrph. = Syrphidae
Cocc. = Coccinellidae
Neur. = Neuroptera (Chrysopidae)
Staph. = Staphylinidae

(L.) = Larvae
(P.) = Pupae
(A.) = Adults

but, once established, the incidence of parasitism appeared to increase fairly rapidly.

Apparently the Terylene netting afforded the aphids little protection against invertebrate predation, even by the larger predators such as syrphids and coccinellids. Both of these groups had gained access into the cage by the 9th August (Table VII). Adults were probably attracted by the large aphid population and either entered the cage when the door was opened or oviposited on the outside of the cage. Newly-hatched larvae were small enough to crawl through the apertures in the netting and may have succeeded in reaching the infested plants within the cage.

The most common predator on the plants from treatment I and III was Anthocoris nemorum.

Three types of mummy were found on the plants infested with green A. pisum. The most common type was that produced by Aphidius species. Black mummies, possibly caused by Aphelinus sp., were also numerous. The third type was characteristic of Praon spp. Unhatched mummies were removed from the plants and retained for identification but only hyperparasites emerged. These were identified as Charips sp. and (probably) Asaphes sp.

Parasitised aphids were not counted in the field and laboratory counts were almost certainly an underestimate of the total number produced on each plant. Some of them, particularly those from which the parasite had emerged, probably dropped from the plant. Others may have been missed because the parasitised aphids left the plants before becoming mummified. This sometimes occurred when parasitised aphids were reared under laboratory conditions.

As a result of the high level of infestation attained in treatment II before the start of the experiment, many of the plants died. Those in

treatment I survived the attack but were permanently affected. They remained weak and thin-stemmed and their yield must have been greatly reduced.

(e) Interspecific Competition

The population trends shown by each species in the presence of other species are presented graphically in Figure 7. Details of the numbers on individual plants are given in appendix 7.

As each plant was infested with only one species initially, inter-specific competition could only have occurred when aphids migrated from their original host plants and colonised plants infested by one or more of the other species. In treatment II, trivial movement of this kind occurred to only a limited extent. With the exception of the pink biotype of A. pisum, a large proportion of the aphids remained on their original hosts (Table VIII) and the actual numbers colonising other plants in the cage were relatively low. The low incidence of migration in this treatment was partly due to the fact that the populations were controlled by various agents before intraspecific-competition- for space or food - became an important factor. In any case, migrants were not confined to the plants within the treatment as they were in treatment I and could therefore have migrated further afield.

In treatment III, the proportion of each species found on plants other than their original hosts was much higher than that in treatment II. In this case, however, the actual numbers were so low that encounters between individuals would have occurred only infrequently and inter-specific competition was therefore unlikely. The increased restlessness of the aphids in treatment III was probably the result of continual disturbance by birds which were chiefly responsible for the decline in numbers of M. viciae and both biotypes of A. pisum. A. fabae was apparently not

Figure 7 : Interspecific competition:- Weekly estimates of the average number of aphids in each treatment.

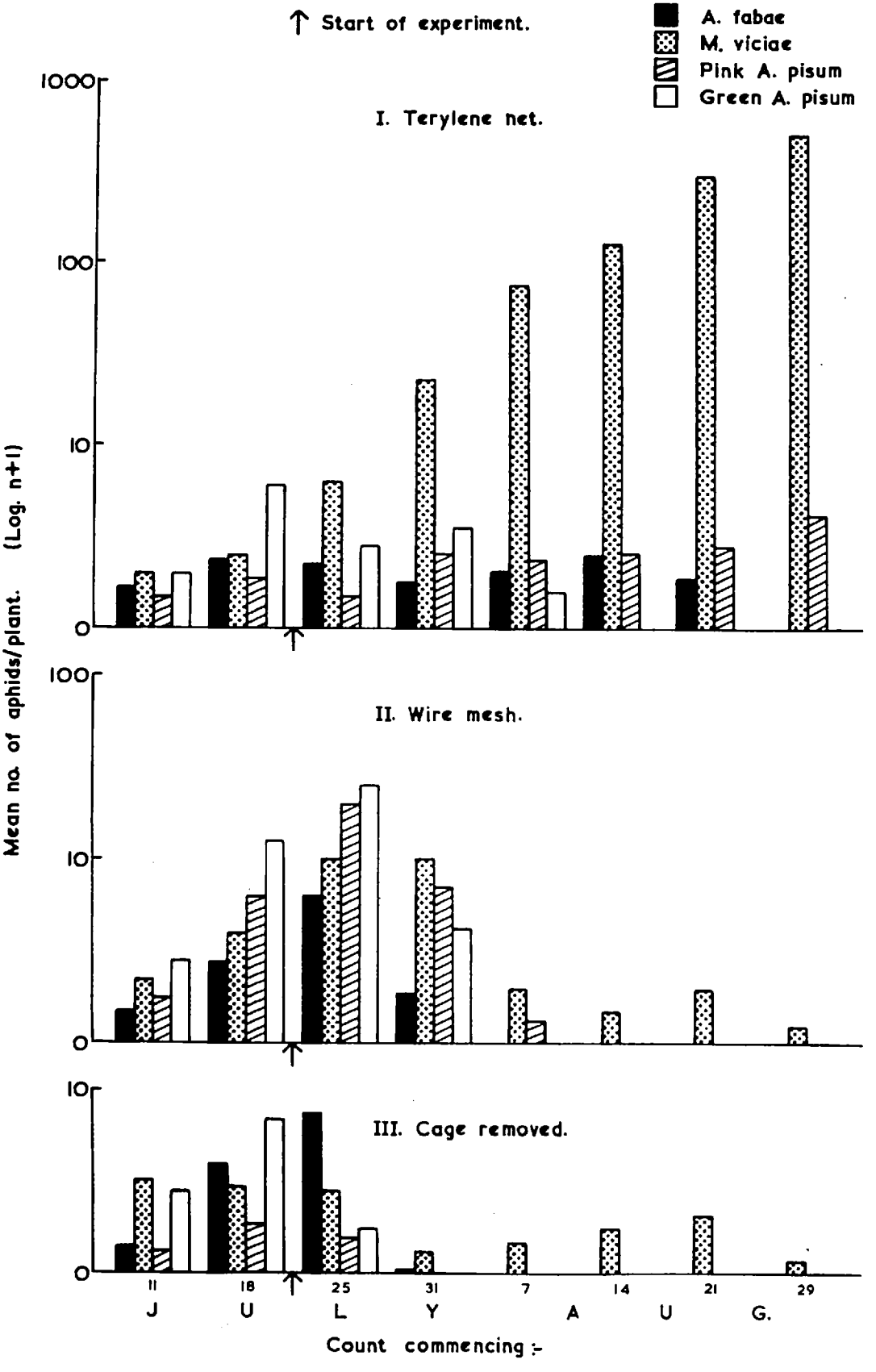

↑ Start of experiment.
A. fabae
M. viciae
Pink A. pisum
Green A. pisum
I. Terylene net.
II. Wire mesh.
III. Cage removed.
Mean no. of aphids/plant. (Log. n+1)
1000
100
10
0
11
18
25
31
7
14
21
29
J
U
L
Y
A
U
G.
Count commencing :-

Table VIII : The proportion of each species in treatment II found on the original host-plants on successive sampling dates, expressed as a percentage of the total number of that species found in the treatment.

Date	*A. fabae*		*M. viciae*		*A. pisum* (Pink)		*A. pisum* (Green)	
	Total No. in Cage	% on Original Hosts	Total No. in Cage	% on Original Hosts	Total No. in Cage	% on Original Hosts	Total No. in Cage	% on Original Hosts
11/7	12	100	64	98.4	27	77.7	127	98.4
18/7	133	97.0	300	97.3	221	88.7	596	86.6
25/7	615	92.7	765	91.5	276	33.7	1287	80.1
31/7	22	81.8	248	53.2	130	33.8	61	13.1
7/8	0	-	21	0	7	57.1	0	-
14/8	0	-	25	12.0	0	-	0	-
21/8	0	-	55	18.2	0	-	0	-

affected by bird predation; its rapid decline was effected by the epizootic *Entomophthora* sp.

The population trends shown by each species in treatments II and III were very similar to those observed when the species were confined in separate cages (Figs. 2, 3, 5 and 6). Apparently interspecific competition did not occur in these treatments or, if it did, its effect could not be distinguished from that of intraspecific competition.

Only in treatment I did the populations increase to a sufficiently high level for interspecific competition to have been a possible factor. In this treatment, migrants were unable to escape from the cage and plant-to-plant movement increased progressively as the populations increased in size. (Table IX)

Table IX : The proportion of each species in treatment I found on the original host-plants on successive sampling dates, expressed as a percentage of the total number of that species found in the cage.

Date	*A. fabae*		*M. viciae*		*A. pisum* (Pink)		*A. pisum* (Green)	
	Total No. in Cage	% on Original Hosts	Total No. in Cage	% on Original Hosts	Total No. in Cage	% on Original Hosts	Total No. in Cage	% on Original Hosts
11/7	39	100	64	100	15	60.0	133	100
18/7	148	97.3	221	99.1	29	10.3	298	88.6
25/7	315	100	334	82.9	46	4.3	194	95.9
31/7	352	99.4	1709	69.0	36	19.4	100	76.0
7/8	470	95.7	2350	46.0	41	48.8	11	63.6
14/8	965	93.3	4130	45.3	47	6.4	0	-
21/8	1231	97.5	7220	34.6	50	40.0	0	-
29/8	0	-	14850	45.7	76	17.1	0	-

(i) *Aphis fabae*

The majority of the aphids remained on the plants originally infested. These plants were all subsequently colonised by other species - predominantly *M. viciae* - so there was still a possibility of competition between *A. fabae* and the other species.

The maximum numbers of *A. fabae* (1200 individuals) and *M. viciae* (1170 individuals) infesting any one plant were recorded on plant 5 on 21st August. (The actual number of aphids belonging to each species was probably very much higher than the field counts suggest). Up to that time, however, there was no evidence of interspecific competition. *A. fabae* is a relatively sedentary species which feeds primarily on the very young and senescing leaves of bean plants, whereas *M. viciae* prefers the stems and

seed pods. Apparently, even at the level of infestation attained on plant 5, the two species were not competing against each other for space. Furthermore, there was no evidence that infestation by M. viciae rendered the plant less suitable for A. fabae. In fact, the population trend of A. fabae in this treatment was very similar to that shown in Figure 2 when it was the only species introduced.

The factor responsible for the sudden collapse of the population during the last week of August was the epizootic, Entomophthora sp.

(ii) Megoura viciae

This was by far the most successful species in treatment I and there was no indication of its being adversely affected by the presence of other species within the cage. The population maintained a steady logarithmic rate of increase up until the end of August when the experiment was terminated. By comparison, when all the plants were infested with M. viciae (Figure 3, treatment I) the population curve began to level off at the end of July. This was due to the fact that all plants were heavily infested with M. viciae and intraspecific competition resulted in a decreased rate of reproduction and, probably, of development. In the interspecific cage, however, M. viciae was able to exploit space on the plants which the other species were prevented - by the action of natural enemies - from utilizing.

The success of this species was due to its immunity to attack by fungus disease, which accounted for the decline of A. fabae, and its resistance to parasitism, which was mainly responsible for mortality in both biotypes of A. pisum.

(iii) Acyrthosiphon pisum - Pink biotype

The pink biotype of A. pisum was extremely restless in treatment I, as evidenced by the fact that, on 18th July, only 10.3% of the aphids were

found on the original host plants. Its mobility would soon have brought it into contact with other aphid species, and results suggest that it was adversely affected by their presence. It fared worse in this treatment than it did in the absence of other species (figure 5, treatment I). Furthermore, the numbers remained lower in this treatment than in treatment II. The relatively higher number of the pink biotype in the latter instance might have been due to a higher proportion remaining on the original host-plants (Table VIII), thus reducing the risk of encounters with other species.

The numbers remained more or less constant until 21st August, after which they declined - presumably as a result of parasitism.

This biotype of A. pisum is known to be extremely sensitive to contact with other aphids of the same species, and to avoid them wherever possible (Sutherland, 1969). Other species would probably have a similar effect. Contact with other individuals causes a significant increase in the production of alate offspring (Sutherland, loc. cit.), and is almost certain to have other adverse effects such as a reduction in the rate of development and reproduction.

The pink biotype survived longer than the green biotype of A. pisum. Although both biotypes are highly susceptible to parasitism, the pink form frequently reacts to the presence of adult parasites by dropping from the plant. This defence mechanism generally results in a lower percentage parasitism than in the green biotype. Frequent disturbance by parasites would probably contribute to a decreased rate of development and reproduction, and would stimulate plant-to-plant movement.

The effect of inter-specific competition might not be more adverse than that of intra-specific competition, although comparison with results presented in Figure 5 suggest that it does have a greater effect. However,

the total number of aphids was lower in the cage containing only the pink biotype, so contact between individuals would have occurred less frequently than in the inter-specific competition cage.

(iv) Acyrthosiphon pisum - Green biotype

As in the case of the pink biotype, the numbers were consistently lower in treatment I than in treatment II (Fig. 7). There is no obvious reason for this discrepancy but, as the actual numbers in cage I were lower from the first count on 11th July, the effect of parasites and invertebrate predators would probably be noticeable at an earlier stage.

The population in treatment I started to decline a week earlier than the green A. pisum population on its own (figure 6). It is unlikely that this was due to the effect of interspecific competition, however, because the decrease in numbers was evident when over 80% of all the aphids (except the pink biotype) were still on the original host plants. The decrease in numbers was probably due entirely to the activity of natural enemies, particularly parasites.

Appraisal of the Exclusion Technique used in 1967 and recommended modifications in subsequent investigations

1. Because of the large number of plants in each cage, it was almost impossible to examine a particular plant closely without disturbing the aphids on other plants. This factor contributed to the inaccuracy of field counts, particularly in the case of M. viciae and the pink biotype of A. pisum. It was therefore decided to reduce the number of plants per cage from twelve to six in future investigations.

2. Terylene netting did not effectively exclude invertebrate predators from the cages. In preference to using a finer gauge of netting, it was proposed to supplement the exclusion technique in subsequent experiments by manual removal of predators from cages completely covered by Terylene netting.

3. Alatae were unable to escape from cages which were completely enclosed by Terylene netting and their continued presence resulted in an artificial build-up of the population. A possible solution would be to use a coarser gauge net on the roofs of the cages. The apertures in the net would have to be sufficiently large to permit the egress of alate adults.

4. As the treatments were not replicated, it was not possible to establish whether differences between treatments were statistically significant or due to chance. Replication of treatments was considered desirable in future experiments.

It was also felt that more information about individual factors could be obtained by increasing the number of treatments to include all possible combinations of Terylene netting, wire mesh, or removal of, roof and/or sides of cages. This would increase the number of treatments to 9. An

experiment in which there were two replicates would therefore require 18 cages.

Because of the limited number of cages available and the amount of time required to count the aphids in each treatment, it was decided to concentrate on only one species in 1968. The pink biotype of A. pisum was selected because of its susceptibility to most biotic and abiotic factors. This species was also chosen because its conspicuous colour and its distribution on the host plant facilitated counting.

2. Further Studies on the Pink Biotype of Acyrthosiphon pisum in 1968

For the purpose of constructing the bar diagrams in Figures 8 and 9, the transformed data from the two replicates were pooled.

Bird predation had an immediate impact on the aphid populations (Figure 9). By mid-July - less than two weeks after the experiment was begun - the aphids had virtually diaappeared from all treatments which allowed access to birds. Over the same period, populations which were protected from birds (except in one replicate of Treatment IV) either continued to increase or remained at approximately the same level as just before the start of the experiment (Figure 8).

The rate of decline appeared to be greater when the sides of the cage had been removed (Treatments VII, VIII and IX) than when only the roof was removed (Treatments III and VI). In order to determine whether this difference was significant and to compare the effects of the other four treatments on the aphid populations, an analysis of variance was performed on the rate of increase shown by the populations over the two periods 1st - 8th and 8th - 16th July.

As the number of aphids on individual plants (Appendix 8) had already been transformed to log n+1, the weekly rate of increase shown by the population in a particular treatment could be measured directly as the difference between the calculated averages for two consecutive counts. If the population were decreasing, a negative value would be obtained.

The design of the experiment - a randomised block on which successive observations were made - lends itself to analysis as a split plot in time (Steel and Torrie, 1960).

As expected, the differences between treatments were highly significant ($P < .005$) (Table X(a)). There were no significant differences

Figure 8 : Population trends (of pink A. pisum) in cages from which birds were excluded.

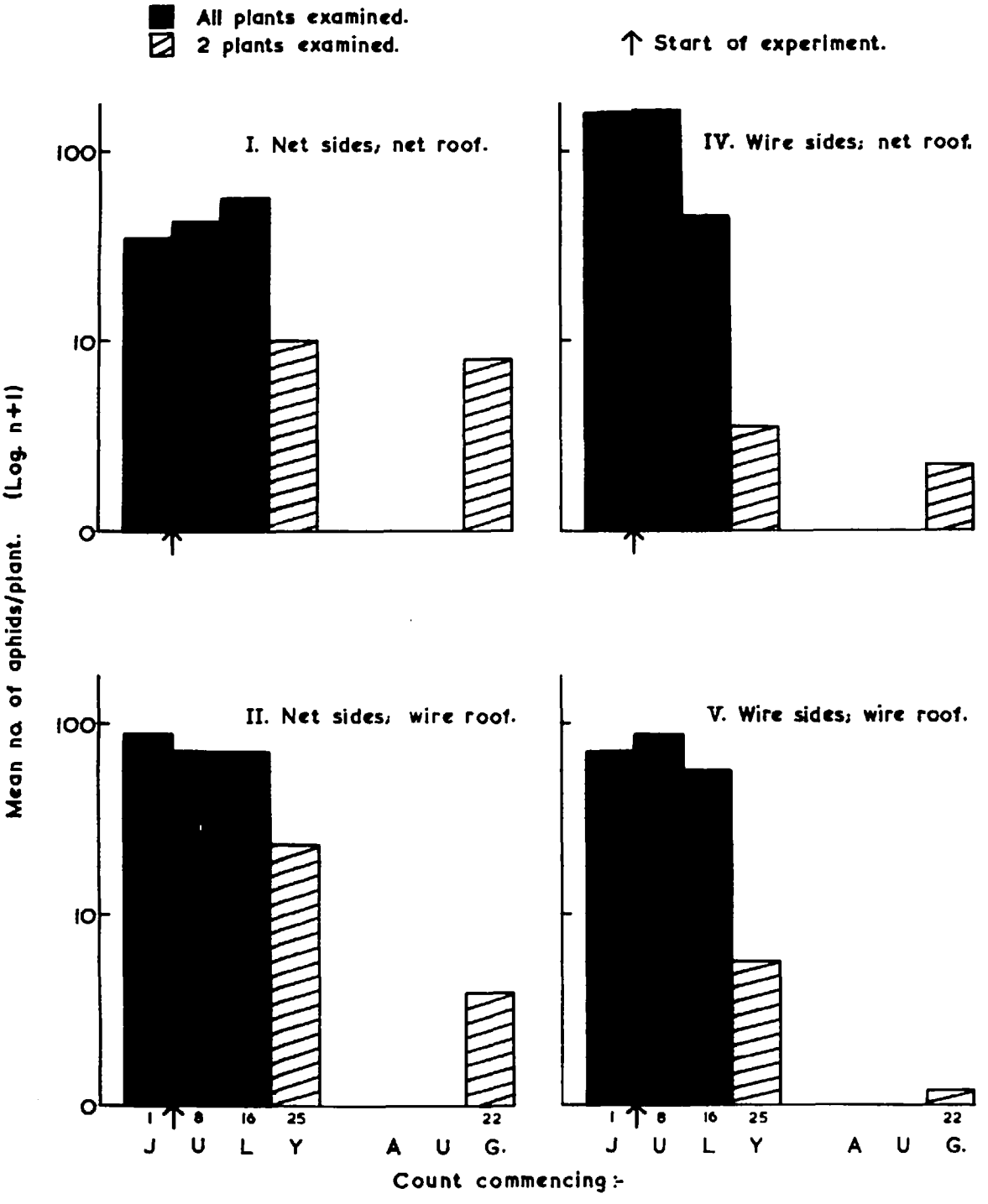
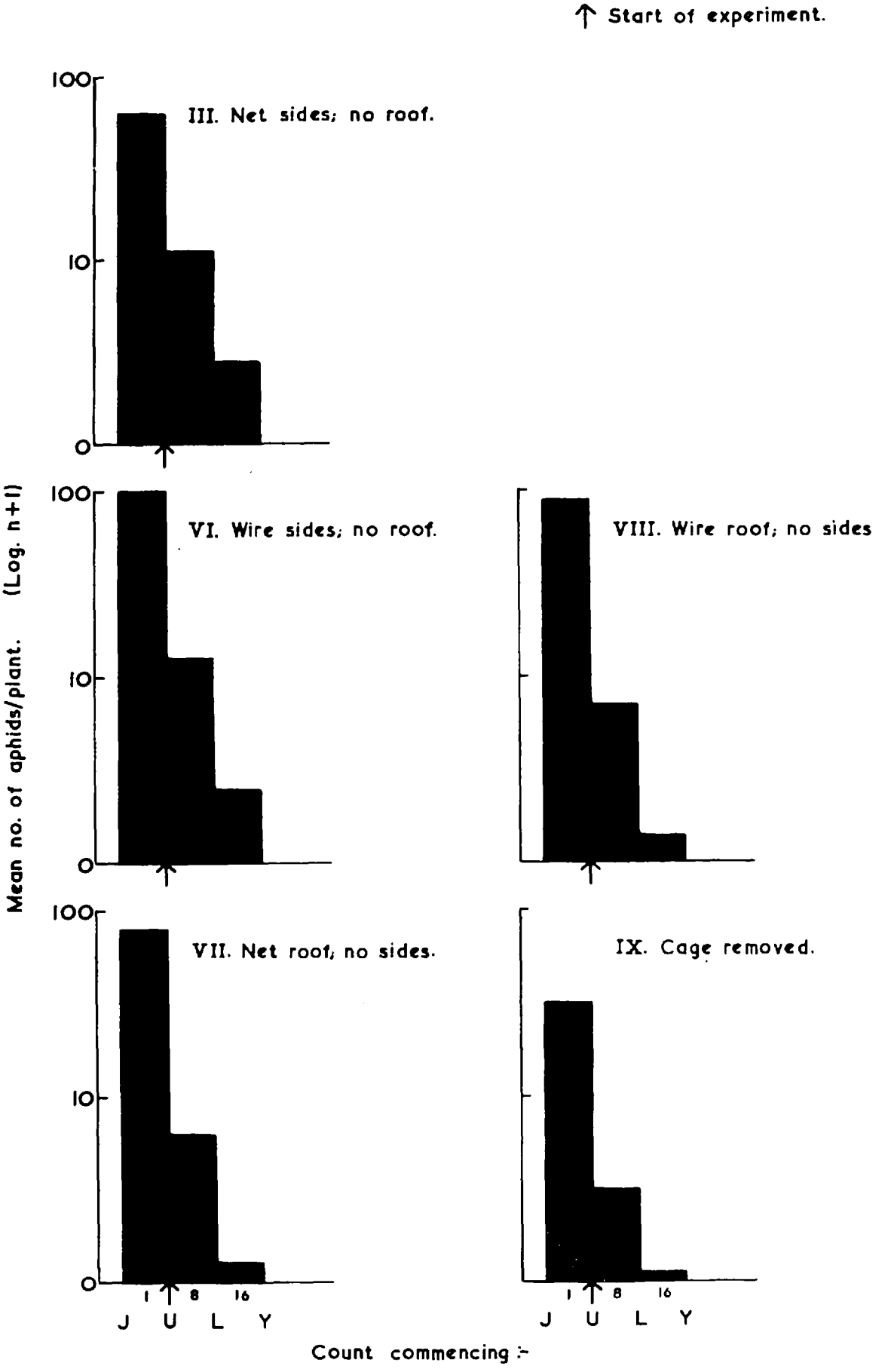

All plants examined.
2 plants examined.
↑ Start of experiment.
I. Net sides; net roof.
IV. Wire sides; net roof.
II. Net sides; wire roof.
V. Wire sides; wire roof.
Mean no. of aphids/plant. (Log. n+1)
100
10
0
1
8
16
25
22
J U L Y A U G.
Count commencing :-

Figure 9 : The effect of bird predation on caged populations of pink *A. pisum*


↑ Start of experiment.
III. Net sides; no roof.
VI. Wire sides; no roof.
VIII. Wire roof; no sides
VII. Net roof; no sides.
IX. Cage removed.
100
10
0
Mean no. of aphids/plant. (Log. n+1)
1
8
16
J U L Y
Count commencing :-

between blocks or periods.

Table X(a) : Analysis of variance of rate of increase shown by the pink biotype of A. pisum in different treatments in 1968.

Source	d.f.	S.S.	M. Sq.	V.R. (F)	
Blocks	1	0.1828	0.1828	2.9155	N.S.
Treats	8	5.4334	0.6792	10.8325	**
Error (a)	8	0.5019	0.0627		
Whole units	17	6.1181			
Periods	1	0.1171	0.1171	0.4200	N.S.
Periods x blocks	1	0.6813	0.6813	2.4437	N.S.
Periods x treats	8	0.9867	0.1233	0.4423	N.S.
Error (b)	8	2.2307	0.2788		
Total	35	10.1339			

't' tests were used to compare the differences between treatment means.

The standard error of the difference between two treatment means,

$$S_m = \sqrt{\frac{2 \times 0.0627}{2 \times 2}}$$

$$= 0.1771$$

For 8 degrees of freedom, $t_{.05} = 2.306$ and $t_{.01} = 3.355$.

The difference between two treatment means would only be significant if it exceeded $t \times S_m$

$= 0.4084$ ($P < .05$) or 0.5942 ($P < .01$).

The treatment means are arranged in order of magnitude in Table X(b).

The rate of decline in treatments which allowed access to birds was significantly higher ($P < .01$) than in those which were protected against bird predation, with the exception of treatment IV. There were no

Table X(b) : Mean rate of increase shown by populations of the pink biotype of A. pisum in various treatments during the first two weeks of July, 1968.

	Treatment	Mean Rate of Increase
Birds excluded	I	+ 0.1122
	V	- 0.0333
	II	- 0.0361
	IV	- 0.2640
Birds not excluded	III	- 0.6551
	IX	- 0.7159
	VI	- 0.7904
	VIII	- 0.9142
	VII	- 0.9210

significant differences between treatments I, II, IV and V, nor was the rate of decline significantly higher in treatments from which the sides of the cage were removed than in those from which only the roof was removed.

The population in one of the replicates of treatment IV (block B) suffered a high mortality during the second week of July as a result of invertebrate predation. The overall rate of decline was therefore higher than in the other treatments which excluded birds and did not differ significantly from that in treatment III. It was, however, significantly lower than the rate of decline in the other four treatments in which the populations were exposed to birds.

In the absence of bird predation, mortality was due to invertebrate predation, fungus disease and parasitism. There was no evidence to suggest that rain had any direct effect on the populations. The most common predators found on the sample plants in July were staphylinid larvae (Table XI) which constituted 64.6% of all the predators, excluding spiders. Other predators were Anthocoris nemorum (15.2%), syrphids (11.4%), coccinellids (5.1%) and Neuroptera (3.8%).

Although staphylinids are not generally considered to be predators of aphids, larvae were successfully reared to adulthood on a diet of pink A. pisum in the laboratory and Way and Banks (1968) observed them feeding on A. fabae in the field.

Block B was sampled a week later than block A. The relatively higher number of predators on the plants from block B was apparently due to the build-up of predators in the field during the intervening period.

Examination of sample plants revealed that the majority of the predators were missed when the plants were examined in the field. Field estimates of number of predators in each treatment were therefore very inaccurate and were only used as an indication as to whether the predator population was increasing or decreasing.

Aphid numbers were also underestimated in the field - usually by about 30%.

3.9% of the aphids on the sample plants taken from block A, and 2.1% of those from block B, were diseased. The fungus responsible was apparently the epizootic, Entomophthora thaxteriana. Infected aphids show no obvious signs of the disease until shortly before death occurs, therefore many of the apparently healthy aphids may, in fact, have been diseased. Furthermore, this particular species of Entomophthora does not produce rhizoids and, as Rockwood (1950) pointed out, many of the diseased aphids may be dislodged from the plant and never observed. The proportion of aphids affected by the disease may therefore have been considerably greater than suggested by the number of diseased aphids found on the sample plants.

Parasitism was apparently not an important factor at this stage. The maximum number of mummies found on any plant was two. All of the fourth

Table XI : Numbers of aphids and predators on sample plants in July, 1968.

Date	Block	Treat	APHIDS			PREDATORS					
			*Healthy	Diseased	+Mummies	Staph.	Cocc.	Syrph.	A. nem.	Neur.	Spiders
9/7	A	I	71	4		1 L.					
12/7	"	II	97	4	2 (1 h.)	5 L.					1
12/7	"	III	18	2		3 L., 1 A.					
9/7	"	IV	278	7	2						
12/7	"	V	174	4		5 L.			2 N.		
8/7	"	VI	105	9	1						
8/7	"	VII	29	1	1 (h.)						
8/7	"	VIII	19		2		1 L., 1 A.		1 A.		
9/7	"	IX	4		1		1 L.				
18/7	B	I	76					1 L.	1 A.	1 L.	
17/7	"	II	161			6 L.	1 L.				
18/7	"	III	1			6 L.		1 L.	1 N., 1 A.		
19/7	"	IV	16		1	15 L.		4 L.	1 A.		
18/7	"	V	65	8	1	3 L.		1 L.	1 N., 1 A.		
18/7	"	VI	5					1 L.	1 N., 1 A.		
17/7	"	VII	0						1 N.	2 L.	
17/7	"	VIII	0			5 L., 1 A.		1 L.			2
N.S.	"	IX									

N.S. = Not sampled
*Apparently healthy (See text)
+Total mummies outside brackets; followed by no. hatched in brackets

L : Larvae ; A ; Adults ; N : Nymphs
Staph. = Staphylinids
Cocc. = Coccinellids
Syrph. = Syrphids
A. nem. = Anthocoris nemorum
Neur. = Neuroptera

instar aphids were dissected but none contained parasite larvae.

The aphid populations on only three of the sample plants (those collected from treatments A II, A III and A V on the 12th July) had developed a stable-instar distribution. The potential rate of increase (λ) was calculated for each population using Hughes' equation

$$e^{\lambda} = \frac{a_1 + a_2}{a_2 + a_3}$$

where a_1, a_2 and a_3 are the number of individuals in the first, second and third instars respectively (Hughes, 1962, 1963).

Both treatments II and V afforded complete protection from bird predation and the populations were increasing in both cases, the potential rate of increase being 0.53 and 0.74 respectively. In treatment III, birds had access to the aphids through the top of the cage and, in this case, the population was declining. The potential rate of increase per instar period for treatment III was calculated as - .36 .

The proportion of first instar nymphs was invariably lower in populations which were exposed to bird predation than in those which were protected from birds. This was particularly striking in the samples from treatments III and VI in block A where the proportion of adults was relatively high (Table XII). Presumably the frequent disturbance of the aphids by birds hopping about on the plants resulted in a lowering of the reproductive rate. The instar-distribution in treatments VII, VIII and IX from block A and treatment VI from block B suggested that birds fed selectively on the larger aphids, particularly adults.

The populations in treatments which did not allow access to birds continued to decline until the experiment was terminated towards the end of August. By that time, only the population in treatment V in block B

Table XII : Instar distribution of aphids on sample plants in July, 1968

Block	Treatment	No. of Aphids on Plant	Percentage of Total Aphids on Plant						
						APTERAE		ALATAE	
			1st Inst.	2nd Inst.	3rd Inst.	4th Inst.	Adults	4th Inst.	Adults
A	I	71	70.0%	4.3%	4.3%	4.3%	17.1%		
"	II	97	38.0	17.4	15.2	16.3	13.0		
"	III	18	11.1	16.7	22.2	38.9	11.1		
"	IV	278	48.9	10.4	9.4	15.1	16.2		
"	V	174	42.8	20.2	9.8	16.8	10.4		
"	VI	105	11.7	39.8	21.4	15.5	10.7	1.0	
"	VII	29	0	44.8	37.9	13.8	0	3.4	
"	VIII	19	0	47.4	31.6	15.8	5.3		
"	IX	4	0	50.0	50.0	0	0		
B	I	76	19.5	40.3	28.6	7.8	3.9		
"	II	161	29.4	20.0	23.8	13.7	10.0	1.9	1.3
"	IV	16	18.2	45.5	9.1	27.3	0		
"	V	65	35.9	40.6	6.3	9.4	7.8		
"	VI	5	0	60.0	20.0	20.0	0		

had died out. During the third week in August, two plants were removed from each of the bird exclusion treatments for detailed examination in the laboratory. The relative abundance of the various groups of predators had changed quite considerably since the previous sample plants were examined five weeks earlier. Anthocorids were now the most numerous predators (Table XIII); there were very few staphylinids and no coccinellids.

Spiders were found on most of the plants and may have contributed to the decline of the populations. The most common species were Meta segmentata (Fam.: Argiopidae) and Theridion bimaculatum (Fam.: Theridionidae).

Fifteen adult parasites emerged from aphid mummies removed from the sample plants. Twelve of these were identified as Aphidius ervi, two as A. smithi and one as Praon sp. - probably P. volucre.

The manual removal of predators from plants which were completely enclosed by Terylene netting (Treatment I) was singularly unsuccessful because most of the predators were missed during field counts. In order to locate all the predators, each plant would need to be examined very carefully. This is not practicable when the plants are infested with the pink biotype of A. pisum because the aphids react to any disturbance by dropping from the plant.

Because of the extreme sensitivity of the aphids, even six plants per treatment proved to be too many. Ideally, the field cages should be considerably larger or the number of plants should be further reduced. If there were only one or two plants in a cage of the dimensions used in the field experiments, it would be possible to approach the plants from all sides without disturbing the aphids. This should lead to greater accuracy of field counts.

Table XIII : Numbers of aphids and predators on sample plants in August, 1968

Date	Block	Treat.	APHIDS			PREDATORS					
			Healthy	Diseased	Mummies	Staph.	Syrph.	A. nem.	Neur.	Derm.	Spiders
22/8	A	I	4.5		3.0 (2 h.)			5.5 N.	0.5 A.		1.5
22/8	"	II	13.0			0.5 L.; 0.5 A.		4.0 N.			4.0
26/8	"	IV	5.0			1.0 A.		1.5 N.		0.5	3.5
26/8	"	V	0.5	1.0	1.0 (h.)			0.5 N.			0.5
28/8	B	I	14.5	0.5	1.0		0.5 L.	1.0 N.; 0.5 A.			
28/8	"	II	1.5		2.5	2.0 A.			0.5 L.		0.5
29/8	"	IV	0.5		1.5 (1.0 h.)			2.0 N.; 0.5 A.			2.5
29/8	"	V	0.0					1.0 N.	0.5 L.		2.0

Derm. = Dermaptera

N.B. Two plants were examined from each treatment. The numbers given in Table XIII represent the mean number of aphids and predators per plant.

For explanation of abbreviations, please refer to Table XI.

D. DISCUSSION

Hughes (1962, 1963) pointed out that the potential and intrinsic rates of increase and the overall mortality rate of an aphid population should be related to a physiological rather than an absolute time-scale. These parameters, and others such as the emigration rate, may be calculated from an analysis of the instar distribution of the population, provided that the instar distribution has become stable.

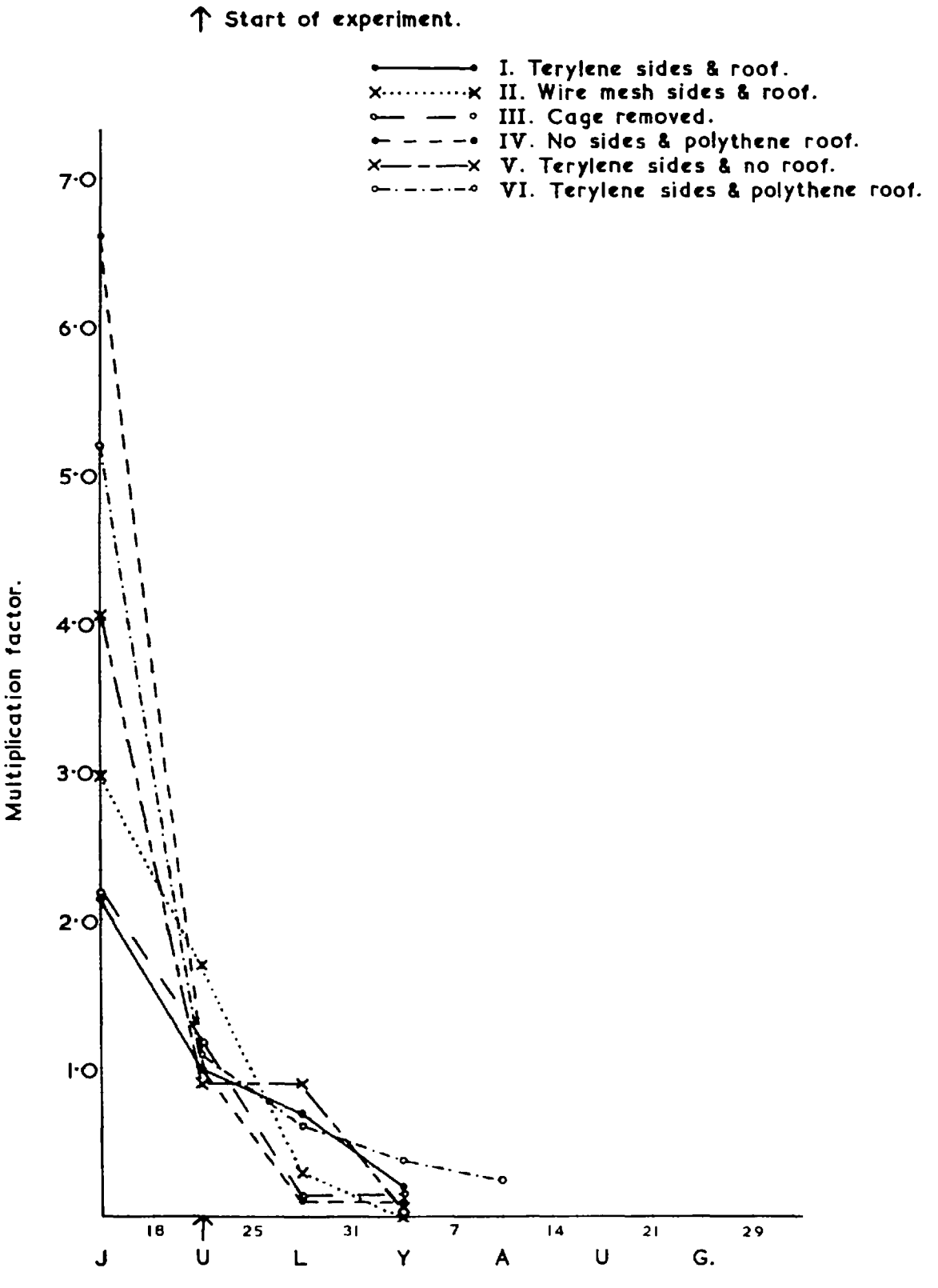
Hughes' method could not be used to interpret changes in the caged populations of the various aphid species investigated in 1967 and 1968 because of the infrequent occurrence of stable-instar distributions (Pages 39 and 71). However, for the purpose of comparing the effect of the various treatments on aphid populations, an estimate of the weekly rate of increase (F) may be obtained by determining the factor by which the population increased between successive counts. Thus

$$F = \frac{n_i}{n_{i-1}}$$

where n_i is the estimated mean number of aphids per plant at the count in the week i, and n_{i-1} the number at the previous count. Values greater than 1.0 will indicate an overall increase in the population size, and values less than 1.0 will indicate a decline in numbers. The weekly rates of population increase of A. fabae and M. viciae in the various treatments to which they were subjected in 1967 are given in Figures 10 and 11.

In the case of A. fabae (Figure 10), there was very little difference between treatments except on the 18th July, prior to the removal of Terylene net from any of the cages. Presumably the variation at this time was due to differences in the reproductive capacity of the adults used to infest the plants initially, or perhaps to the aphids becoming more quickly established in some cages than in others.

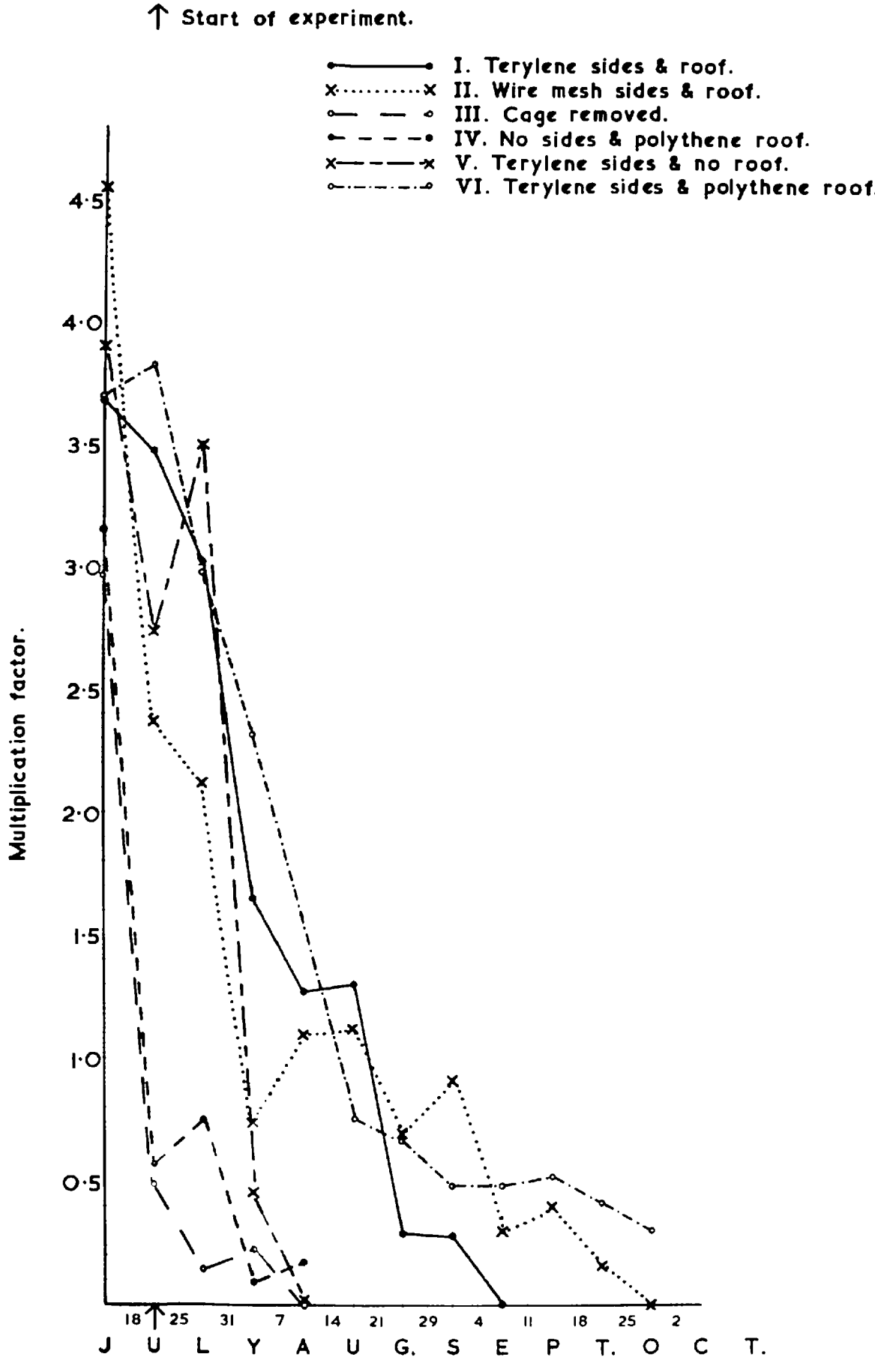
Figure 10 : Weekly rate of increase in populations of A. fabae subjected to various treatments


↑ Start of experiment.
I. Terylene sides & roof.
II. Wire mesh sides & roof.
III. Cage removed.
IV. No sides & polythene roof.
V. Terylene sides & no roof.
VI. Terylene sides & polythene roof.
Multiplication factor.
7·0
6·0
5·0
4·0
3·0
2·0
1·0
18
25
31
7
14
21
29
J
U
L
Y
A
U
G.

On the other hand, the rate of increase of populations of M. viciae (Figure 11) appeared to be markedly affected by the various treatments. In treatments III and IV, the rate of increase dropped sharply (to less than 0.6) during the week when the populations were first exposed to bird predation. Populations in the remaining treatments continued to increase, though at a progressively reduced rate, at least until the end of July. The rate of increase was generally higher in the Terylene net-covered cages (Treatments I and VI) than in Treatments II and V. The more rapid decline in the rates of increase in the latter two treatments was mainly due to emigration of alatae. Birds had access to the aphids in treatment V via the open roof of the cage but they had no noticeable effect on the population until the beginning of August when the rate of increase dropped from 3.45 (for the week up to the 31st July) to 0.46 the following week. During the latter part of August and most of September, the weekly rate of increase in treatment II was similar to that in treatment VI. The plants deteriorated more rapidly in treatment I than in the other two treatments, apparently because of the relatively larger aphid population. This presumably accounted for the more rapid decline of the aphid population in Treatment I in September.

Bird predation drastically reduced populations of M. viciae and both biotypes of A. pisum but A. fabae was unaffected. A. fabae may be avoided by birds because it is distasteful or perhaps because of its colour. It has a noticeably acrid flavour to man, whereas the other species are virtually tasteless. Other possible - though less likely - reasons for its immunity to bird predation are its relatively smaller size and greater tenacity. Smith (1957) found that birds tend to feed selectively on larger aphids. This was borne out to some extent by the instar distribution of M. viciae and the pink biotype of A. pisum on plants which were accessible to birds in this investigation. However, the rapid rate of

Figure 11 : Weekly rate of increase in populations of M. viciae subjected to various treatments


↑ Start of experiment.
I. Terylene sides & roof.
II. Wire mesh sides & roof.
III. Cage removed.
IV. No sides & polythene roof.
V. Terylene sides & no roof.
VI. Terylene sides & polythene roof.
Multiplication factor.
4·5
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
18
25
31
7
14
21
29
4
11
18
25
2
J U L Y A U G. S E P T. O C T.

decline of the populations suggested that smaller aphids were also consumed. A. fabae adults are larger than the first and second instars of the other two species, but they were apparently ignored by birds - even in the competition experiments where all species occurred on the same plants. It therefore seems unlikely that size alone would account for the disinterest shown by the birds. Neither is it very probable that the tenacity of the aphids would deter birds from feeding on them. Way et al. (1969) observed greenfinches scraping Brevicoryne brassicae from the lower leaves of brussels sprout plants. Similar tactics would effectively remove A. fabae but there was no evidence that birds attacked the aphids in this manner.

In spite of the fact that birds fed readily on A. pisum, this species is a serious pest of peas and lucerne in many countries. The susceptibility of an aphid species to bird predation must, therefore, be governed by other factors besides their suitability as prey. In the first instance, the nature of the host plant is important - it would need to be sufficiently sturdy to support the weight of the birds. Lucerne does not fulfil this requirement and bird predation is therefore unlikely to have much effect on aphid infestation in this crop. Secondly, only aphids which are feeding on relatively exposed parts of the plant will be affected. A. pisum and M. viciae which were feeding within the furled leaves at the tip of the plant escaped predation.

The distribution of the aphid population in the crop might also be an important factor. Clark (1964) investigated bird predation in relation to the population density of the psyllid , Cardiaspina albitextura. He found that birds effectively controlled sudden localised increases of the psyllid population but were ineffective when other environmental factors favoured a general increase over a large area. A similar situation might arise in the case of aphids on certain crops, particularly if the crops cover a large area. The bean plot used in these investigations was relatively small and

the infestations of M. viciae and A. pisum confined to a very small proportion of the plants. Furthermore, there was a clump of trees situated near the plot in which some of the insectivorous birds appeared to be nesting. Conditions were therefore particularly favourable to bird predation.

The control of A. fabae in 1967 was effected by an epizootic, Entomophthora sp. Way (1967) recorded that populations of A. fabae at Rothamsted were virtually eliminated as a result of Entomophthora infection in 1954. It is an extremely efficient mortality factor but its appearance is sporadic and several years may elapse between outbreaks of the disease. Its incidence is dependent on an abundance of spores in the atmosphere and suitable weather conditions. High humidity and moderate temperatures favour the rapid spread of the disease. Outbreaks of Entomophthora spp. generally occur towards the end of July which in most years is too late to prevent the aphids from causing economic injury to the crop.

A. pisum was also affected by a fungus disease - apparently caused by Entomophthora thaxteriana - which killed a significant proportion of the population in 1968.

The role of invertebrate predators in controlling aphid populations is more difficult to assess because of the complexity of the factors involved. van Emden (1966) pointed out that the effectiveness of predators is governed by three main criteria:- synchronization with the aphid prey, voracity of the predators and reproductive rate of the aphids.

From an economic point of view, predators will only be effective if they are able to suppress the aphid population below the threshold of economic injury (Hodek, 1967). If the aphids escape early predation, the populations are liable to build up to a very high level (Way et al., 1954; Szalay-Marzso, 1958; Skuhravy and Novak, 1966). Although many predators may be attracted to these high populations, they are seldom able to control

the aphids and in any case their impact comes too late to be of economic importance (Hodek et al., 1965 Hagen and van den Bosch, 1968).

In the field experiments described in this section, the artificially-infested plants were all initially enclosed in Terylene net-covered cages to allow the population to become established on the plants. Although the net did not completely exclude predators, it delayed their effect and they were therefore unable to prevent the build-up of the populations. The only species which apparently suffered significant mortality due to invertebrate predation was the pink biotype of A. pisum. The rate of increase was considerably lower in this biotype than in any of the other aphids and the populations were consequently relatively small.

In theory, a comparison of the populations in wire mesh- and Terylene net- covered cages should give a measure of the effect of invertebrate predation but, as the net did not effectively exclude predators, such a comparison would give an underestimate of the effect of predators on the pink biotype of A. pisum. Even though the gauge of the Terylene net used was fine enough to exclude most of the larger insect predators, syrphids and coccinellids were sometimes found on the plants in the cages. Sailer (1966) suggested that adult predators are attracted to the large aphid populations within the cages and lay their eggs on the netting. Some of the newly-hatched larvae may find their way into the cages and eventually reach the aphids. Adults may also occasionally have entered unnoticed when the cage door was opened.

The populations of M. viciae and the green biotype of A. pisum increased rapidly and the preferred feeding sites soon became overcrowded, resulting in the production of alatae. The aphids were unable to escape from cages covered with Terylene netting and this factor largely accounted for differences between populations in Terylene net and wire mesh cages. The difference between treatments was particularly marked in the case of A.

pisum where the removal of the Terylene net from the wire cage was followed by a rapid decline of the population. In this instance, the deterioration in the condition of the host plants intensified crowding effects which further stimulated alate production. It probably also induced large numbers of apterae to leave the plants.

The plants were less affected by high populations of M. viciae and the population in the wire cage remained at a high level throughout August. The subsequent decline was partly due to emigration but was also the result of a decrease in rate of development and reproduction caused by lower temperatures and the appearance of oviparae. The latter two factors were mainly responsible for the decline of the populations in treatments covered with Terylene net. Only in treatment I did the high population cause the premature death of the host plants.

These results emphasise the need to determine the incidence of alatae in the different types of cage. Without information on the proportion of alatae in the populations, a comparison of the total populations in different treatments might lead to the conclusion - erroneous in this case - that the smaller populations in wire mesh cages were due to the effect of predators. Samples taken early in the experiment would give some indication of the rate of build-up of predators in the various treatments.

Anthocoris nemorum was the most common predator in 1967 but it only appeared at the beginning of August and was therefore too late to prevent the increase of aphid populations. In some instances, they apparently arrived on the plants after the aphids had disappeared which suggests that they were not specifically attracted to aphid-infested plants. Smith (1969) reached the same conclusion in her investigations on Brassica aphids.

The relative scarcity of coccinellids on plants infested with M. viciae was probably due to the toxic effect of the aphids Blackman (1966).

The high number of staphylinids on the plants in 1968 was interesting because this group is not generally mentioned in connection with aphid control. Dunn (1949) recorded the occurrence of Tachyporus sp. on potato plants but believed them to be scavengers. However the late W. O. Steel (personal communication) suggested that they might prey on aphids. During 1969, larval stapylinids were successfully reared in the laboratory on a diet of aphids.

Parasitism contributed to the mortality of both biotypes of A. pisum but M. viciae was apparently unaffected. A. fabae populations died out too soon for parasitism to become established.

The incidence of parasitism appeared to be greater in the green biotype of A. pisum than in the pink form. This was probably largely due to the higher density of aphids in the former instance but the behaviour of the pink biotype might have reduced its susceptibility to parasitism. Adults and advanced nymphs of the pink form become very agitated in the presence of adult parasites and take evasive action, often dropping from the plant. Small nymphs react less violently but may nevertheless deter the parasites to some extent.

In the green biotype, this type of avoiding reaction is developed to only a minor extent and it may therefore be more susceptible to parasitism.

Rain is considered to be an important mortality factor in some aphid species, including A. pisum (Dunn, 1951; Dunn & Wright, 1955). In 1967, heavy rain fell on the 22nd July (14.6 mm. in 2.0 hours) and 23rd July (35.2 mm. in 2.9 hours). This was immediately after the start of the experiment and it was therefore difficult to separate the effect of rainfall from that of other factors such as emigration. It seemed likely that the rain was partly responsible for the decline of the green A. pisum population in the wire mesh cage (Treatment II) and there was some indication that the

pink biotype was also affected. In the competition experiment, however, the populations of all the species, including the pink and green biotypes, of A. pisum increased steadily in Treatment II over this period. It can therefore be assumed that on field beans none of the species is particularly affected by rain.

Wadley (1931) found that the effect of rain on populations of Toxoptera graminum on oats varied with the intensity of the rain. Miskimen (1970) observed that heavy rain (1 inch or more over a short period) caused high mortality in populations of the sugar cane aphid, Sipha flava. Less rainfall had no significant effect. Dunn and Wright (loc. cit.) gave no indication of the intensity or even of the total rainfall which reduced populations of the pea aphid on lucerne. It is unlikely, however, that it would have greatly exceeded the intensity of the rain which fell on the 23rd July, 1967 at Silwood Park. The effect of rain on aphid populations must therefore be influenced by other factors besides intensity.

The nature of the host plant might be important, broad-leaved plants affording more protection than those with small or narrow leaves such as lucerne and cereals. This hypothesis conflicts with that of Smith (1957) who suggested that populations on broad-leaved plants might suffer a higher mortality because 'sheets of water' would flow over the leaves and wash the aphids off.

Manglitz and Hill (1964) found that rain caused a higher mortality in populations of the sweet clover aphid, Therioaphis riehmi, on 1st year then on 2nd year plants. They attributed the differential mortality to the greater protection afforded by the larger plants.

The effect of rain might also be modified by the distribution of the aphids on the plants; those feeding in relatively exposed situations are more likely to be affected than those on protected areas of the plant.

It is not possible at this stage to explain why none of the species in this investigation - particularly green A. pisum, which feeds on the young leaves at the tip of the plant and would therefore be expected to be especially vulnerable - were significantly affected by rain.

Neither the exclusion technique nor the manual removal of predators proved very satisfactory. The insecticidal check method might be a more successful means of eliminating invertebrate predators but it would have to be used in conjunction with the exclusion technique if the aphid species were subject to bird predation. A finer gauge net than the one used in these investigations would probably increase the efficiency of the exclusion technique. Alternatively, the net could be treated with insecticide (Way & Banks, 1968; Eldin, 1970). This might have the added advantage of killing any aphids attempting to escape and thus prevent them from returning to the plants. (The continued presence of alatae in caged populations of M. viciae and green A. pisum resulted in an artificial build-up of the populations). It would not, however, affect soil-inhabiting predators which would have to be controlled by the application of insecticide to the soil. In studies of aphids which fall readily from the plants, such as M. viciae and pink A. pisum, it would be essential to use a selective insecticide which would not harm the aphids.

Manual removal of predators was only used in studies on the pink biotype of A. pisum (in 1968). It proved to be particularly unsuitable because the aphid is extremely sensitive to any disturbance. It might give more satisfactory results in studies on the effect of predators on A. fabae populations as this species is not readily disturbed. The plants could therefore be subjected to a more thorough search for predators.

SECTION II : STUDIES ON BIOTIC FACTORS AFFECTING APHID POPULATIONS IN THE FIELD

A. INTRODUCTION

The effectiveness of invertebrate predators is largely determined by their ability to prevent aphid populations from increasing above the threshold of economic injury to the crop (Hagen and van den Bosch, 1968). Van Emden (1966) emphasised the importance of synchronisation between the arrival of aphids and predators on the host plants. Although it is generally accepted that invertebrate predators do exert some check on aphid populations, many workers have found that their impact comes too late to prevent economic injury to the plants (Way et al., 1954; Hodek, 1967). In years of aphid abundance, however, the predator population generally builds up to a high level towards the end of the season and causes high mortality among aphids on late-sown crops and weeds (Way and Banks, 1958; Meier, 1966). Only a small proportion of the aphids survive to lay eggs and the population the following year is consequently low. Thus the long-term effect of predators may be of considerable significance.

The most important invertebrate predators of aphids are the coccinellids and syrphids. Research relating specifically to aphidophagous coccinellids has been reviewed by Hagen (1962) and Hodek (1967) and to syrphids by Schneider (1969).

Several species of aphidophagous coccinellids occur in Britain, the most important being Adalia bipunctata (L.), Coccinella septempunctata L. and Propylea quattuordecimpunctata (L.) (Banks, 1953; 1955). All three species overwinter as adults and are generally univoltine (Bodenheimer, 1943; Banks, 1955; Bonnemaison, 1966). A. bipunctata may, under favourable weather conditions, produce a second generation (Banks, 1953). Smee (1922) claimed that coccinellids in Britain may have three or even four generations per year but this seems highly unlikely. Banks (1953) observed that over-wintered females of A. bipunctata laid the majority of their eggs on

nettles and relatively few on beans, although more eggs were laid on beans later in the season by first generation adults from the nettle brood.

Many species of Coccinellidae appear to be primarily attracted to a specific type of host plant and feed mainly on the aphids occurring in that habitat (Hodek et al., 1959; Iperti, 1965; Blackman, 1965a). Hodek et al found that, in Czechoslovakia, A. bipunctata occurs almost exclusively on trees and shrubs whereas C. septempunctata is common only in fields. In England, this distinction is less marked, perhaps because the fields tend to be relatively small and bounded by hedgerows and trees, and A. bipunctata is usually the most common coccinellid predator of aphids on beans.

The various species show particular height preferences for oviposition which are closely associated with their preferred habitat (Blackman, 1965 a and b, 1967 b; Iperti, 1966). C. septempunctata invariably lays its eggs near the base of the plant; A. bipunctata tends to oviposit at a much higher level, although it appears to be less restricted than the former species.

The relative suitability of various aphid species as prey of A. bipunctata and C. septempunctata has been studied by Iperti (1966), Blackman (1965 a and b, 1966, 1967a) and El Hariri (1966). Megoura viciae proved to be toxic to both larvae and adults of A. bipunctata, and to young adults of C. septempunctata. Mature adults of the latter species survived on a diet of M. viciae but did not lay any eggs. A. fabae proved to be a less suitable prey than Acyrthosiphon pisum for both species of coccinellids.

The biology of the Syrphidae is extremely diverse. Most species hibernate as mature larvae but a few, such as Syrphus luniger and S. balteatus, hibernate as flies (Schneider, 1948, 1969). Although the majority of syrphids are bi- or oligovoltine, a few species are univoltine and others may have as many as five generations per year. S. eligans and

S. nitidicollis are univoltine species which are active only in the spring and early summer.

Adult syrphids feed mainly on pollen and nectar. Smith (1957) and Dixon (1959) suggested that the adults are initially attracted to a particular area by the presence of flowering plants. Chandler (1967) distinguished between phytozetic syrphid species (Melanostoma spp. and most species of Platychirus), which laid significant numbers of eggs on uninfested plants, and aphidozetic species (Syrphus spp., P. scutatus and Scaeva pyrastri) which almost invariably oviposited on infested plants. Aphidozetic species are strongly attracted to aphids and lay a high proportion of their eggs within 5 mm of the nearest aphid colony (White, 1958;Dixon, 1959; Chandler, 1968 c). Most investigations have shown a positive correlation between aphid density and syrphid oviposition (Banks, 1953; White, 1958; Peschken, 1965; Chandler, 1968 c). Both Banks and Chandler found, however, that the relationship tended to become inverse at high aphid densities.

Female syrphids are attracted to aphid colonies mainly by chemical (olfactory) stimuli although visual and mechanical stimuli may also be important (Dixon, 1959; Bombosch, 1962; Volk, 1964; Chandler, 1966).

Many species show marked height preferences for oviposition (Chandler, 1967).

Oviposition may also be affected by the density of the plant stands. Peschken (1965) reported that oviposition was greater in dense than in sparse stands. Smith (1969) found that Platychirus spp. deposited significantly more eggs on brussels sprout plants surrounded by bare soil than on those surrounded by weeds but that the reverse was true for Melanostoma spp. Species of Syrphus laid more eggs on sprouts surrounded by weeds early in the season, but tended to prefer plants surrounded by

bare soil later in the season.

Although Syrphus spp. show a positive repponse to aphid density, various species have different optimum sizes of aphid population and also different colony sizes. Chandler (1968 b) pointed out that selection of specific sites by different species would reduce the likelihood of inter-specific competition.

Little is known about the relative attractiveness of aphid species to syrphids or the suitability of aphids as prey. Chandler (1968 b) found that S. balteatus laid more eggs on plants infested with pink Acyrthosiphon pisum than on those infested with the green biotype. His experiments revealed that this response was elicited by the colour of the aphids rather than by a specific preference for the pink biotype. Larvae of S. corollae are apparently able to distinguish between Brevicoryne brassicae and Myzus persicae and show a marked preference for the former species (Ruzicka, 1969).

Aphids are subject to attach by several other groups of predators, including anthocorids, cecidomyids, chrysopids and hemerobiids. These groups are generally considered to be less important than coccinellids or syrphids, although they have been known to cause high mortality among aphid populations from time to time.

Anthocorids have been studied in Britain by Hill (1957), Anderson (1961, 1962 a and b) and Russel (1970). The most common species affecting aphids on agricultural crops is Anthocoris nemorum. It usually has two generations per year in southern England, the first occurring mainly on trees, particularly Salix sp. (Anderson, 1961). Anderson found that A. nemorum developed more slowly and was less fecund when reared on a diet of A. fabae than when it was fed on A. pisum. In spite of its relative unsuitability, A. fabae constitutes a common prey of A. nemorum in the field. Way and Banks (1968) stated that A. nemorum was the most common

predator of Aphis fabae on spindle in September and October, and the first predator to appear on spindle in spring.

Davis (1916) believed cecidomyids to be important predators of the pea aphid in America and Hafez (1961) attributed the mid-seasonal decline of Brevicoryne brassicae on brussels sprout plants in the Netherlands largely to the activity of the cecidomyid, Phaenobremia aphidivora. Most of the common aphidophagous cecidomyids in Britain belong to the genus Phaenobremia. Wood-Baker (1964) recorded them as predators of several aphid species, including Aphis fabae and Megoura viciae. Cecidomyids are generally bivoltine in England, eggs being laid in early June and at the end of July. Smith (1957) found eggs apparently belonging to a third generation at the end of September, 1956, on broom.

Several species of chrysopids and hemerobiids prey on aphids, usually in the adult as well as the larval stage. Others are aphidophagous only in the larval stage. The latter group includes the species Chrysopa carnea which is one of the most common chrysopid predators of aphids in Britain. According to Killington (1937), C. carnea has two generations per year in England. Withycombe (1922) observed that newly-hatched larvae of C. septempunctata sometimes prey on unhatched eggs.

Neuroptera are seldom sufficiently numerous to reduce aphid populations significantly although Dunn (1954) found that Micromus variegatus was as abundant, and killed as many pea aphids, as syrphid larvae in one field.

Aphids are sometimes attacked by more general feeders such as carabids, staphylinids and spiders (Fluke, 1929) but these predators generally have little effect on aphid populations in the field.

The most important primary parasites of aphids occur in the hymenopterous families Braconidae (Ichneumonoidea) and Eulophidae (Chalcidoidea).

Braconid adults feed mainly on honeydew and are very active in warm weather. During oviposition, the female faces the aphid, bending the ovipositor forward between its legs (Stary, 1970). Adults of many species are seemingly unable to distinguish between parasitised and healthy aphids and superparasitism frequently occurs, although only one larva reaches maturity. Messenger and Force (1963) reported an increase in the incidence of superparasitism at low temperatures (12.5°C) as a result of the decreased activity of the parasites.

The Aphelininae differ in many respects from the Braconidae, particularly with regard to the feeding and oviposition behaviour of the adults. The female wasps feed on the body fluids of aphids after puncturing the integument with the ovipositor. During oviposition the female faces away from the aphid and lunges backwards with her ovipositor. Although Aphelinus species are less active than braconids, superparasitism is relatively rare. Hartley (1922) and Spencer (1926) found no evidence of superparasitism in Aphelinus semiflavus but Lundie (1924) frequently found more than one egg of A. mali in Eriosoma lanigerum. In the event of multiparasitism by Aphidius sp. and Aphelinus sp., Aphidius larvae generally develop at the expense of Aphelinus (Hartley, 1922; Spencer, 1926; Force and Messenger, 1965). Hartley found this to be true even when the Aphidius egg was laid 24 hours later than that of Aphelinus.

Stary (1964 b) asserted that the presence of aphid parasites in a particular area is primarily determined by the nature of the habitat. He found that dioecious aphids, such as Aphis fabae, are attacked by one group of parasites on the primary host plants and by a different group on the secondary hosts. Only when primary and secondary hosts are closely associated in the field are the aphids likely to be attacked by both groups of parasites simultaneously. Monoecious species, for example Acyrthosiphon pisum and Megoura viciae, have only one group of parasites.

The parasites of A. fabae have been studied in Czechoslovakia by Hodek et al (1959, 1962) and Stary (1966). The aphids were parasitised mainly by Trioxys angelicae on spindle and by Aphidius fabarum on beet. Trioxys sp. has also been recorded as a parasite of A. fabae in England (Way and Banks, 1968).

Parasites of Acyrthosiphon pisum have been accorded a great deal of attention in Canada (Mackauer and Finlayson, 1967) the United States (van den Bosch et al., 1966, 1967) and Czechoslovakia (Stary, 1962), where the pea aphid is a serious pest of lucerne. In California, attempts have been made to control populations of A. pisum by means of the parasite Aphidius smithi which was imported from India and first released in 1958 (van den Bosch et al., 1967). Aphidius megourae was imported into Czechoslovakia from Russia and released in large numbers as a control measure against A. pisum (Stary, 1966).

Little is known about parasites which attack the pea aphid in England. Dunn and Wright (1955) reported that a large proportion of the fundatrices of A. pisum was killed by primary parasites but the species responsible was not named.

Megoura viciae is parasitised in Czechoslovakia by Aphidius megourae and Praon dorsale (Stary, 1964 a, 1966). Nothing has been published concerning parasites of this species in Britain.

Aphids are most commonly parasitised while in the second instar. Later instars of many aphid species exhibit defense reactions and are therefore less liable to be parasitised (Fox et al., 1967).

The efficiency of parasites is greatly reduced by hyperparasitism (Dunn and Wright, 1955; Hafez, 1961). There are two main groups of aphid hyperparasites - endo- and ectoparasites. The former lay their eggs in the

third or fourth instar larvae of primary parasites in living aphids. The majority of endoparasites belong to the family Cynipidae, typical examples being Charips spp. and Alloxysta spp. (Haviland, 1921 b; Stary, 1962).

Ectoparasites lay their eggs in mummified aphids, outside the body of the primary host. Two of the most common species in this group are the pteromalids Asaphes vulgaris and Coruna clavata (Stary, 1962; Haviland, 1922; Barnes, 1931). Another genus which occurs as a secondary or tertiary parasite of aphids is Lygocerus (Haviland, 1921 a).

Endoparasites often suffer a high mortality since they are invariably killed if the primary host is subsequently attacked by an ectoparasite (Haviland, 1922; Stary, 1966).

Most hyperparasites are non-specific and attack a variety of primary parasites of several different aphid species.

Various methods have been employed to estimate the percentage parasitism in aphid populations in the field. Pimentel (1961), Otake (1966) and Smith (1969) expressed the number of unhatched mummies as a percentage of living aphids + mummies. Hafez (1961) used a similar method but omitted early instars from his calculations.

In a number of investigations, the percentage parasitism was determined by dissecting a sample of aphids - usually fourth instar nymphs (Evenhuis, 1962, van den Bosch et al., 1966; Hafez, 1960, 1961).

A third method consists of retaining a sample of live aphids in the laboratory for a period - long enough for any parasitised aphids to become mummified. The proportion of the original sample which produces mummies will thus give an estimate of the percentage attacked by primary parasites (Dunn, 1951; George, 1957).

Many workers have obtained a positive correlation between aphid density and percentage parasitism (Evenhuis, 1962; van den Bosch et al., 1966, 1967). Van den Bosch et al. (1966) observed, however, that the relationship was sometimes obscured by other factors, particularly weather conditions, competition from other biotic agents and cultural practices. Pimentel (1961) and Shiga (1968) suggested that larger aphid colonies are more easily located by the adult parasites. Shiga obtained an inverse relationship between aphid density and percentage parasitism at high aphid densities. Beirne (1942) in his work on the mealy plum aphid, Hyalopterus arundinis and its parasite, Praon volucre, observed that the highest percentage parasitism occurred when aphid numbers were low and the aphids scattered.

Experiments conducted in 1967 and 1968 indicated that bird predation was a major mortality factor in the case of Megoura viciae and the pink and green biotypes of Acyrthosiphon pisum. The aphids were counted only at weekly intervals, however, and the decline of the populations may have been due to other factors besides bird predation. It was therefore decided to conduct further experiments to assess the impact of bird predation.

The main objectives of the experiments described in this section were to determine:-

(i) Seasonal variation in the relative abundance of various groups of invertebrate predators and parasites in the field.

(ii) The relative susceptibility of the four aphid species/biotypes to attack by invertebrate predators and parasites.

(iii) The effect of bird predation on aphid populations over short periods of time (24 - 48 hours).

B. MATERIALS AND METHODS

1. Studies Concerning Invertebrate Predators and Parasites

a) Experiments using caged field beans to determine the build-up of predators and the incidence of parasites in 1969

Field beans were planted in two adjacent plots at Silwood Park at the end of March(Plot I) and in mid-May (Plot II). Four field cages 5 ft. high x 4 ft. x 3 ft. were placed in each plot and the twelve beans within each cage were artificially infested with aphids from the stock greenhouse cultures. The cages were covered with ½ inch wire-netting to protect the aphids from bird predation. The roofs of the cages were also covered by a single layer of Terylene netting to reduce the effect of rain.

Aphis fabae, Megoura viciae and the pink and green biotypes of Acyrthosiphon pisum were introduced into separate cages in each plot. The beans in plot I were infested on the 27th May and those in plot II on 19th June.

Sample plants (usually two for each aphid species) were removed each week between the 12th June and the 2nd August. The first two samples were taken exclusively from plot I. Subsequent samples consisted mainly of plants from plot II.

All predators and mummified aphids found on the plants were recorded. Immature predators were transferred to infested bean seedlings. Unhatched mummies were retained and the adult parasites were identified by Mr. R. D. Eady, Dr. B. R. Subba-Rao and Mr. J. Quinlan at the British Museum of Natural History.

b) Experiments using bean seedlings in pots to assess the seasonal variation in the incidence of predators and parasites in the field from May to September, 1970

Every week from the end of April until the beginning of September, dwarf broad beans (Variety: The Sutton) were planted in 16 5-inch flower pots at the rate of five per pot. About 20% of the seeds failed to germinate so there were generally four seedlings in each pot. When the plants were 3 - 4 inches high, they were infested with aphids from the stock greenhouse cultures. A. fabae, M. viciae and both biotypes of A. pisum were used in the experiments, each species being introduced into four pots.

The pots were placed in a large field cage covered with 1 inch wire netting situated at the eastern end of the bean plot in a narrow strip of lucerne. They were arranged in the form of a Latin square on a table 30 inches high. A week later, the plants were removed from the pots (the stems were cut just above the level of the soil) and transferred to the laboratory in polythene bags secured by means of rubber bands. The pots were replaced by a new lot containing newly-infested seedlings.

The first lot of bean plants was placed out in the field on the 5th May. The experiment was repeated each week until the 23rd September when the last batch of plants was examined. The position of the species on the table was changed each week to reduce the risk of biased results in case the adult predators approached the plants predominantly from one particular direction.

In the laboratory, the plants were carefully examined and all the predators found were recorded. From the 2nd June onwards, syrphid eggs were stored in Pampel's fluid (6 parts 35% Formaldehyde, 15 parts 95% Ethyl Alcohol, 2 parts Glacial Acetic acid and 30 parts distilled water)

and later identified by means of the chorionic sculpturing (Chandler, 1967, 1968a). Adult predators were killed and retained for identification. Immature stages (including eggs other than syrphid eggs) were placed on infested bean plants in order to obtain as many adults as possible for identification.

From the 25th May onwards, a sample of aphids was taken from the plants and retained so that the percentage parasitism could be determined for each aphid species. Approximately equal numbers were taken from each replicate and the entire sample (from all four replicates) was placed on a bean seedling growing in a 3 inch or 5 inch plastic pot. Whenever possible, the total sample for each species consisted of 60 - 100 aphids. In some cases, however, there were very few aphids remaining on the plants and, on these occasions, virtually all the survivors were retained.

The number of aphids in the sample was recorded and the plant was covered with a lamp-glass or plastic propagator. The tops of the 'cages' consisted of fine Terylene muslin, the plastic tops of the propagators having been previously removed. The plants were transferred to a controlled environment room and maintained at a constant temperature of 20°C and a 16 hour photoperiod. The plants were examined three times per week when all the mummies found were carefully removed and placed separately in 2 x ½ inch glass tubes with cork stoppers. The mummies were stored in the laboratory and the adults which emerged were later identified.

c) Rearing of predators for identification

Immature stages of all predators (except syrphid eggs throughout most of 1970) were placed on young bean seedlings growing in 3 inch or 5 inch plastic pots. The seedlings were infested with the same species of aphid as the plants on which the predators were found. They were then enclosed in lamp-glass cages or plastic propagators with Terylene muslin

'roofs'.

The pots were transferred to a controlled environment room having a constant temperature of 20°C and a photoperiod of 16 hours.

The plants were examined once a week and the progress of the predators recorded. Unhealthy plants were discarded, the predators being transferred to fresh seedlings. The remaining plants were reinfested. If necessary, the plants were again reinfested mid-week.

d) Identification of adult predators

Syrphids were identified from keys devised by Verrall (1901), Sack (1930), Lindner (1928 - 1932) and Coe (1953). Coccinellids and staphylinids were identified by the late Mr. W. O. Steel, and anthocorids and Orius spp. by Professor T. R. E. Southwood.

e) The relationship between aphid density and percentage parasitism on individual leaves

Field beans were planted in the field at Silwood Park at the beginning of April, 1970. Field cages 5 ft. high x 4 ft. x 3 ft. covered with Terylene netting were placed over some of the beans which were infested at the end of May with aphids from the greenhouse cultures. A. fabae and both biotypes (the pink and the green) of Acyrthosiphon pisum were used in the investigation, each species or biotype being introduced into a separate cage. The green biotype of A. pisum was sampled on the 21st June, A. fabae on the 28th June and pink A. pisum on the 3rd July.

Each sample consisted of 10 leaves taken more or less at random from the plants in the cage. In the case of A. pisum, leaves which were close together were rejected because of the difficulty of manoeuvreing the sampling container into position without disturbing the aphids.

The container (a circular plastic dish 4 in. in diameter and 2 in. deep) was held beneath the leaf to be sampled while the petiole was cut so that any aphids falling from the leaf would not be lost. The leaf was placed in the dish which was immediately covered with a tightly-fitting lid to prevent any of the aphids escaping.

In the laboratory, the aphids were counted and classified into instars. They were then transferred onto bean seedlings growing in 3 inch plastic pots. The aphids from different leaves were placed in separate pots. The seedlings were enclosed in lamp-glass cages with Terylene muslin tops.

After the aphids had been removed from the leaves, the outline of each leaf was traced onto graph paper. The leaf area was calculated, and the aphid density per square centimetre determined.

The aphids were kept at a constant temperature of 20°C and 16 hour photoperiod for over two weeks. They were examined three times a week when the number of mummies found on each plant was recorded. The mummies were transferred to glass tubes and stored in the laboratory until the adults emerged and were identified.

2. Experiments on Bird Predation

During 1970, three experiments were conducted to determine the effect of bird predation on aphid populations over periods of 24 or 48 hours.

Broad beans were grown singly in plastic pots 7" in diameter and infested with aphids when 6 - 8" high. Newly-infested plants were all initially protected by cylindrical ½" gauge wire netting cages 15" high and 10 - 12" in diameter until the aphids had settled down. The aphids were then counted and their position on the plant recorded. The cages were replaced over half of the pots (the controls); the remainder were left unprotected. When the experiment was terminated, the aphids were counted

once more.

All experiments were conducted in the field. The pots were placed on a large table 30 inches high situated at the southern edge of the bean plot.

The total population on each plant was divided into sub-populations according to the position of the aphids on the plant. Records were kept of the number of aphids on (i) expanded leaves and stem, (ii) apex i.e. unfurled leaves at the top of the plant, (iii) flowers, and (iv) side shoots. The sub-populations from all replicates were summed and the totals found at each count were used to calculate the change in size of the sub-populations on the various parts of the plants. This was expressed as the percentage increase or decrease in numbers since the first count. Grand totals for all replicates were used to determine the overall percentage change shown by the populations in each treatment.

The first experiment was intended to determine the 'knock-down' effect of birds i.e. the proportion of the aphid population which fell from the plants as a result of disturbance by birds, as distinct from the proportion actually consumed by birds. The aphid species used in the experiment was the green biotype of A. pisum, and the plants in this instance were dwarf broad beans, variety 'The Sutton'.

After the plants had been infested and the aphids had settled down, overlapping sheets of cellulose acetate coated with 'Ostico' tree-banding grease were placed around the bases of two of the four plants. The cellulose acetate sheets were supported by a piece of hardboard 2 ft. square with a central hole for the plant. Birds were prevented from walking on the 'Ostico' and from eating any aphids which had fallen from the plants by a wire mesh screen consisting of ½ inch wire netting. The netting was secured to a wooden frame 18 in. square and was also provided with a hole in the centre for the plant. The space between the wire mesh

and the hardboard was approximately 2 inches. The other two plants were provided with hardboard bases and wire mesh screens but without the 'Ostico' -covered plates. Two of the plants - one with and one without 'Ostico'-coated plates - were exposed to bird predation for 24 hours; the others were protected by wire cages throughout the experiment. The experiment began at midday on the 22nd July, 1970. The weather during the ensuing 24 hours was cool (mean temperature between 12 and 13°C) with intermittent sunshine. 1 mm. of rain was recorded.

In the second and third experiments, only the gross effect of bird predation on aphid populations was determined. In both experiments the beans used were Sutton's Green Windsor. Each treatment was replicated four times and the experiments ran for approximately 48 hours.

The aphids used in the second experiment were the pink and green biotypes of A. pisum. The plants were each infested with only one biotype. The experiment started at 18.45 on the 18th September and was terminated at 16.15 on the 20th September. The weather during the experiment was dry and sunny; the mean temperature was about 15°C.

In the last experiment, the aphids investigated were Aphis fabae and the pink biotype of A. pisum. Once again the aphid species were introduced onto separate plants. The experiment commenced at 12.30 on the 22nd September and was terminated at 10.15 on the 24th September. The weather was dry but rather cloudy. The average temperature was approximately 13°C.

C. RESULTS

1. The Incidence of Invertebrate Predators and Parasites in Field Cages in 1969

a) Predators

Megoura viciae failed to become established in either of the cages into which it had been introduced. The plants were reinfested but the populations remained low and many of the plants - particularly in the cage in plot II - were subsequently colonised by Aphis fabae. Predators found on the sample plants were probably feeding mainly on the latter species. For this reason, the results obtained for M. viciae were inconclusive and will be omitted.

The other aphid species rapidly established themselves on the plants and were attacked by a variety of predators of which syrphids were the most numerous. The term 'predator' in this section refers not only to the active stages but also to the inactive stages i.e. eggs and pupae.

(i) Syrphidae

A total of 102 unhatched eggs and 122 larvae were found on all the sample plants. Syrphids constituted over 50% of the predators associated with each of the aphid species/biotypes (Figure 12).

Eggs were laid throughout the course of the experiment with peak numbers occurring in mid-June and mid-July (Figure 13). Although relatively fewer unhatched eggs were found on plants infested with green A. pisum than on those infested with pink A. pisum or A. fabae, the average number of larvae per plant was higher (Table XIV). These differences may have been due to chance. Alternatively, there may have been a higher survival rate of larvae feeding on the green biotype. Survival rates of the larvae on the different aphid species could not be determined, however, as the number

Figure 12 : Relative abundance of groups of predators (as a percentage of total number of predators associated with each aphid species).

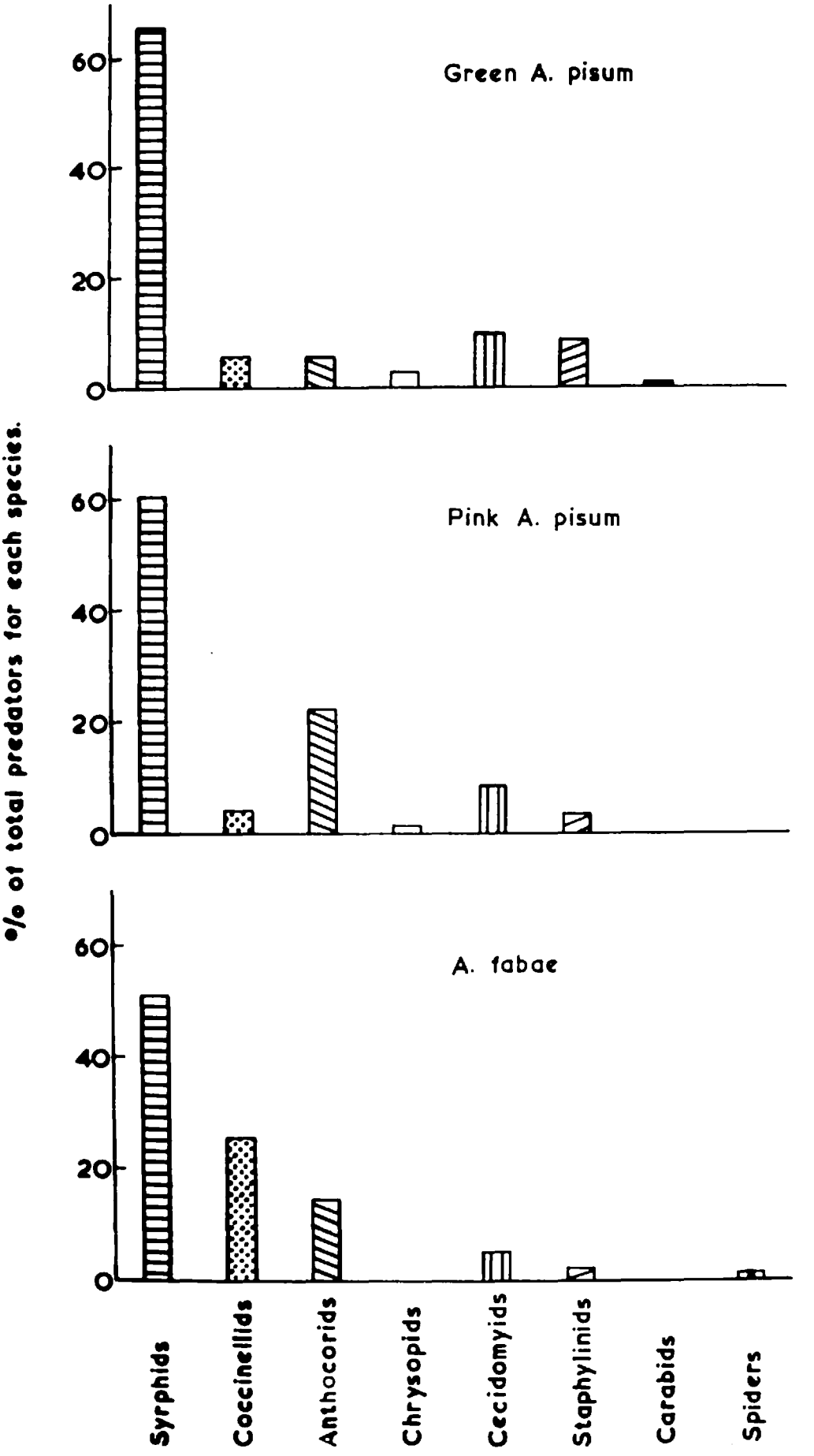
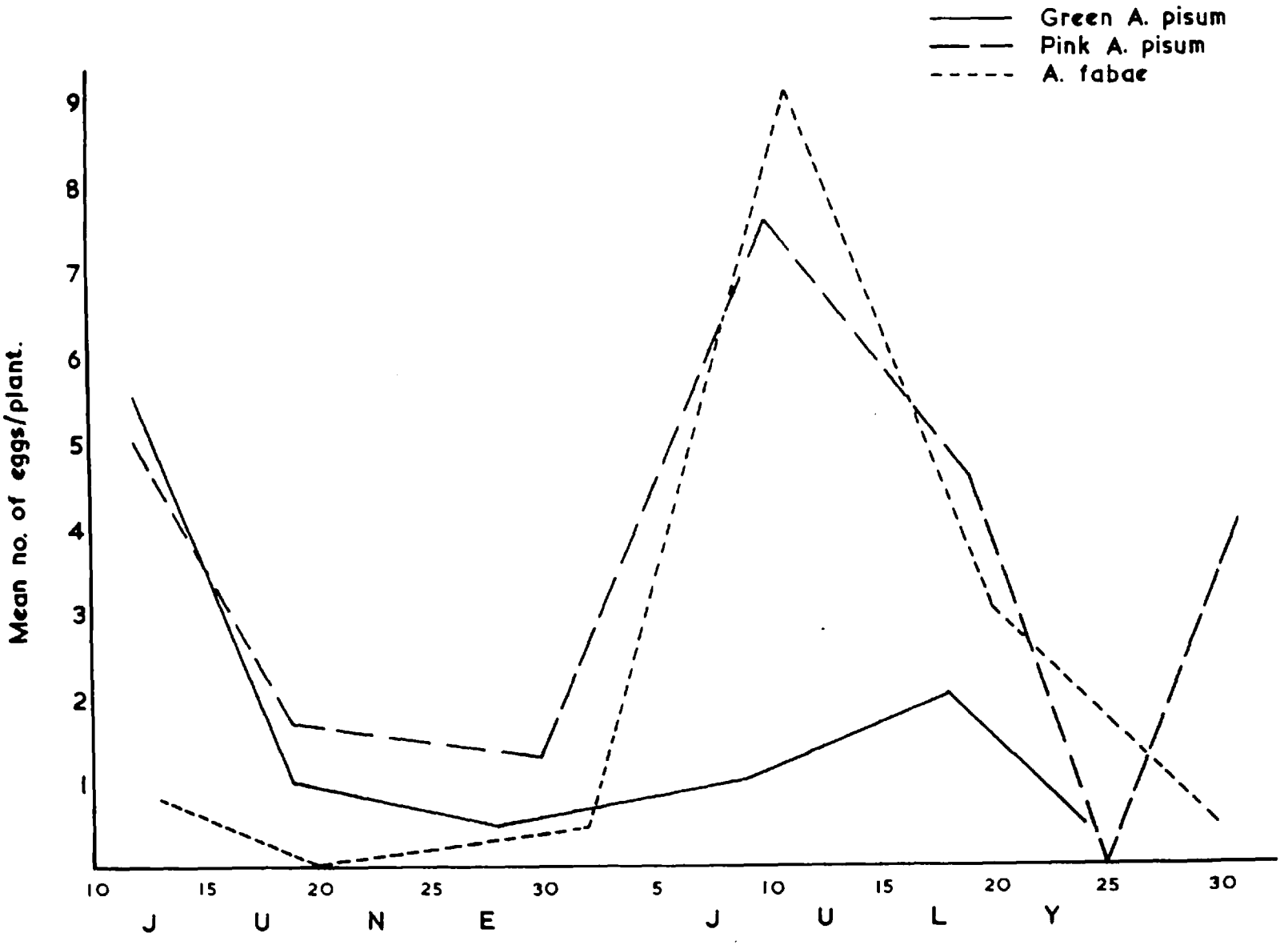

Green A. pisum
Pink A. pisum
A. fabae
% of total predators for each species.
0
20
40
60
Syrphids
Coccinellids
Anthocorids
Chrysopids
Cecidomyids
Staphylinids
Carabids
Spiders

Figure 13 : Incidence of unhatched syrphid eggs on sample plants in 1969


Green A. pisum
Pink A. pisum
A. fabae
Mean no. of eggs/plant.
9
8
7
6
5
4
3
2
1
10
15
20
25
30
5
10
15
20
25
30
J U N E
J U L Y

of hatched eggs was not recorded.

Table XIV : Average number of syrphid eggs and larvae on sample plants infested with A. fabae and the pink and green biotypes of A. pisum in 1969.

Aphid Species	Av. No. of Syrphids	
	Eggs	Larvae
A. fabae	2.0	2.7
A. pisum (Green)	1.8	3.8
A. pisum (Pink)	3.2	2.3

The larvae suffered a high mortality under experimental conditions. Mortality may have been relatively greater in some species than in others, in which case the adults obtained would not have been representative of the species occurring in the field.

The majority of the adults belonged to two species:- Syrphus balteatus and S. ribesii. Five other species were also reared from eggs or larvae, namely:- S. vitripennis, S. corollae, S. latifasciatus, Platychirus scutatus and Sphaerophoria scripta.

(ii) Anthocoridae

Anthocoris nemorum was found only occasionally during June and early July but there was a sudden increase in number towards the end of July, particularly on plants infested with the pink biotype of A. pisum. Of the 59 anthocorids (nymphs and adults) recorded from all the sample plants, 32 were associated with pink A. pisum, most of them in the last sample on the 2nd August.

(iii) Coccinellidae

This group was relatively uncommon in the field cages throughout June and most of July. By the 25th July, only 11 larvae, 3 pupae and 3 adults had been found on all the sample plants. They occurred in approximately

equal numbers on plants infested with pink and green A. pisum and A. fabae and belonged to four species, namely Propylea 14 - punctata, Coccinella septempunctata, Adalia decempunctata and A. X - biabilis.

On the 30th July, however, 27 first-instar larvae and 3 pupae were found on the two sample plants infested with A. fabae. The larvae were subsequently identified as Adalia bipunctata. Although it appeared in only one sample, this species accounted for 57% of all coccinellids found on sample plants. 20 hatched A. bipunctata eggs were recorded on one of the plants on the 30th July. This was the only occasion on which eggs were observed during the course of the investigation. Presumably oviposition by overwintered females had ceased by the time sampling commenced on 12th June and the A. bipunctata eggs laid on the plants towards the end of July represented a partial second generation. It is unlikely that first generation eggs would have been laid so late in the season.

(iv) Cecidomyidae

29 larvae were recorded, mainly during the latter part of June. Most of the larvae occurred on plants infested with the two biotypes of A. pisum. Attempts to rear the larvae through to the adult stage were unsuccessful so the species could not be identified.

(v) Staphylinidae

A staphylinid, identified as Tachyporus pallidus, was sometimes present on the plants and may have been preying on the aphids. A total of 17 individuals (mainly larvae) was obtained from all plants.

(vi) Chrysopidae

Five chrysopids, including eggs, larvae and pupae were found during June on plants infested with pink and green A. pisum.

(vii) Carabidae

A single adult, identified as Harpalus sp. (probably H. latus) was

recovered from a plant infested with green A. pisum.

(viii) Arachnida

This group was represented by two spiders, both of them on a plant infested with A. fabae. They were not identified.

b) Parasites

Megoura viciae was virtually unaffected by parasites. Only one mummy was found during the course of the investigation. The adult which emerged was identified as Praon dorsale. This species also parasitised Aphis fabae but, again, only a single mummy was recovered.

A. fabae is subject to parasitism by Lysiphlebus fabarum and Trioxys sp. but no mummies characteristic of these species were seen on the plants. It is possible that they were overlooked because they are difficult to distinguish from living aphids in dense colonies.

The pink and green biotypes of Acyrthosiphon pisum were attacked by four species of primary parasites, of which Aphidius ervi was the most common, followed by Praon volucre. A. avenae and Aphelinus sp. were rare. Aphidius spp. constituted 52.6% of the 133 mummies found on all the plants infested with A. pisum. Praon volucre and Aphelinus sp. accounted for 42.1% and 4.5% respectively.

43.5% of the adults which emerged from mummies of both biotypes were hyperparasites. The incidence of hyperparasitism appeared to be greater in the pink than in the green biotype (Table XV).

Figures obtained for the green biotype indicated that a significantly higher proportion of hyperparasites emerged from Aphidius - type mummies than from Praon - type mummies ($\chi^2 = 7.39$; $P < .01$). The figures for pink A. pisum were too low to be analysed by χ^2 but the percentage hyperparasitism again appeared to be higher in Aphidius than in Praon.

Table XV : The incidence of primary and secondary parasites in the pink and green biotypes of Acyrthosiphon pisum in 1969

Green Biotype

Type of Mummy	Total No. From All Plants	No. of Adults Emerged		*Percentage Hyperparasitised
		Primary	Secondary	
Aphidius	44	21	19	47.5%
Praon	32	19	3	13.6%
Aphelinus	2	2	0	0
TOTAL	78	42	22	Mean= 34.4%

Pink Biotype

Type of Mummy	Total No. From All Plants	No. of Adults Emerged		*Percentage Hyperparasitised
		Primary	Secondary	
Aphidius	26	2	9	81.8%
Praon	24	7	9	56.3%
Aphelinus	5	1	0	0
TOTAL	55	10	18	Mean= 64.3%

* Assuming that there was no selective mortality of primary or secondary parasites in 'unhatched' mummies.

The most common hyperparasite of both biotypes was the pteromalid, Asaphes vulgaris Walk. (Table XVI). Two other species occurred in moderate numbers. They were the cynipid Alloxysta victrix (mainly from the green biotype) and another pteromalid, Coruna clavata Walk. (mainly from the pink biotype). The three remaining species, Phaenoglyphis sp. (Cynipidae), Lygocerus sp. (Ceraphronidae) and Aphidencyrtus sp. (Encyrtidae), were relatively rare.

A large proportion of mummies of the pink biotype failed to produce adult parasites - over 35% as opposed to only 15% in the green biotype.

Table XVI : Hyperparasites which emerged from A. pisum mummies in 1969

Hyperparasite	Number obtained from each biotype	
	Green biotype	Pink biotype
Pteromalidae		
Asaphes vulgaris	12	9
Coruna clavata	1	5
Cynipidae		
Alloxysta victrix	9	1
Phaenoglyphis sp.	1	2
Encyrtidae		1
Aphidencyrtus sp.	1	
Cerophronidae		
Lygocerus sp.	1	
TOTAL	25	18

General Comments on Predator Studies in 1969

The results obtained in 1969 suggested that certain of the aphid species might be more attractive than others to the various groups - or species - of predators. There was, however, considerable variation in the number of predators on individual plants taken from the same cage on the same day. Any apparent differences in the susceptibility of the aphid species to attack by a particular group of predators may therefore have been due purely to chance. The results emphasised the inadequacy of the sampling method and the need for increased replication.

Ideally, there should be several replicates (i.e. field cages) for each aphid species and the total predator population in each cage should be determined. Results obtained in 1968 proved, however, that predator counts *in situ* in the field were very inaccurate. It was therefore decided to abandon the use of field cages in 1970, in favour of infested bean seedlings growing in pots. This would impose no limit on the number of replicates and would enable the plants to be changed at frequent intervals and carefully examined for predators in the laboratory.

2. Seasonal Variation in the Incidence of Predators and Parasites in the Field from May to September, 1970

a) Predators

(i) Syrphidae

Syrphids were potentially the most numerous predators throughout the summer of 1970 (Figure 14). Eggs were laid on the infested bean seedlings throughout the course of the investigation, except between the 21st and 28th July, and the total number greatly exceeded that laid by any other group of predators. There were three main peaks of oviposition - in early June, mid-July and late August/early September.

During most weeks, more eggs were laid on plants infested with Aphis fabae and, to a lesser extent, with Megoura viciae, than on those infested with green or pink Acyrthosiphon pisum (Figures 15 and 16). This trend is particularly noticeable when egg totals recorded from the individual aphid species are compared (Table XVII) and is remarkably consistent for all the common syrphid species.

Not all hatched eggs found on the plants in September were retained for identification and eggs were sometimes lost from earlier samples. On these occasions, the total number of eggs belonging to individual syrphid species was estimated on the basis of the eggs which were identified. Any differences in the relative abundance of syrphid species between hatched and unhatched eggs were taken into account in the estimates.

The relatively high number of eggs associated with A. fabae suggested that ovipositing syrphids might be particularly attracted by this species. M. viciae and both biotypes of A. pisum take defensive action in the presence of certain natural enemies and it seemed possible that this might have deterred oviposition to some extent. In some weeks, however, (e.g. between the 9th and 16th September) similar numbers of eggs were recorded

Figure 14 : Incidence of syrphid eggs, coccinellids and anthocorids on bean seedlings after one week's exposure in the field.

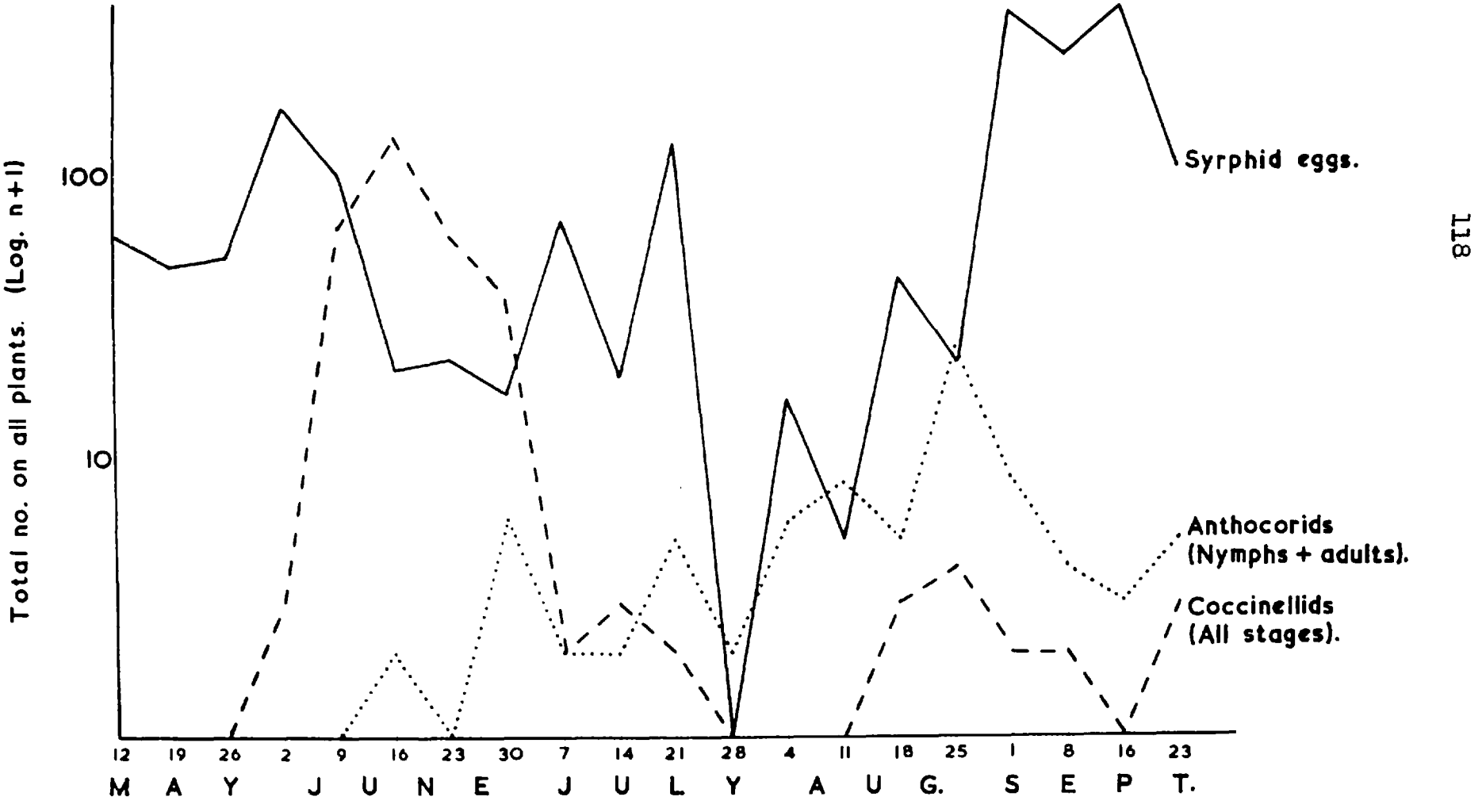

Total no. on all plants. (Log. n+1)
100
10
Syrphid eggs.
Anthocorids
(Nymphs + adults).
Coccinellids
(All stages).
12 19 26 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
M A Y J U N E J U L Y A U G. S E P T.

Figure 15 : Number of syrphid eggs and larvae on plants infested with A. fabae and M. viciae.

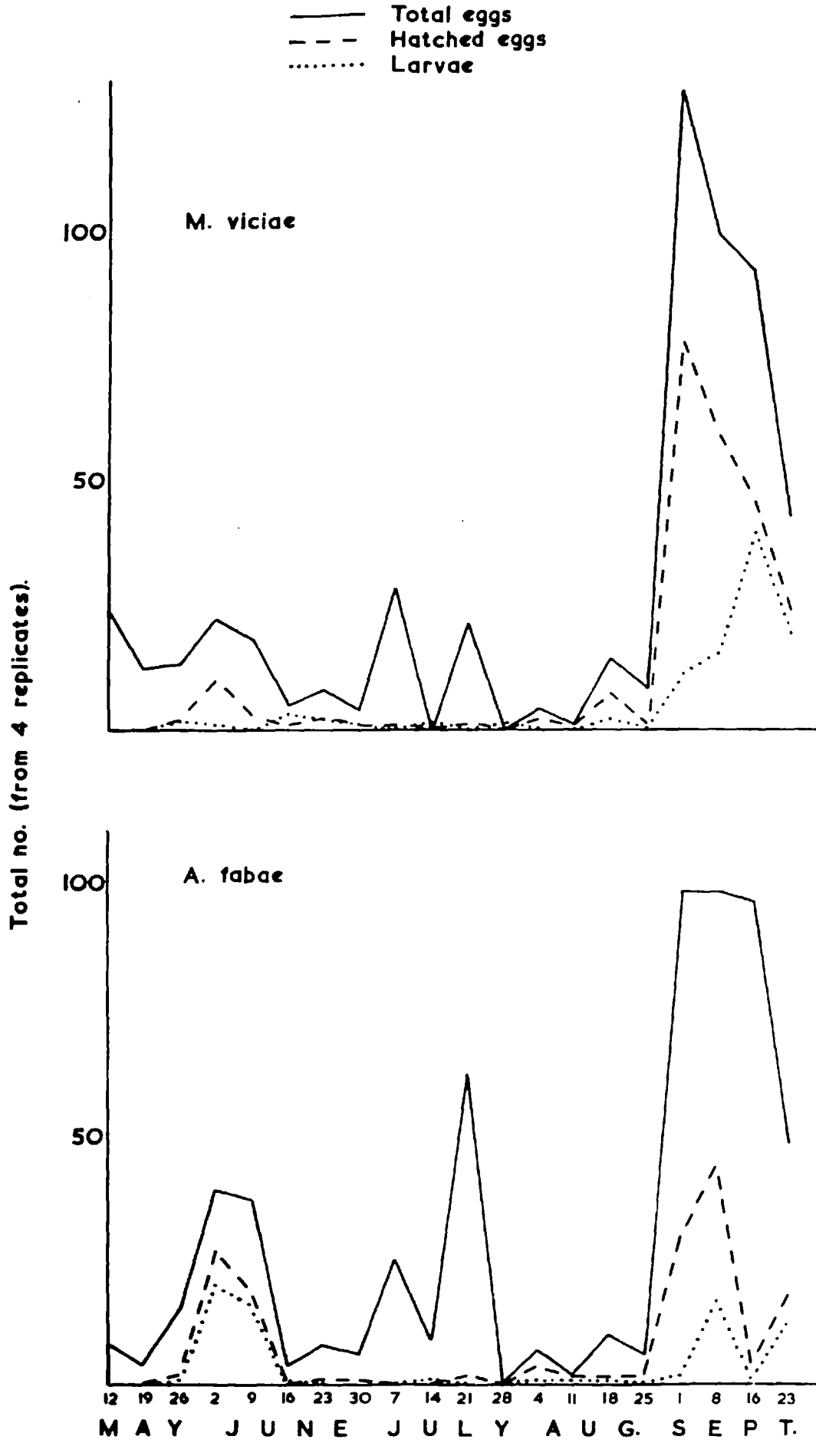

Total eggs
Hatched eggs
Larvae
M. viciae
100
50
A. fabae
100
50
Total no. (from 4 replicates).
12 19 26 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
MAY JUNE JULY AUG. SEPT.

Figure 16 : Number of syrphid eggs and larvae on plants infested with *A. pisum*

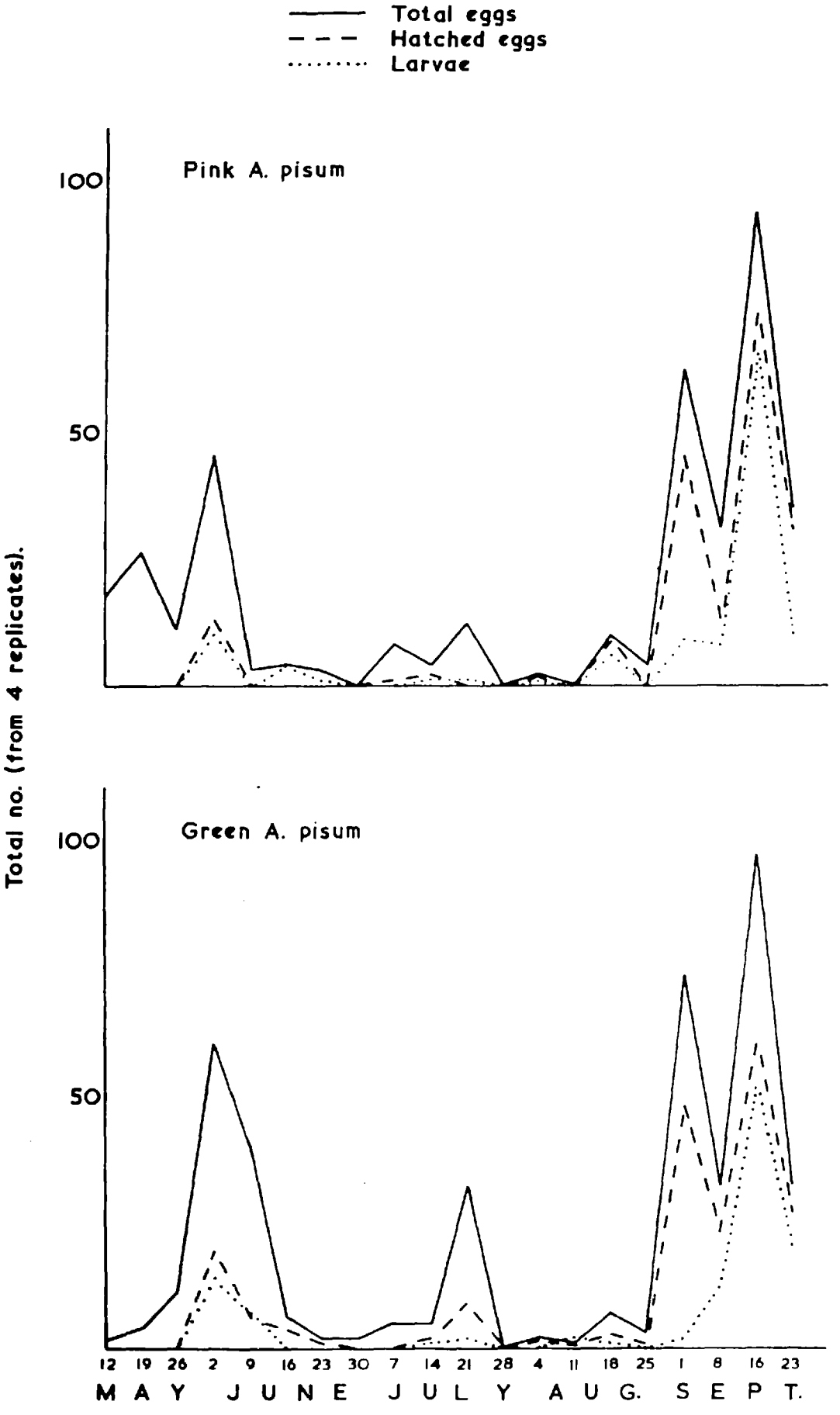

Total eggs
Hatched eggs
Larvae
Pink A. pisum
Green A. pisum
100
50
Total no. (from 4 replicates).
12 19 26 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
MAY JUNE JULY AUG. SEPT.

Table XVII : Estimated total numbers of eggs laid by individual syrphid species on plants infested with A. fabae, M. viciae, green A. pisum and pink A. pisum

Syrphid species	APHID SPECIES				Total
	A. fabae	M. viciae	Green A. pisum	Pink A. pisum	
+Unidentified	12	35	16	57	120
*S. eligens	88	39	76	42	245
*S. nitidicollis	2	5	5	2	14
S. luniger	191	186	137	127	641
S. vitripennis	46	37	42	30	155
S. balteatus	9	5	11	11	36
S. corollae	1	0	1	1	3
S. latifasciatus	2	2	1	0	5
S. ribesii	186	183	103	70	542
Platychirus spp.	46	46	34	34	160
TOTAL	583	538	426	374	1921

+Collected on 12th and 19th May, except 3 from pink A. pisum

*Numbers underestimated because eggs collected on the 12th and 19th May were not identified.

for all the aphid species. Furthermore, most of the eggs recorded on the 2nd June were found on plants infested with green and pink A. pisum. Although this does not eliminate the possibility that certain syrphid species might exhibit a preference for A. fabae there were obviously other factors involved, one of which appeared to be aphid density.

Approximately 200 - 300 aphids were introduced into every pot at the beginning of each experiment, giving an average of 50 or more aphids per plant. In many instances, the aphid populations declined while in the field

to such an extent that, by the end of the week, there were fewer than 10 aphids per plant in all four replicates of a particular aphid species. Decreases of this magnitude occurred most frequently in green and pink A. pisum. M. viciae was affected to a much smaller extent and populations of A. fabae invariably remained at a high level.

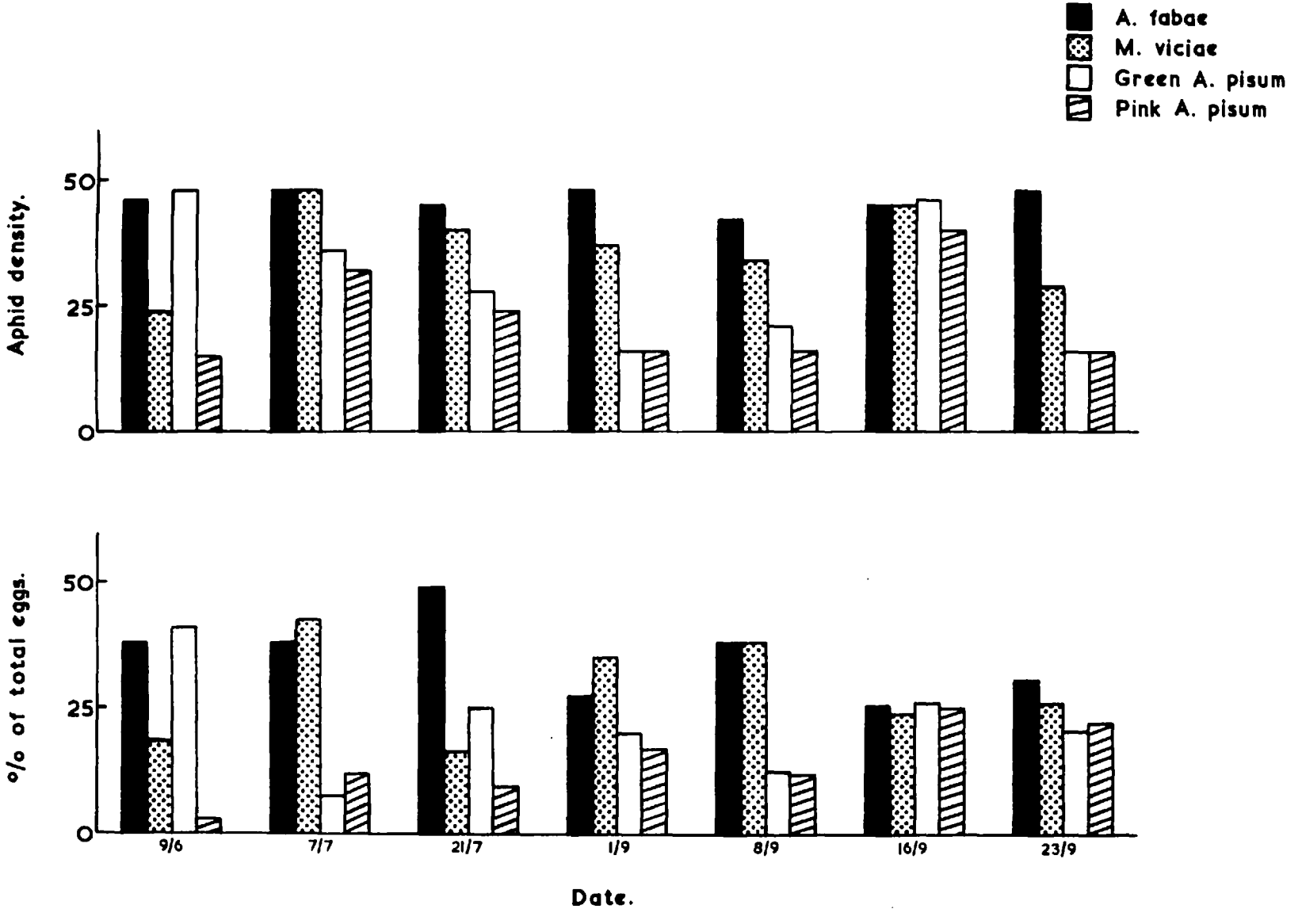
From the 9th June onwards, the number of aphids remaining on individual plants at the end of each week was estimated and the estimates were subsequently used to calculate the weekly density for each aphid species. Each plant was assigned to a category:- Category (1) if there were 0 to 9 aphids, Category (2) - 10 to 19 aphids and Category (3) - 20 or more aphids. The categories corresponded to the arbitrary density of the aphids so that the maximum possible density on individual plants was '3'. The overall density for each species was then calculated by summing the densities for individual plants. For example, if there were 7 plants in category (1), 3 in category (2) and 6 in category (3), the overall density for the species would be $(7 \times 1) + (3 \times 2) + (6 \times 3) = 31$.

The relative densities of the individual aphid species were then compared with the proportion of the total eggs associated with each aphid species (Figure 17). Only weeks in which the egg total exceeded 50 were considered.

There seemed to be a positive correlation between aphid density and syrphid oviposition, although this was more apparent in some weeks (e.g. 9th June and 16th September) than in others. The relationship between the two variables was tested by comparing the expected distribution of the eggs, based on the relative densities of the aphids each week, with the observed distribution for the week in question. The differences were tested by χ^2 (3 degrees of freedom). The results are presented in Table XVIII.

The smallest value of χ^2 was obtained for the week ending 16th

Figure 17 : Comparison between aphid density and oviposition by syrphids


A. fabae
M. viciae
Green A. pisum
Pink A. pisum
Aphid density.
50
25
0
% of total eggs.
50
25
0
9/6
7/7
21/7
1/9
8/9
16/9
23/9
Date.

September - the only week during which populations of all four species/ biotypes remained at a high level. Only on two out of the seven occasions (7th and 21st July) were the differences between observed and expected distributions highly significant ($P < .01$).

Assuming that there is a correlation between aphid density and syrphid oviposition, the correlation would be most obvious in weeks when aphid numbers declined early in the week, and least obvious when they declined towards the end of the week. Neither the rate of aphid decline nor that of syrphid oviposition was determined, and the proportion of hatched eggs was generally too low for them to be used as an indication of when the eggs were laid. Nevertheless, the fact that fewer eggs were found on plants on which the aphid populations had declined than on those on which the populations remained high throughout the week, suggests that aphid density was one of the major factors affecting oviposition by syrphids. Presumably most eggs in the former instance were laid during the early part of the week when aphids were relatively plentiful.

Prior to the 1st September, all the plants brought in from the field were examined the same day. Because of the large numbers of eggs laid in September, however, it took much longer to examine each plant and transfer the eggs to Pampel's fluid. Examination of plants infested with green and pink A. pisum was therefore delayed - usually until the following day. The highest number of eggs occurred on plants brought in on the 16th September and, on this occasion, only the plants infested with A. fabae were examined the same day. Those infested with M. viciae were examined on the 17th September and with pink and green A. pisum on the 18th September.

The delay in examining plants infested with the two biotypes of A. pisum accounted for the relatively high number of hatched eggs and larvae recorded from these species in September (Figure 16) as compared with those recorded from A. fabae and M. viciae (Figure 15).

Table XVIII : Relationship between aphid density and syrphid oviposition

(See text)

Date		Distribution of syrphid eggs (expressed as a percentage of the weekly total)			
		A. fabae	M. viciae	Green A. pisum	Pink A. pisum
9th June	Expected	34.6	18.0	36.1	11.3
	Observed	37.8	18.4	40.8	3.1
		χ^2 = 6.87 N.S.			
7th July	Expected	29.3	29.3	22.0	19.5
	Observed	37.9	42.4	7.6	12.1
		χ^2 = 20.61 ** (P < .01)			
21st July	Expected	32.8	29.2	20.4	17.5
	Observed	48.8	16.5	25.2	9.4
		χ^2 = 18.21 ** (P < .01)			
1st Sept.	Expected	41.0	31.6	13.7	13.7
	Observed	27.3	35.1	20.3	17.2
		χ^2 = 9.04 * (P < .05)			
8th Sept.	Expected	37.2	30.1	18.6	14.2
	Observed	37.8	37.8	12.4	12.0
		χ^2 = 4.39 N.S.			
16th Sept.	Expected	25.6	25.6	26.1	22.7
	Observed	25.5	24.1	25.7	24.7
		χ^2 = 0.27 N.S.			
23rd Sept.	Expected	44.0	26.6	14.7	14.7
	Observed	30.6	26.8	20.4	22.3
		χ^2 = 10.22 * (P < .05)			

Identity of syrphid eggs

On the basis of the chorionic sculpturing, ten syrphid species were identified, eight of which were Syrphus species and the remainder, Platychirus species. Estimates of the total number of eggs for each syrphid species and the number associated with each aphid species are given in Table XVII.

Syrphus eligans (Harris)

This is a univoltine species which occurred only in spring (Figure 18). It was largely responsible for the first oviposition peak on the 2nd June. No eggs were found on plants after the 9th June.

A high proportion of the eggs found on the 2nd and 9th June had hatched and several larvae were found on plants infested with A. fabae nd the pink and green biotypes of A. pisum. Only one larva was recorded from M. viciae - on the 2nd June.

Most of the eggs collected on the 12th and 19th May were placed on infested bean seedlings and maintained at a constant temperature of 20°C. Larvae which appeared to be S. eligans subsequently found on all plants except those infested with M. viciae. The virtual absence of larvae from plants infested with M. viciae - both in the laboratory and in the field - suggested that this aphid might be toxic to S. eligans. Further evidence of its toxicity was obtained when attempts were made to rear the larvae separately in leaf cages. Eggs collected on the 9th June were introduced into separate leaf cages containing either green A. pisum or M. viciae. The newly - hatched larvae thrived on a diet of green A. pisum, but those provided with M. viciae died within a few hours of hatching.

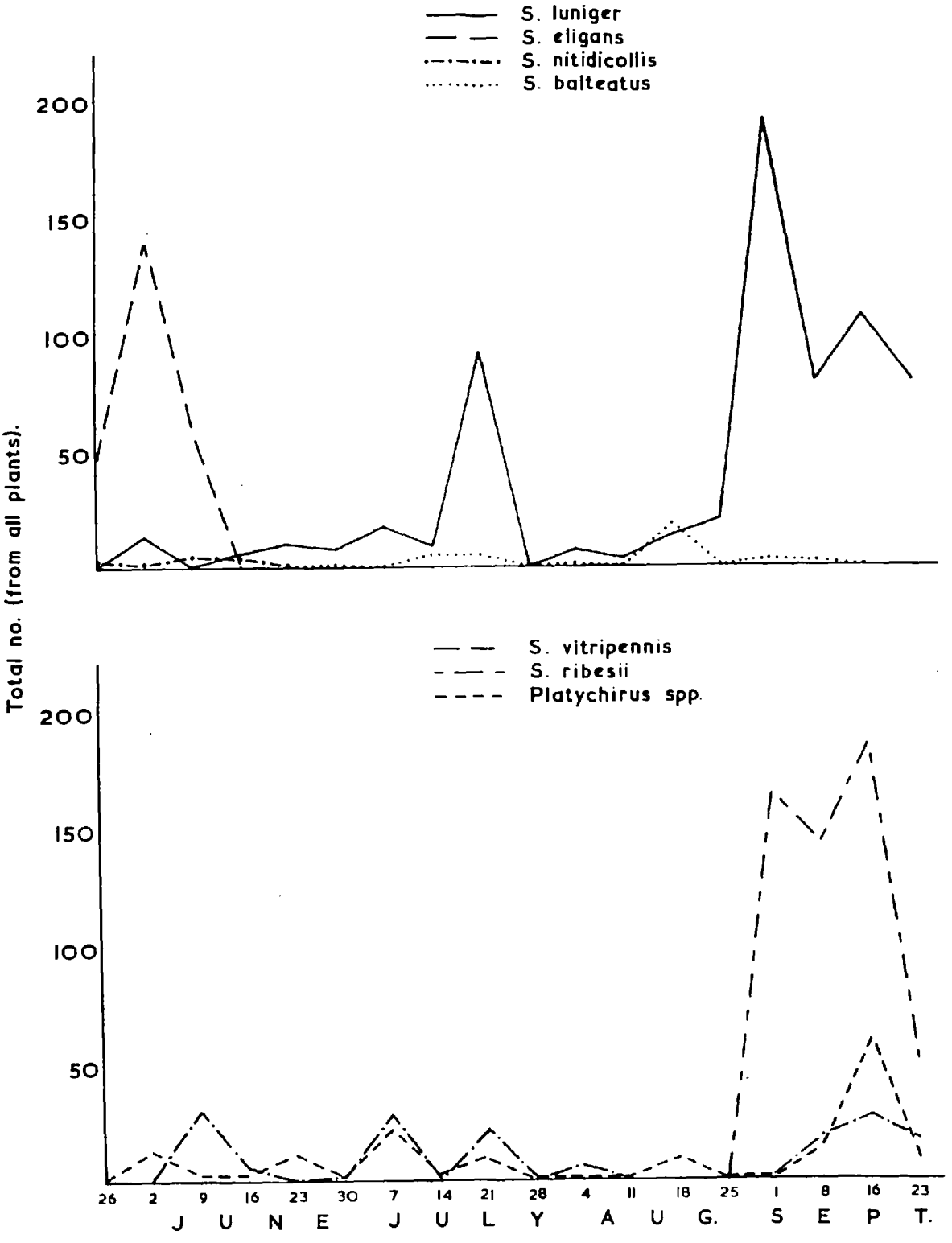
Although many of the larvae reared on A. fabae or A. pisum reached an advanced stage of development under experimental conditions, no adults were obtained. All the larvae entered diapause.

Syrphus nitidicollis Meigen

This is another univoltine species whose eggs were found only in spring (Figure 18). Eggs were found on the plants until the 16th June but only in very small numbers. Oviposition might have been affected by the height of the plants. Chandler (1967) found that S. nitidicollis females laid almost twice as many eggs on potted plants 1 ft. above the ground as on plants raised 4 ft. above the ground. The tendency to oviposit at low levels

Figure 18 : Weekly totals of Syrphus eligans, S. nitidicollis, S. luniger and S. balteatus eggs laid on infested bean seedlings.

Figure 19 : Weekly totals of Syrphus vitripennis, S. ribesii and Platychirus scutatus eggs laid on infested bean seedlings.


S. luniger
S. eligans
S. nitidicollis
S. balteatus
S. vitripennis
S. ribesii
Platychirus spp.
Total no. (from all plants).
200
150
100
50
26 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
J U N E J U L Y A U G. S E P T.

was more marked in this species than in most of the other species which he studied.

On the 4th June, another set of 16 pots containing infested bean seedlings was placed at ground level at the southern end of the bean plot. A wire mesh cage was placed over the pots to protect aphids from bird predation. Only 15 S. nitidicollis eggs were found on all the plants when they were examined a week later, but this figure was three times as large as that recorded from the plants in the main experiment (30 in. above the ground) which were exposed between the 2nd and 9th June.

No adults were obtained from eggs or larvae introduced onto infested seedlings in the laboratory. Presumably the larvae entered diapause but, as the larvae are virtually identical to those of S. eligans, it was not possible to determine the relative survival rates of the two species.

Syrphus luniger Meigen

This was the most abundant species, eggs being laid virtually continuously throughout the season. There were two distinct peaks of oviposition - in the third week of July and at the end of August/beginning of September (Figure 18). Apparently this species is oligo- or polyvoltine. Only three adults were reared from larvae in the laboratory - one on M. viciae, one on green A. pisum and the third on pink A. pisum.

Syrphus balteatus (Degeer)

This species was relatively uncommon, although eggs were found on the plants between the end of June and the beginning of September. There was a small but distinct oviposition peak on plants exposed between the 11th and 18th August (Figure 18). Six adults were reared from larvae found on the plants - two each on M. viciae, pink A. pisum and green A. pisum.

Syrphus vitripennis Meigen

Eggs were laid sporadically between mid-June and early August and appeared in all samples in September (Figure 19). The total number

oscillated from week to week and there were no distinct oviposition peaks. The highest number found in any one week was 30 - on the 9th June.

The larvae proved to be relatively easy to rear under experimental conditions. 20 adults were obtained - 3 from A. fabae, 4 from M. viciae, 7 from green A. pisum and 6 from pink A. pisum. It was not possible to determine the percentage mortality of larvae reared in the laboratory because the larvae closely resemble those of several other species of syrphids; nor could the initial number of larvae be deduced from the number of hatched eggs found on the plants when they were brought in from the field because many larvae had disappeared from the plants when they were collected.

Syrphus corollae (Fabricius)

Eggs which were positively identified as belonging to this species were found on only two occasions - on the 14th July and 16th September. Two adults were reared from eggs collected on the 19th May (eggs were retained for identification from the 26th May onwards). A third adult was reared from a larva collected on the 8th September when no S. corollae eggs were recorded. The larva may have strayed onto the bean plant from the lucerne which surrounded the table on three sides. Alternatively the egg from which the larva had hatched may not have been included in the sample or it could have been wrongly identified as S. luniger.

Syrphus latifasciatus Macquart

This species was rare, eggs being found only on the plants brought in on the 18th August and 8th September.

Syrphus ribesii (Linnaeus)

Eggs were found on the plants from the end of August until the experiment was terminated (Figure 19) but, despite the fact that oviposition occurred over such a short period, S. ribesii ranked second to S. luniger in terms of the total number of eggs laid (Table XVII).

25 adults were reared in the laboratory - on all four species/biotypes of aphid.

Platychirus spp.

Oviposition occurred virtually continuously throughout the season but the total number of eggs laid was usually small. There was only one distinct peak of oviposition - on the plants exposed between the 9th and 16th September (Figure 19).

With the exception of one egg found on the 2nd June which appeared to be P. albimanus (Fabricius), all the eggs were identified as P. scutatus (Meigen).

Only one adult was reared under experimental conditions - on A. fabae.

Melanostoma scalare (Fabricius)

No eggs were found on the plants between the 26th May and the 23rd September but one adult was reared from an egg found on one of the plants on the 19th May.

General comments on identification of syrphid eggs

The chorionic sculpturing of S. eligans, S. balteatus and S. latifaciatus is characteristic for each species and there is little likelihood of the eggs being confused with those of any other species.

Difficulty was experienced in distinguishing between hatched eggs of S. ribesii and S. vitripennis because the chorionic projections were frequently distorted. Those which had dried out were particularly difficult to identify. It is therefore likely that S. ribesii eggs were occasionally wrongly identified as S. vitripennis and vice versa.

The chorionic sculpturing on the dorsal surface of S. corollae eggs is identical to that of S. luniger eggs. Eggs of the two species can only be distinguished on the basis of the sculpturing on the ventral surface. In some cases, the ventral surface was damaged or even torn away completely when the eggs were removed from the plant. As most of the eggs which could

be positively identified were S. luniger, those of doubtful identity were also recorded as belonging to this species. The number of S. corollae eggs might therefore have been underestimated.

S. nitidicollis eggs bear a superficial resemblance to those of P. scutatus but the chorionic sculpturing of the former is more regular and it is unlikely that the two species were confused. There is, however, a very strong similarity between eggs of P. scutatus and those of other species of Platychirus, especially P. albimanus. Eggs which were identified as P. scutatus may occasionally have been wrongly identified.

Larvae suffered a high mortality - both in the field and in the laboratory - even when aphids were plentiful. Cannabalism might have accounted for some mortality, particularly under experimental conditions when up to 10 larvae were confined on a single plant. In the field, mortality may sometimes have resulted from the larvae becoming desiccated, particularly when the weather was warm and dry, but there is no specific evidence to support this. Alternatively, some of the larvae may have wandered off the plants or been dislodged as a result of avoiding action, such as kicking, taken by the aphids. This type of response is particularly well-developed in A. pisum and M. viciae.

(ii) Coccinellidae

Although Coccinella septempunctata adults were occasionally found on the plants in the main experiment (30 in. above the ground) no eggs were recorded for this species. On the 4th June, a second set of pots containing infested bean seedlings was placed on the ground at the southern end of the bean plot. Approximately 140 eggs were found when the plants were examined a week later and, in this case, over 50% of the eggs were laid by C. septempunctata. The remainder were laid by Adalia bipunctata (about 40%) and Propylea quattuordecimpunctata (6%). Presumably the plants in the main experiment were placed above the level which C.

septempunctata normally chooses for oviposition (Iperti, 1965; Blackman, 1967 a).

All the eggs recorded from plants in the main experiment were laid by A. bipunctata and P. 14 - punctata, most of them by the former species.

Eggs were laid only in June and there was a pronounced peak during the second week when 126 eggs were recorded from all plants. 102 of the eggs were found on plants infested with A. fabae (Figure 20). Over the same period, no eggs were recorded from pink A. pisum and only six from green A. pisum. The low incidence of eggs on plants infested with A. pisum may have been related to the fact that populations of both biotypes declined to a very low level during the week in question.

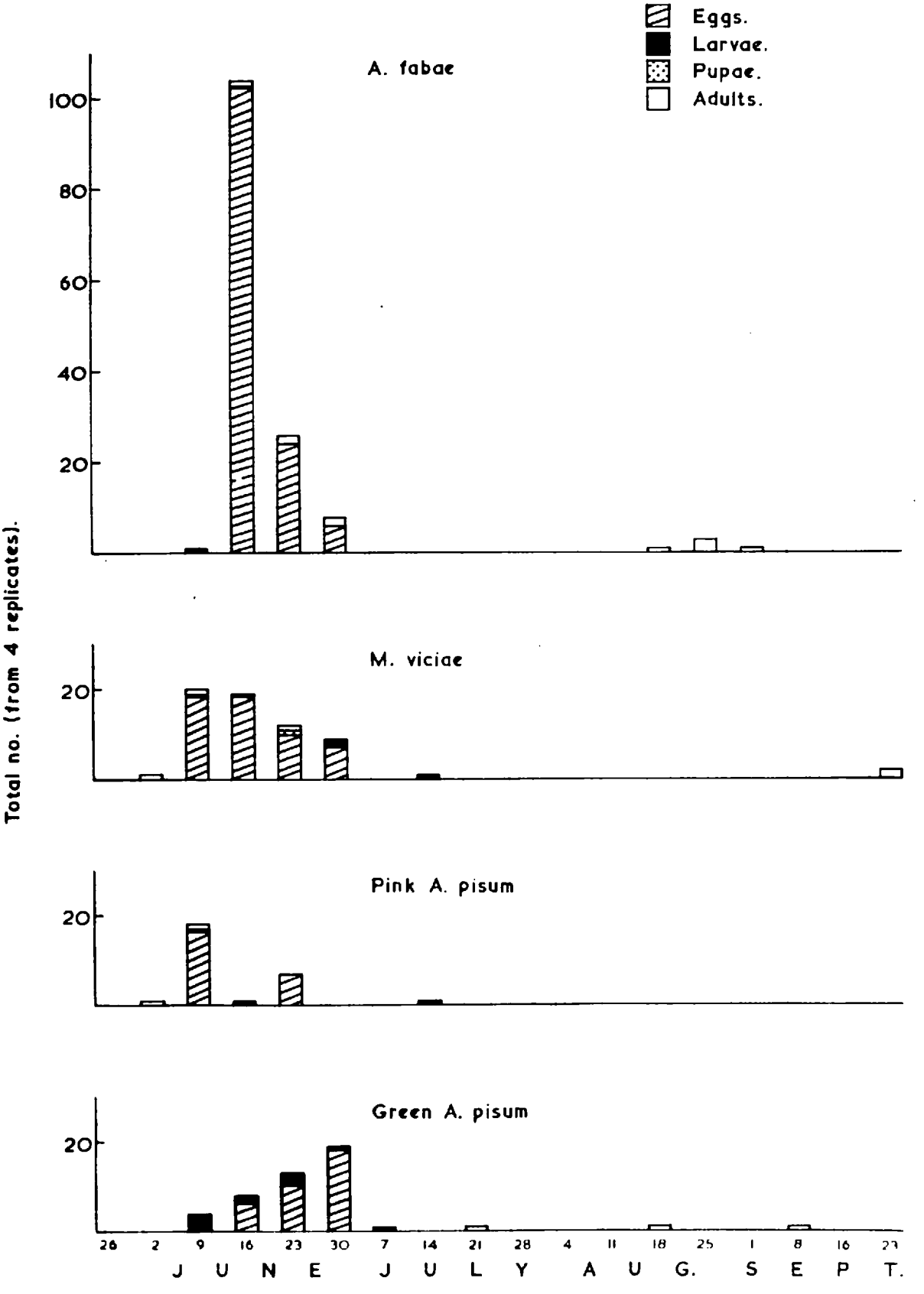
Despite the fact that M. viciae populations remained high, only 18 eggs were recorded from plants infested with this species on the 16th June.

Many of the eggs found on plants infested with M. viciae were tentatively identified as A. bipunctata but none of the larvae survived.

Although no C. septempunctata eggs were laid on plants in the main experiment, larvae belonging to this species were occasionally found on the plants. Presumably the eggs were laid on the lucerne surrounding the table on which the pots were placed, and the larvae subsequently found their way onto the bean plants. This would also account for the presence of second and third instar larvae and, in one case, a pupa of the other coccinellid species on the bean seedlings as they could not have reached such an advanced stage of development within a week of the eggs' being laid.

No larvae or adults of A. bipunctata were recorded after the 30th June. The majority of the adults found during the latter part of the season were C. septempunctata. P. 14 - punctata adults were found on only two occasions after the end of June but three larvae were found on the plants in July.

Figure 20 : Number of coccinellids found on infested bean seedlings each week between May and September, 1970


Eggs.
Larvae.
Pupae.
Adults.
A. fabae
100
80
60
40
20
Total no. (from 4 replicates).
M. viciae
20
Pink A. pisum
20
Green A. pisum
20
26 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
J U N E J U L Y A U G. S E P T.

Both C. septempunctata and P. 14 - punctata were still active in the field when the experiment was terminated. The final sample on the 23rd September included one adult of each species.

(iii) Anthocoridae

Only one species of Anthocoris was found on the bean seedlings - A. nemorum. Numbers remained low throughout June and July but increased in August, particularly on plants infested with A. fabae (Figure 14; Figure 21). The maximum number (25 nymphs from all plants) was recorded on the 25th August. Numbers dropped to a low level again during September.

Eggs may have been laid on the plants but were not specifically looked for. If significant numbers of eggs were laid on the plants, the potential importance of this group of predators will have been greatly underestimated in Figure 14.

In addition to A. nemorum, two other species of anthocorids were occasionally found on the plants. They belonged to the group commonly known as flower bugs and were identified as Orius minutus and O. niger.

(iv) Chrysopidae

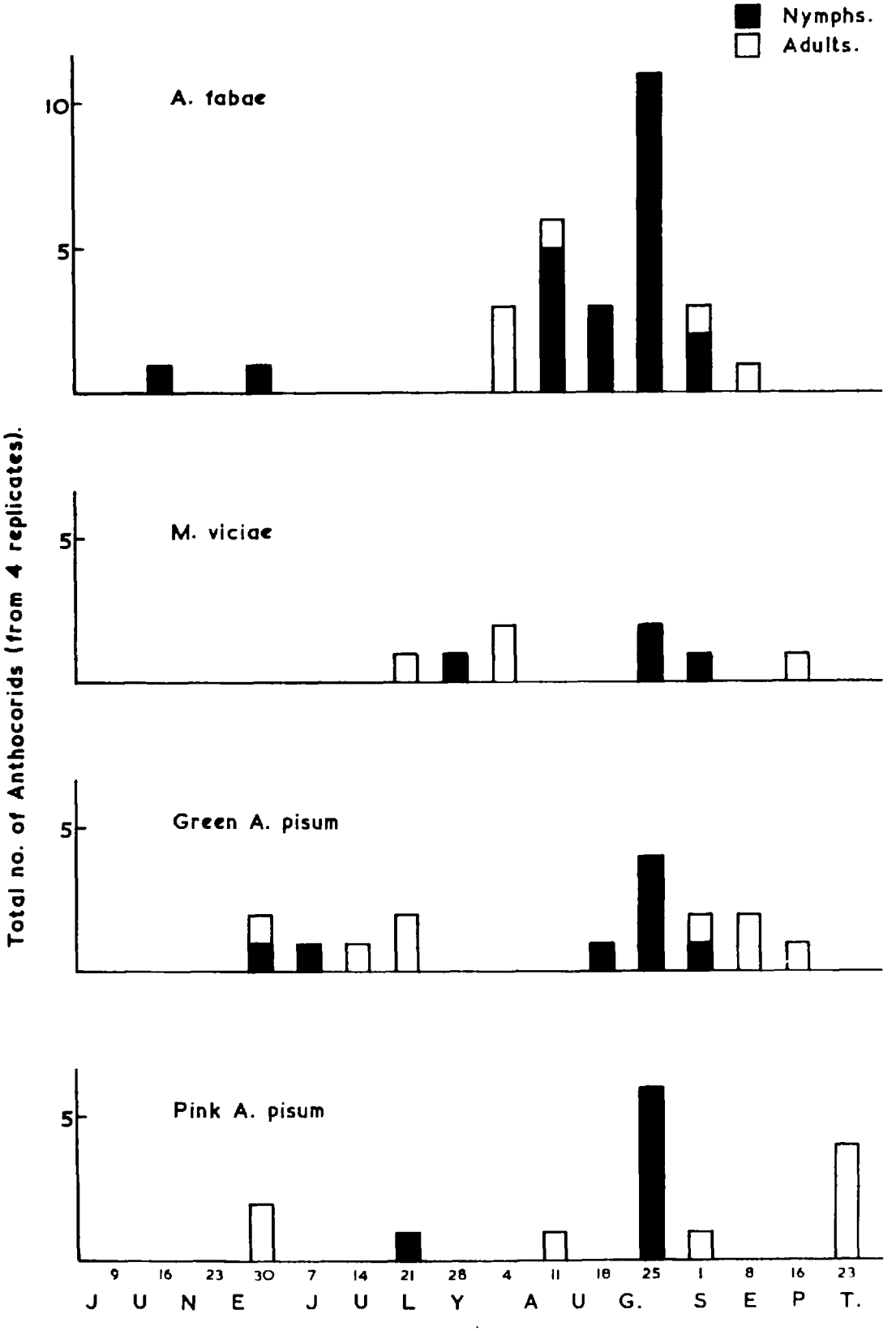
This group was relatively uncommon, only 12 eggs and 6 larvae being recorded from all plants throughout the experiment. Eggs were found on the 16th and 23rd June. Larvae occurred very sporadically between June and September; all of them had reached a relatively advanced stage of development and must have found their way onto the plants - probably from the lucerne.

No chrysopid eggs or larvae were recorded on the plants exposed at ground level between the 4th and 11th June.

(v) Cecidomyidae

14 cecidomyid larvae were recorded during June, 13 of these on the

Figure 21 : Incidence of anthocorids on bean seedlings infested with *A. fabae*, *M. viciae* and *A. pisum* after one week's exposure to predators in the field


Nymphs.
Adults.
A. fabae
M. viciae
Green A. pisum
Pink A. pisum
Total no. of Anthocorids (from 4 replicates).
10
5
5
5
5
9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
J U N E J U L Y A U G. S E P T.

9th June on plants infested with A. fabae. 16 larvae were recovered from plants exposed at ground level between the 4th and 11th June. Four of the latter were associated with A. fabae, 5 with M. viciae and 7 with green A. pisum.

b) Parasites

(i) Aphis fabae

Populations of A. fabae invariably remained at a high level during the time that they were exposed in the field and it was therefore possible to retain fairly large samples of aphids to determine the percentage of parasitism each week. The samples usually consisted of between 70 and 110 aphids.

All except two of the samples collected between the 26th May and the 25th August inclusive were parasitised, but the total percentage parasitism never exceeded 11.8% (Figure 22 a).

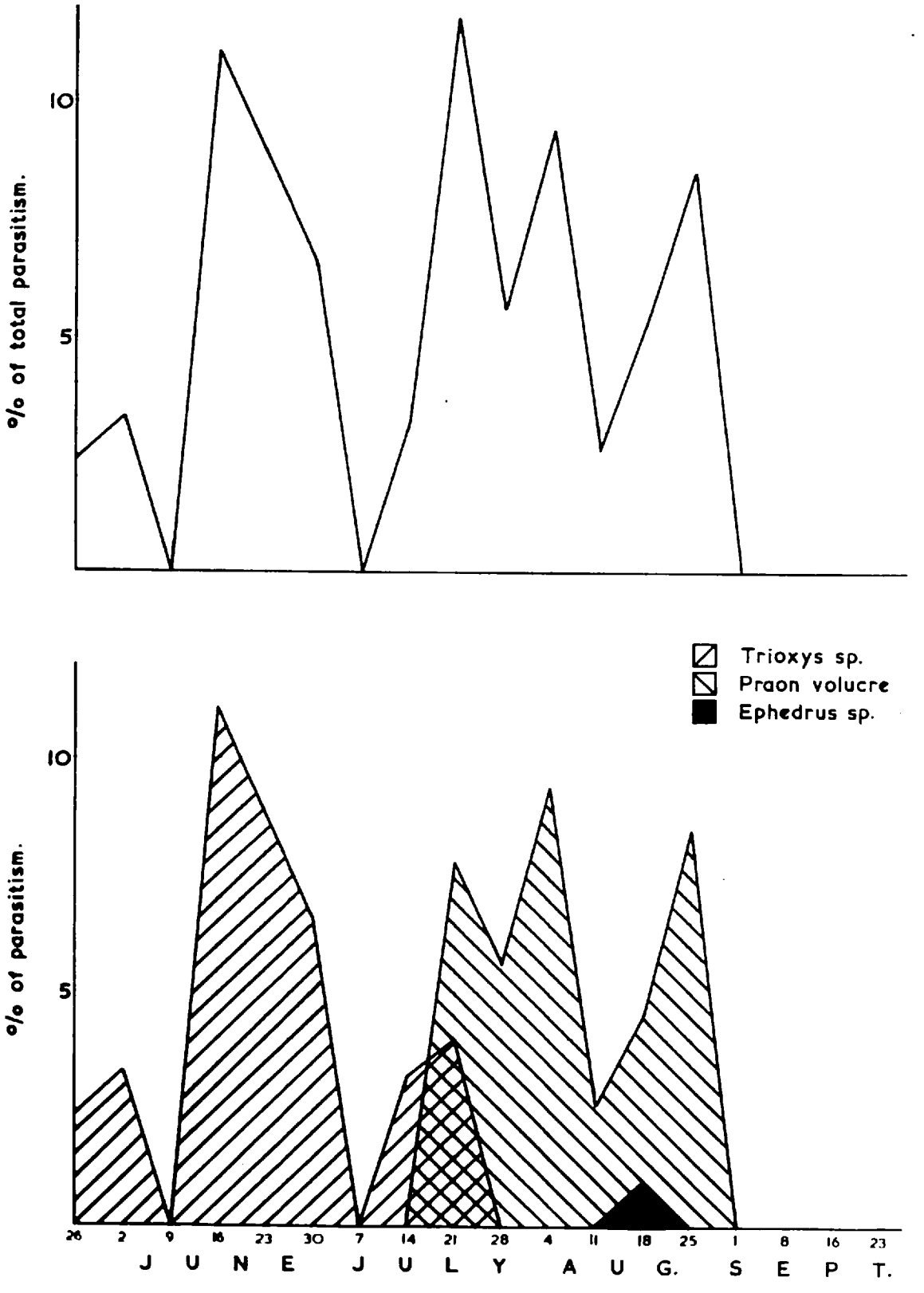
A. fabae was attacked by three species of primary parasites, namely the braconids Praon volucre, Trioxys sp. and Ephedrus sp. The latter species was represented by only one parasite which emerged from the aphid sample collected on the 18th August. Trioxys sp. occurred mainly in June, while Praon volucre was reared only from aphids exposed in the field in July and August. There was very little overlap in time between the two species (Figure 22 b).

The percentages presented in Figure 22 a and b are based on the total number of mummies produced, not the number of primary parasites which emerged. A relatively high proportion of the mummies failed to hatch - 25% in the case of Trioxys sp. and 26.3% of the Praon mummies.

No hyperparasites were recorded from P. volucre but a cynipid hyperparasite - Alloxysta victrix - emerged from Trioxys mummies in samples

Figure 22(a): Total percentage parasitism in weekly samples of *A. fabae*

Figure 22(b): Incidence of *Trioxys* sp., *Praon volucre* and *Ephedrus* sp. in weekly samples of *A. fabae*


10
5
% of total parasitism.
Trioxys sp.
Praon volucre
Ephedrus sp.
10
5
% of parasitism.
26 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
J U N E J U L Y A U G. S E P T.

collected on the 16th and 30th June. The incidence of hyperparasitism could not be determined for the earlier sample because the parasites emerged before the mummies were removed from the cage and only one of the adults (the hyperparasite referred to above) was found.

4 of the 76 aphids collected on the 30th June were parasitised by Trioxys sp. but one of the mummies failed to 'hatch'. Of the three adults which emerged, two were Trioxys sp. and the third was A. victrix. No hyperparasites were obtained from any of the samples taken after the 30th June.

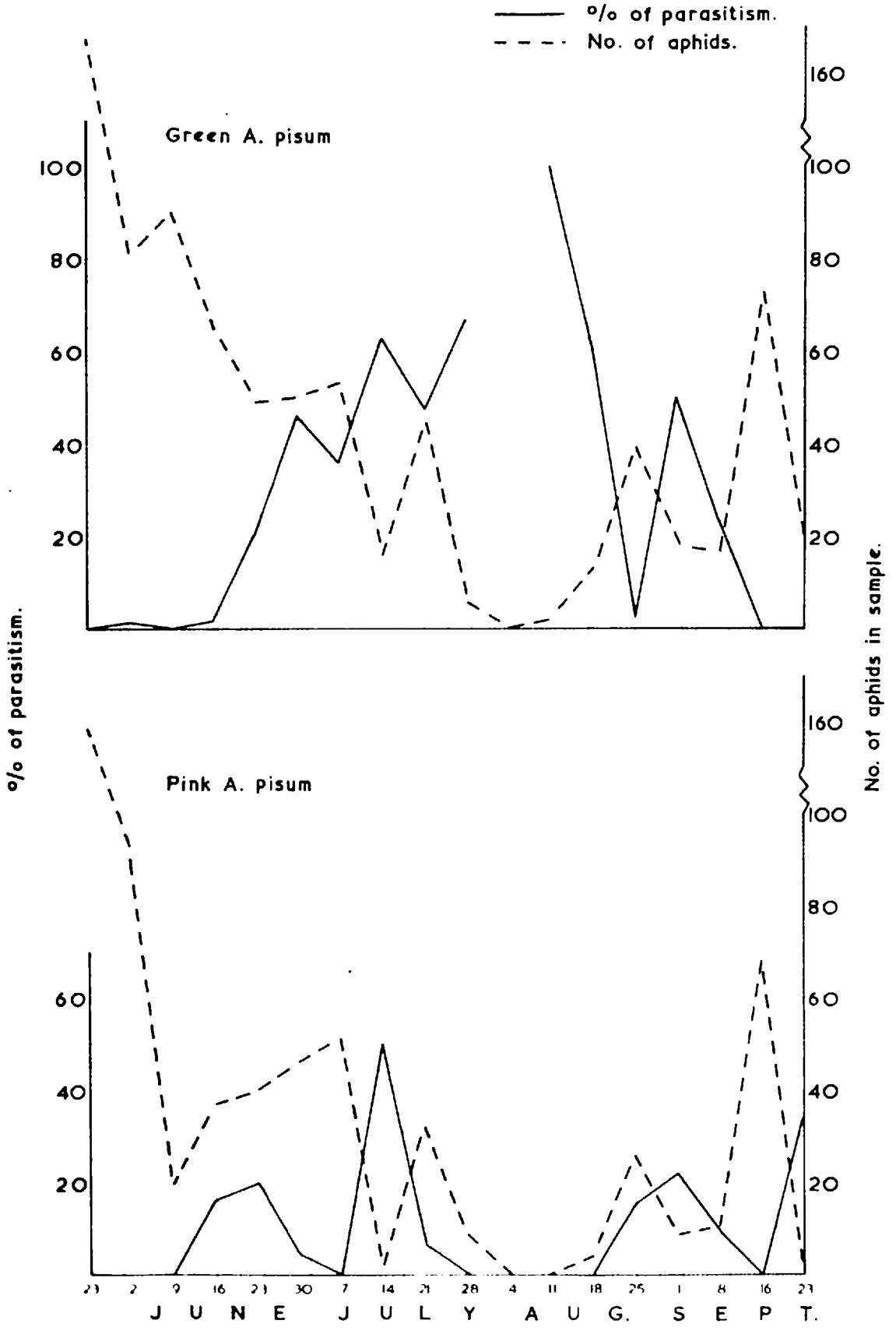
(ii) Megoura viciae

As in previous years, this species was virtually unaffected by parasites. In only one sample - that collected on the 11th August - were any parasitised aphids found. The sample in this instance consisted of only 5 aphids as the aphids had virtually diappeared from the plants when they were brought into the laboratory at the end of the week. Two of the aphids in the sample were subsequently found to be parasitised by Praon volucre.

(iii) Acyrthosiphon pisum

In both biotypes of A. pisum, there was considerable variation in the percentage parasitism from week to week and this largely obscured any seasonal trend which may have existed. Nevertheless, there appeared to be a fairly rapid increase in the incidence of parasitism during June and July (Figure 23). A very high percentage of the aphids brought in from the field during August was found to be parasitised but, as the estimates of parasitism over this period were based on very small aphid samples, they are not necessarily indicative of parasitism in natural aphid populations in the field. There appeared to be an inverse correlation between the size of the aphid sample - which was largely determined by the number of aphids remaining on the plants - and the percentage parasitism of the aphids in

Figure 23 : Number of aphids and percentage parasitism in weekly samples of green and pink A. pisum


% of parasitism.
No. of aphids.
Green A. pisum
Pink A. pisum
% of parasitism.
No. of aphids in sample.
100
80
60
40
20
160
23 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
J U N E J U L Y A U G. S E P T.

the sample. The relationship between the two variables was tested for each biotype by means of Spearman's method of rank correlation. The correlation coefficient was - .6 for green A. pisum and - .7 for pink A. pisum. The possible significance of the relationship between aphid density and percentage parasitism will be discussed later in this section (Page 175).

The incidence of parasitism was almost invariably lower in the pink than in the green biotype.

Primary Parasites

Four species of primary parasites were common to both biotypes of A. pisum. With the exception of Aphelinus sp. (Family : Eulophidae) all were braconids, namely Praon volucre, Aphidius ervi and A. urticae. A fourth braconid - Ephedrus sp. - was recorded only from pink A. pisum.

The proportion of the samples affected by the various primary parasites each week is presented in Figure 24. Percentages are based on the number of mummies which developed in each sample. Those given for Aphidius include both A. ervi and A. urticae as it is not possible to distinguish between individual species in the mummy stage. The total number of mummies recorded from each biotype is given in Table XIX. Although the total number of mummies recorded from green A. pisum was considerably higher than that recorded from pink A. pisum, the relative abundance of the primary parasites did not differ significantly (χ^2 = 2.26 ; 2 degrees of freedom).

Aphelinus sp.

This was the most common primary parasite of green A. pisum (Table XIX). It occurred throughout most of the summer from mid-June until early September but was particularly numerous in late June and July (Figure 24).

Pink A. pisum was affected to a much smaller extent, and all but one of the aphelinid parasites occurred in samples collected during June.

Figure 24 : Incidence of primary parasites in weekly samples of A. pisum based on the number of aphid mummies recorded

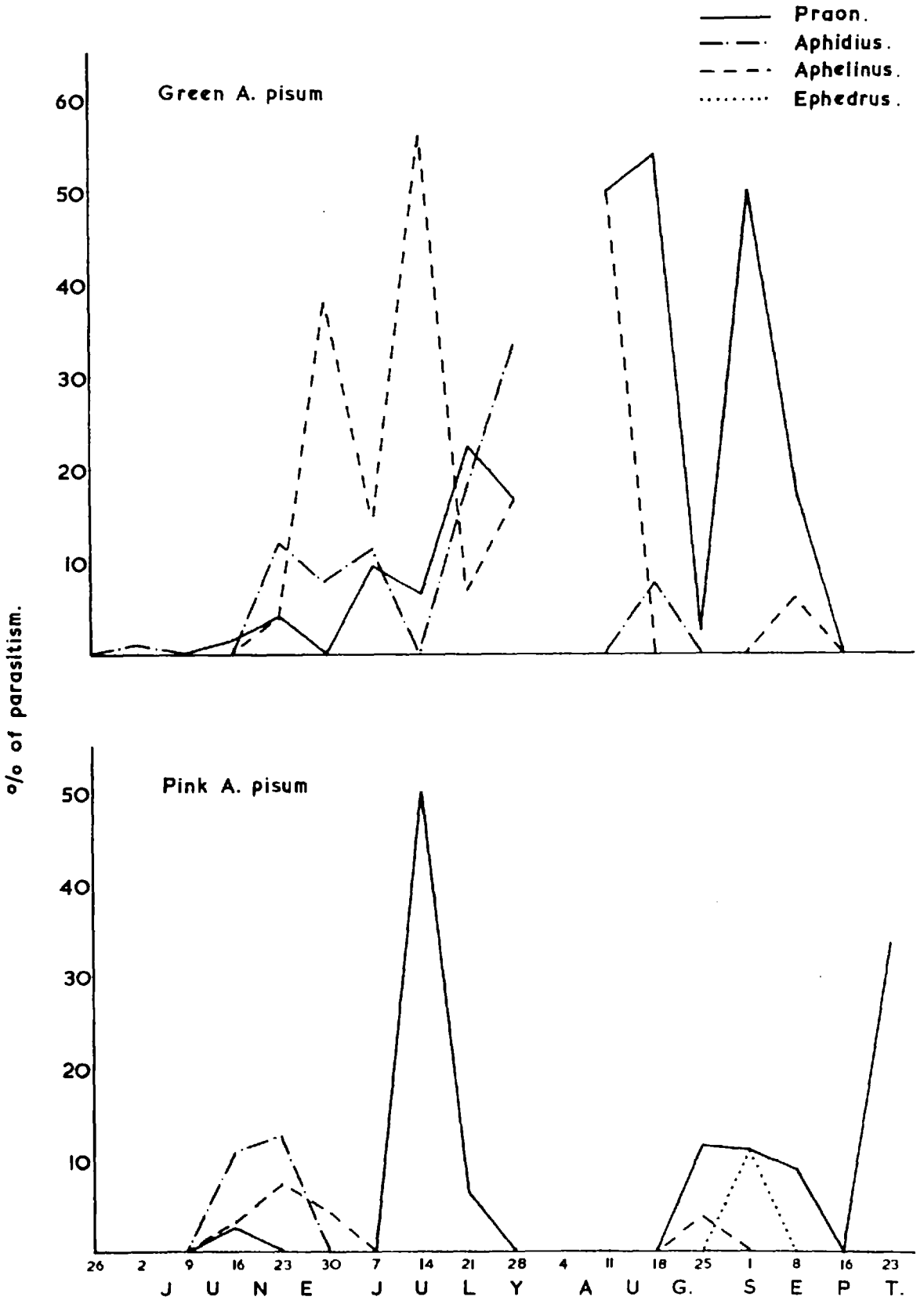

Praon.
Aphidius.
Aphelinus.
Ephedrus.
Green A. pisum
Pink A. pisum
% of parasitism.
60
50
40
30
20
10
50
40
30
20
10
26 2 9 16 23 30 7 14 21 28 4 11 18 25 1 8 16 23
J U N E J U L Y A U G. S E P T.

Table XIX : Total number of mummies obtained from samples of green and pink A. pisum throughout the season

Mummy-type	GREEN BIOTYPE		PINK BIOTYPE	
	No. of Mummies	% of Total	No. of Mummies	% of Total
Aphelinus	44	39.6%	7	26.0%
Praon	40	36.0%	10	37.0%
Aphidius	27	24.3%	9	33.3%
Ephedrus	0	0%	1	3.7%
TOTAL	111		27	

A total of 51 mummies was recorded from both biotypes. All of them hatched and all produced primary parasites.

Praon volucre

This species was only slightly less important than Aphelinus sp. in samples of the green biotype of A. pisum. It occurred in nearly all samples from the 16th June onwards, but the highest incidence of parasitism due to this species was recorded during the latter part of August and early September when Aphelinus sp. and Aphidius spp. were scarce.

P. volucre was one of the main parasites of pink A. pisum and accounted for 37.0% of all mummies recorded from the pink biotype.

50 mummies were obtained from all samples of both biotypes. 49 of them hatched and 48 produced primary parasites.

Aphidius species

Although the first to appear in the samples, Aphidius species accounted for only 24% of all mummies recorded from green A. pisum. A. ervi was the more common of the two species and occurred mainly during June and July. A. urticae was recovered from the samples of both biotypes collected on the 23rd June. Adults of the latter species emerged from 5 out of the 6 green

A. pisum mummies, and 1 out of the 5 pink A. pisum mummies.

Ephedrus sp.

A single adult was reared from the pink A. pisum sample collected on the 1st September. Mummies of Ephedrus resemble those of Aphelinus spp. in that both are black. Those of Ephedrus can usually be identified by their relatively larger size and by the fact that they are more firmly attached to the substratum. The hatched mummy in this instance was readily distinguishable from hatched Aphelinus mummies because of its relatively large emergence hole which was located at the posterior end of the mummy. (Aphelinus adults almost invariably emerged through a small hole in the dorsal surface of the mummy).

Hyperparasites

Two species of Cynipidae - Alloxysta victrix and Phaenoglyphis sp. - were reared from green A. pisum. The former species was obtained on three occasions - on the 2nd June, 28th July and 18th August. The primary host in each case was Aphidius sp. - presumably A. ervi. Phaenoglyphis sp. was represented by a single adult which emerged from a Praom mummy in the sample of green A. pisum collected on the 1st September.

No hyperparasites were reared from pink A. pisum.

c) The relationship between aphid density and percentage parasitism on individual leaves

(i) Aphis fabae

The caged population of A. fabae was sampled on the 28th June, 1970. The number of aphids on individual leaves varied between 33 and 411, and the percentage parasitism between 0% and 26.2% (Table XX).

The relationship between aphid density and the percentage parasitism on individual leaves was tested using Spearman's formula for the coefficient of rank correlation. The calculated value for r was - .1, which suggests

Table XX : Density and percentage parasitism of A. fabae on individual sample leaves

Leaf No.	No. of Aphids	Leaf Area (cm^2)	Density (Aphids/sq. cm.)	% Parasitism
1	65	37.7	1.7	26.2
2	33	18.5	1.8	3.0
3	77	39.4	1.9	0.0
4	89	20.1	4.4	24.7
5	74	12.9	5.7	5.4
6	114	12.5	9.1	0.9
7	411	38.5	10.7	7.1
8	319	24.4	13.1	6.0
9	127	9.0	14.1	3.9
10	119	6.6	18.1	4.2
TOTAL	1428	-	-	Mean= 7.2%

that there was no correlation between aphid density and percentage parasitism in this species.

Similarly, there was no apparent correlation between the number of aphids per leaf and the percentage parasitism (r = .1).

The overall percentage parasitism of the aphids was 7.2% and was due mainly to Trioxys spp. (6.9%). Aphelinus sp. was the other parasite concerned but it attacked only 0.3% of all the aphids. Hyperparasites emerged only from Trioxys mummies. They belonged to two species, namely Alloxysta victrix and Phaenoglyphis sp., both of which are members of the family: Cynipidae. Approximately 10% of the adults which emerged from Trioxys mummies were hyperparasites.

10 unhatched mummies were found at the time of sampling - all of them on leaf 10. One of the mummies was lost but the others all produced hyper-parasites - 5 A. victrix and 4 Phaenoglyphis sp.

(ii) Green biotype of Acyrthosiphon pisum

The leaf samples were removed from the cage on 21st June. The percentage parasitism of the aphids on individual leaves was less than 1% in most cases but was as high as 26.3% in one instance (Table XXI).

Table XXI : Density and percentage parasitism of green A. pisum on individual sample leaves

Leaf No.	No. of Aphids	Leaf Area (cm^2)	Density (Aphids/sq. cm.)	% Parasitism
1	28	19.5	1.4	3.6
2	57	23.0	2.5	26.3
3	97	31.5	3.1	5.2
4	70	11.8	6.0	0.0
5	87	9.8	8.9	2.3
6	274	14.1	19.4	0.7
7	142	6.3	22.7	0.7
8	258	10.6	24.3	0.8
9	169	6.5	26.2	0.6
10	195	6.5	30.2	0.5
TOTAL	1377	-	-	Mean= 2.2%

The correlation between aphid density and percentage parasitism on individual leaves was tested using Spearman's formula for the coefficient of rank correlation. The correlation coefficient, r, was calculated as - .7 which suggests that there is a fairly strong inverse correlation between aphid density and percentage parasitism in this biotype.

The overall percentage parasitism at the time of sampling was very low (2.2%) but must have increased rapidly as large numbers of mummies were found on the dead plants 2 weeks later.

A total of 1377 live aphids was found on the 10 sample leaves, 30 of which were parasitised, mainly by Aphelinus sp. and Aphidius sp. (Table XXII).

Table XXII : Identity of aphid mummies and the incidence of primary and secondary parasites

Mummy-Type	HATCHED MUMMIES		Unhatched Mummies	Total
	Primary	Secondary		
Aphelinus	14	0	0	14
Aphidius	5	6	0	11
Praon	4	0	1	5
TOTAL	23	6	1	30

Only one species of primary parasite emerged from the Aphidius - type mummies, namely A. ervi. Over 50% of the Aphidius mummies produced hyperparasites, all of which were identified as Alloxysta victrix (Family: Cynipidae). No hyperparasites emerged from either Aphelinus - or Praon - type mummies. The primary parasites which emerged from Praon - type mummies were all P. volucre.

Two Aphidius mummies were found on leaf 3 at the time of sampling. Both produced hyperparasites which were identified as Alloxysta victrix.

(iii) Pink biotype of Acyrthosiphon pisum

The caged population of pink A. pisum was sampled on 3rd July, 1970. The number of aphids on individual leaves was generally much lower than in the case of green A. pisum and the number of parasites recorded was correspondingly lower. The possible relationship between aphid density and percentage parasitism could not be analysed statistically because parasites were reared from only four of the ten samples (Table XXIII).

Only 5 parasites were reared from all the aphid samples, giving an overall percentage parasitism of 2.6%. Four of the parasites were Aphelinus sp; the fifth was Praon volucre. One mummy was found on leaf 2 at the time of sampling. The adult which emerged was a pteromalid -

Table XXIII : Density and percentage parasitism of pink A. pisum on individual sample leaves

Leaf No.	No. of Aphids	Leaf Area (cm^2)	Density (Aphids/sq. cm,)	% Parasitism
1	13	29.5	0.4	7.7
2	21	27.9	0.8	0.0
3	10	13.1	0.8	10.0
4	14	17.4	0.8	0.0
5	26	28.3	0.9	0.0
6	41	35.0	1.2	7.3
7	19	13.1	1.5	5.3
8	10	6.8	1.5	0.0
9	23	14.1	1.6	0.0
10	17	7.7	2.2	0.0
TOTAL	194	-	-	Mean= 2.6

Coruna clavata Walk. This species is an ectoparasite of primary parasites.

3. Studies on the Effect of Bird Predation on Aphid Populations

a) The effect of bird predation on the green biotype of A. pisum over a period of 24 hours

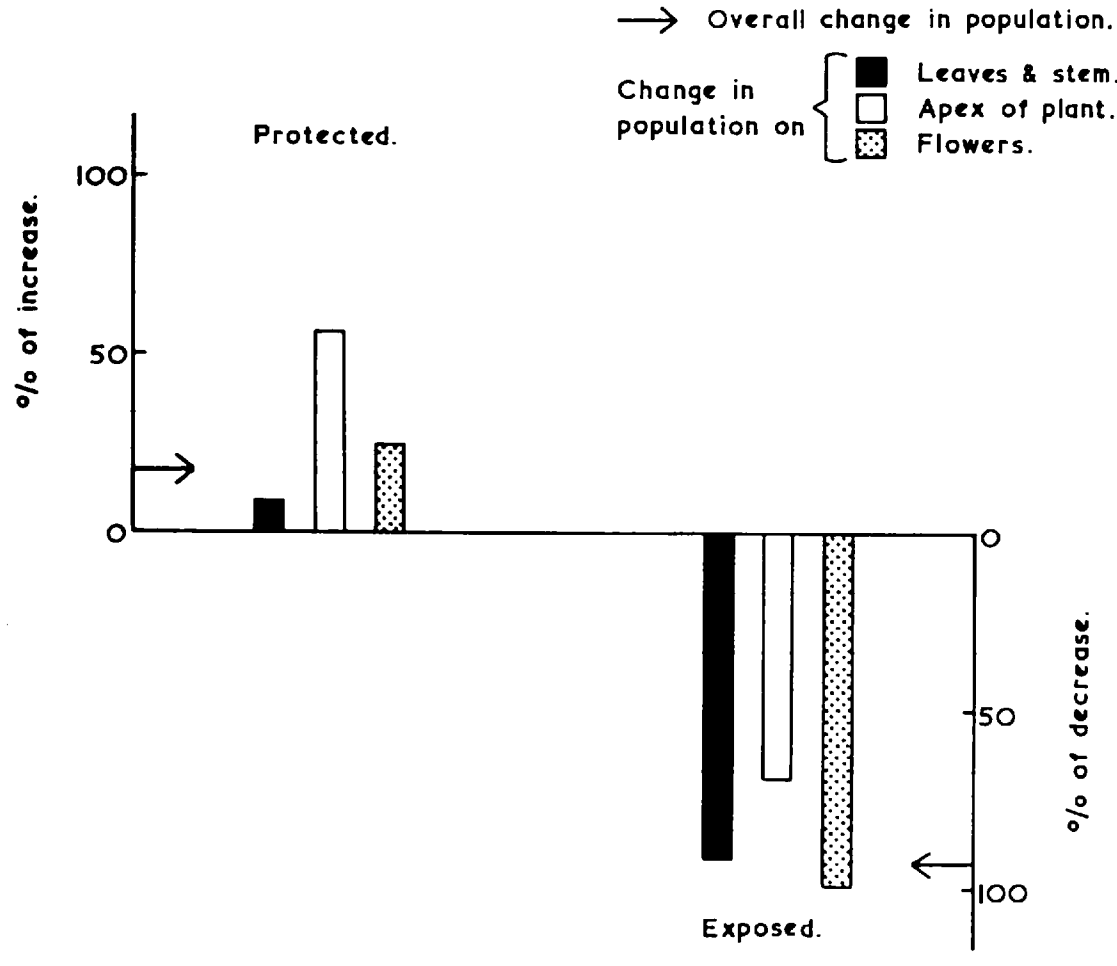
Populations on uncaged plants suffered a high mortality (Table XXIV; Figure 25). The percentages given in Figure 25 represent the change in the number of aphids between the first and second counts in each case. Assuming that the populations on uncaged plants would have increased by a similar amount to those on caged plants had they not been exposed to birds, the true effect of birds may be estimated by subtracting a particular value for uncaged plants from the corresponding value for caged plants. The figure so obtained is the 'Reduction ratio attributable to bird predation' (Table XXIV). The relative susceptibility of the three sub-populations may then be determined by comparing these 'reduction' ratios.

In this experiment aphids feeding on the apices and flowers of the plants apparently suffered a higher mortality due to bird predation than those feeding on the leaves and stems. The reduction in numbers on the leaves and stems between the two counts appeared to be partly due to the aphids' moving up the plant to the apex.

The 'knock-down' effect of birds on the aphids was smaller than expected. In the case of the exposed plant surrounded at its base by Ostico-coated cellulose acetate sheets, only 9.1% of the population (based on the first count) fell from the plant and was trapped by the Ostico, as opposed to 3.1% in the case of the caged plant. These percentages are overestimates as they do not take into account any increase in the population due to natality. A possible explanation for the small knock-down effect of birds in this experiment was that the birds may have perched on the wire mesh rather than on the plant itself while feeding.

The relatively large increase in size of the sub-population on the

Figure 25 : Effect of bird predation on green A. pisum over a period of 24 hours


Overall change in population.
Change in population on
Leaves & stem.
Apex of plant.
Flowers.
Protected.
% of increase.
100
50
0
0
50
100
% of decrease.
Exposed.

apex of caged plants was probably partly due to the movement of aphids from other parts of the plant. Only a small proportion of the total population was feeding on the apex at the first count.

Table XXIV : Populations of green A. pisum on caged and uncaged plants at each count

(Figures represent totals from two replicates)

Position on plant	Caged plants			Uncaged plants			Ratio of reduction attributable to birds (c-u)
	1st count	2nd count	Ratio 2/1 (c)	1st count	2nd count	Ratio 2/1 (u)	
Leaves + stem	277	303	1.09	232	19	0.08	1.01
Apex	35	55	1.57	80	25	0.31	1.26
Flowers	120	150	1.25	400	5	0.01	1.24
TOTAL	432	508	1.18	712	49	0.07	1.11

b) A comparative study of the effect of bird predation on the green and pink biotypes of A. pisum

At the first count there was considerable variation in the distribution of the aphids on the plants, presumably because the count was made only a few hours after the plants were infested. When the aphids were counted at the end of the experiment 48 hours later, the pattern of distribution of the two biotypes on caged plants was noticeably different. In the case of the green biotype, more than half the total population (on the four replicates) was concentrated on the young furled leaves at the apex of the main plant (Table XXV). Some of the aphids must have moved up to the apex from other parts of the plant, particularly the older, expanded leaves where the numbers decreased over the 48 hour period (Figure 26). The pink biotype was more generally distributed over the plant but mainly on the expanded leaves (and stem) of the main plant. The decrease in numbers on

the apices of the plants may have been partly due to the fact that the upper parts of the plants were unshaded. The aphids have frequently been observed to move off leaves which are directly exposed to the sun's rays, presumably because of the high temperatures. This tendency is more marked in the pink than in the green biotype.

Table XXV : Distribution of the aphids on caged plants at the second count

	Green Biotype	Pink Biotype
Expanded leaves + stem	28.0%	45.6%
Apex	56.9%	28.3%
Side-shoots	15.1%	26.1%

The differential distribution of the two biotypes on their host plants could conceivably affect their relative susceptibility to bird predation.

The overall increase in size of the populations on caged plants was greater in the green biotype (35.8%) than in the pink biotype (14.1%). On uncaged plants, both biotypes suffered on high mortality as a result of bird predation (Table XXVI; Figure 26).

Overall mortality due to bird predation was similar in both biotypes of A. pisum (Table XXVI). In the case of the green biotype, aphids feeding on the apices of the main plants were most affected by bird predation. Those on the side-shoots were least affected. The decrease in numbers on the expanded leaves + stem was again partly due to the aphids' moving to the younger leaves of the apex and side-shoots.

The pink biotype suffered a high mortality on all parts of the plant (Figure 26). Those on the expanded leaves + stem appeared to be most vulnerable to bird predation.

Figure 26 : Effect of bird predation on both biotypes of A. pisum over a period of 48 hours

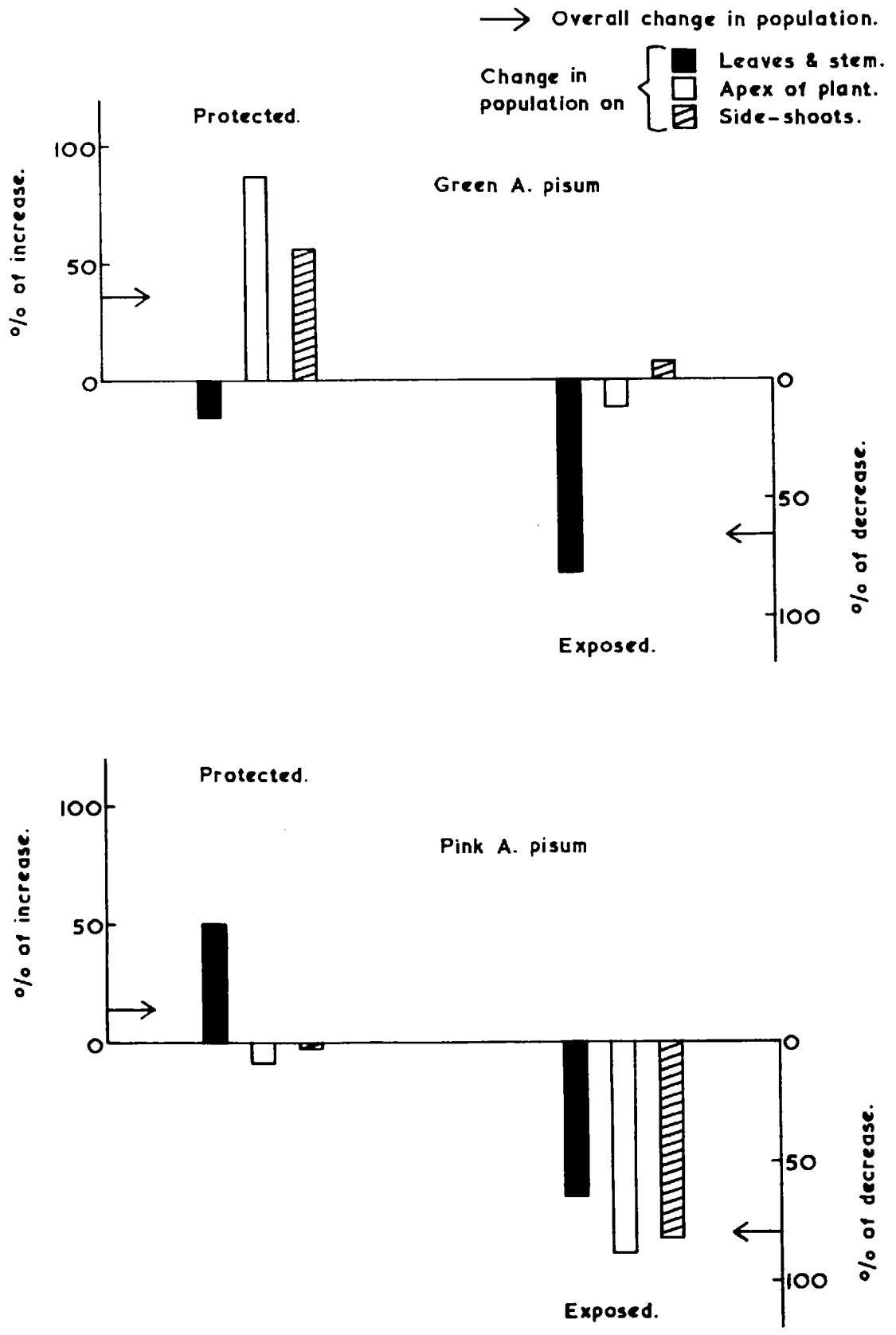

Overall change in population.
Change in population on
Leaves & stem.
Apex of plant.
Side-shoots.
Protected.
Green A. pisum
% of increase.
100
50
0
0
50
100
% of decrease.
Exposed.
Protected.
Pink A. pisum
% of increase.
100
50
0
0
50
100
% of decrease.
Exposed.

Table XXVI : Populations of green and pink A. pisum on caged and uncaged plants at each count

(Figures represent totals from four replicates)

Green A. pisum

Position on plant	Caged plants			Uncaged plants			Ratio of reduction attributable to birds (c-u)
	1st count	2nd count	Ratio 2/1 (c)	1st count	2nd count	Ratio 2/1 (u)	
Leaves + stem	327	274	0.84	870	155	0.18	0.66
Apex	298	556	1.87	250	220	0.88	0.99
Side-shoots	95	148	1.56	13	14	1.08	0.48
TOTAL	720	978	1.36	1133	389	0.34	1.02

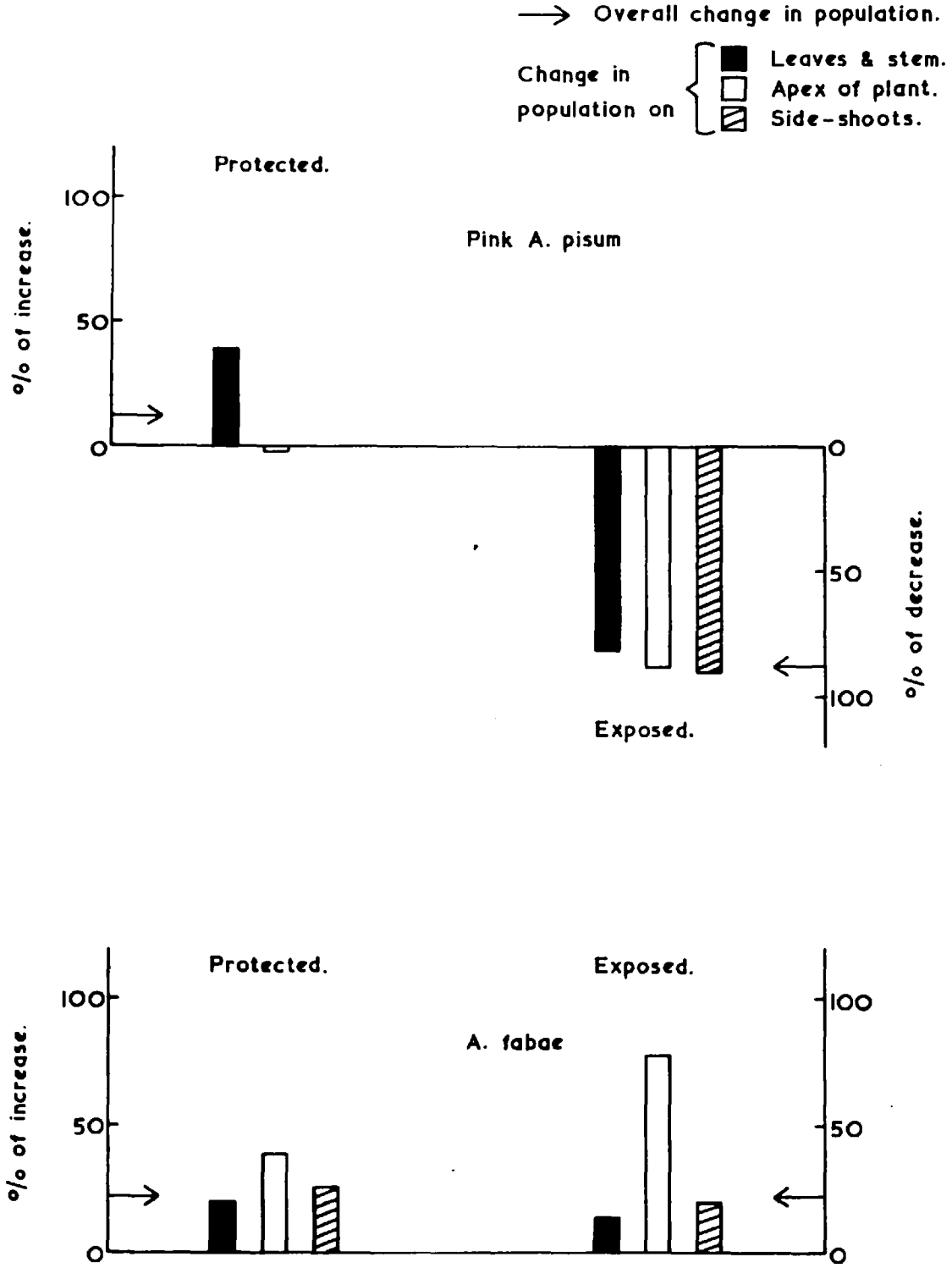
Pink A. pisum

Position on plant	Caged plants			Uncaged plants			Ratio of reduction attributable to birds (c-u)
	1st count	2nd count	Ratio 2/1 (c)	1st count	2nd count	Ratio 2/1 (u)	
Leaves + stem	403	604	1.50	402	140	0.35	1.15
Apex	405	375	0.93	640	72	0.11	0.82
Side-shoots	353	346	0.98	519	88	0.17	0.81
TOTAL	1161	1325	1.14	1561	300	0.19	0.95

c) A comparative study of the effect of bird predation on pink A. pisum and Aphis fabae

As before, populations of pink A. pisum suffered a high mortality on uncaged plants. Those protected from bird predation showed an overall increase of 12.1% (Figure 27). In this experiment, however, most of the

Figure 27 : Effect of bird predation on pink A. pisum and Aphis fabae over a period of 48 hours


Overall change in population.
Change in population on
Leaves & stem.
Apex of plant.
Side-shoots.
Protected.
Pink A. pisum
% of increase.
100
50
0
0
50
100
% of decrease.
Exposed.
Protected.
Exposed.
A. fabae
% of increase.
100
50
0
100
50
0

aphids on the caged plants remained on the apices of the plants (Tables XXVII and XXVIII) and exhibited only a slight tendency to move down to the more mature leaves (the caged plants had no side-shoots). A possible explanation for this is that the weather during the experiment was relatively cool and cloudy, therefore the aphids feeding on the upper parts of the plant were not subjected to the high temperatures which appeared to affect the distribution of pink A. pisum in the previous experiment. Aphids feeding on the expanded leaves + stem once again suffered the highest mortality.

Table XXVII : Distribution of the aphids at the second count

	Pink A. pisum (Caged plants)	Aphis fabae	
		Caged plants	Uncaged plants
Leaves + stem	43.1%	87.6%	83.4%
Apex	56.9%	11.6%	15.2%
Side-shoots	-	0.7%	1.4%

Aphis fabae appeared to be unaffected by birds (Figure 27; Table XXVIII). Populations on exposed plants showed a similar overall increase in size to those on caged plants (20.7% and 22.1% respectively), and the distribution of the aphids on the plants was very similar in both treatments (Table XXVII).

Identity of birds which attacked aphid populations

Species which were most commonly observed feeding on the aphids in the field were hedge sparrows (Prunella modularis), robins (Erithacus rubecula), great tits (Parus major) and, less frequently, blue tits (Parus caeruleus).

Infested bean seedlings which were no longer required in the green-

Table XXVIII:: Populations of pink A. pisum and A. fabae on caged and uncaged plants at each count

(Figures represent the totals from four repliaates)

Pink A. pisum

Position on plant	Caged plants			Uncaged plants			Ratio of reduction attributable to birds (c-u)
	1st count	2nd count	Ratio 2/1 (c)	1st count	2nd count	Ratio 2/1 (u)	
Leaves + stem	218	303	1.39	226	42	0.02	1.37
Apex	409	400	0.98	444	45	0.10	0.88
Side-shoots	-	-	-	43	4	0.09	-
TOTAL	627	703	1.11	713	91	0.13	0.98

Aphis fabae

Position on plant	Caged plants			Uncaged plants			Ratio of reduction attributable to birds (c-u)
	1st count	2nd count	Ratio 2/1 (c)	1st count	2nd count	Ratio 2/1 (u)	
Leaves + stem	1758	2111	1.20	1545	1762	1.14	0.06
Apex	201	280	1.39	180	320	1.78	0.39
Side-shoots	14	18	1.29	25	30	1.20	0.09
TOTAL	1973	2409	1.22	1750	2112	1.21	0.02

house were placed out in the open on a bench about three feet high. The aphids (with the exception of Aphis fabae) were readily attacked by birds, mainly house sparrows (Passer domesticus) and robins. Blue tits and wrens (Troglodytes troglodytes) were also occasionally seen eating the aphids.

D. DISCUSSION

In 1970, the arrival of syrphid adults in the bean plot evidently coincided with, or occurred soon after, the immigration of aphids (notably Aphis fabae) into the plot. Prior to the 9th June, however, most of the eggs and larvae found on the experimental plants 30 inches above ground level were identified as Syrphus eligans. This species is not normally found on beans, presumably because it is only active in spring when the height of bean plants growing in the field is well below the preferred height for oviposition of the species (Chandler, 1967). Conversely, the importance of S. nitidicollis was underestimated as this species lays most of its eggs near ground level and tended to ignore the experimental plants at 30 inches. Thus the effectiveness of syrphids in spring is limited by their restricted height range of oviposition.

Their effectiveness in controlling aphid populations in the field is also determined by the degree to which oviposition is governed by aphid density, and by the survival rate of the larvae. In 1970, more eggs were laid on plants with consistently high aphid populations than on those on which the aphid numbers decreased. If adults in the field are specifically attracted to plants with high aphid populations, the impact of the predators would probably be too late to prevent economic injury to the plants (Bombosch, 1963).

Many of the syrphid larvae disappeared from the plants within a few days of hatching and larvae suffered a high mortality in the laboratory, even when aphids were plentiful. Way et al. (1969) considered that the failure of syrphids to suppress populations of Brevicoryne brassicae was due to the high mortality of newly-hatched larvae. The most likely causes of mortality of young larvae in the field are desiccation and cannabilism.

Syrphid oviposition continued throughout the season and there was a pronounced oviposition peak in September. The apparent build-up of syrphids in autumn provides further evidence in support of the theory proposed by Way and Banks (1958) i.e. that predators may cause high mortality among aphid populations late in the season and that their long-term effect may therefore be of considerable importance.

In contrast to the extended oviposition period of syrphids, coccinellid oviposition occurred only during June. The efficiency of coccinellids in controlling natural aphid populations in the field will therefore depend on the number and distribution of the eggs laid during that period, and on a high survival rate of the larvae.

The abundance of coccinellids was undoubtedly underestimated in 1970 because the height of the experimental plants was above the preferred height for oviposition of Coccinella septempunctata (Blackman, 1965 a). No eggs were laid by this species on the plants 30 inches above the ground, but it accounted for over 50% of the eggs laid on plants exposed at ground level between the 4th and 11th June.

Peak oviposition occurred between the 9th and 16th June, when 102 eggs were recorded from plants infested with A. fabae. Relatively few eggs were recorded for the other aphid species during the same period. The low number of eggs laid on plants infested with Acyrthosiphon pisum may have been due to the low density of the aphids towards the end of the week. In the case of M. viciae, however, the aphid populations remained high throughout the week.

M. viciae is known to be toxic to adults (and larvae) of Adalia bipunctata, and the majority of the eggs on the plants at 30 inches were laid by this species. Although A. bipunctata adults are unable to avoid feeding on unsuitable aphids in the laboratory, Blackman (1965 a) suggested

that they might avoid prolonged contact with M. viciae in the field by becoming restless and flying away. This might explain the relatively low number of eggs found on M. viciae - infested plants on the 16th June.

Larvae suffered a high mortality in the laboratory, possibly as a result of cannabalism. Banks (1956) observed that fertile eggs are frequently attacked by newly-hatched larvae. He claimed that egg batches were often laid some distance from the nearest aphids in the field and that larvae consequently suffered a high mortality, due mainly to cannabalism and starvation (Banks, 1953).

Only one other group of predators - Cecidomyidae - appeared sufficiently early in the season to assist in preventing the build-up of aphid populations in the field. However, the larvae appeared too sporadically and were too localised to have had any significant effect on the aphids.

Although 200-300 aphids were introduced into each pot at the commencement of each experiment, the population of green and pink A. pisum, had frequently declined to a very low level when the plants were transferred to the laboratory a week later. M. viciae was also affected but to a lesser extent. A. fabae invariably remained at a high level throughout the week.

There was no obvious reason for the drastic decrease in aphid numbers, so various biotic and abiotic factors were considered in relation to the density of the aphids at the end of the week. The discussion will be mainly confined to green A. pisum.

(i) Abiotic factors

Weather conditions most likely to have affected the aphids are rainfall and high temperatures. Rainfall did not appear to cause significant mortality among the aphid populations in 1967 and 1968, but the plants used

in 1970 were only about 6 to 8 inches high and would have afforded the aphids little protection from rain.

Alternatively, high temperatures may have induced the aphids to leave the plants. During the course of rate of development experiments in the field, the aphids were frequently observed to move away from leaves which received direct sunlight to more shaded situations. In the greenhouse, a combination of bright sunlight and high temperatures provoked a similar reaction. When the temperature in the greenhouse rose above about 30°C, M. viciae and both biotypes of A. pisum frequently left the plants and clustered around the outside of the pots near the floor of the cage, and occasionally underneath the pots.

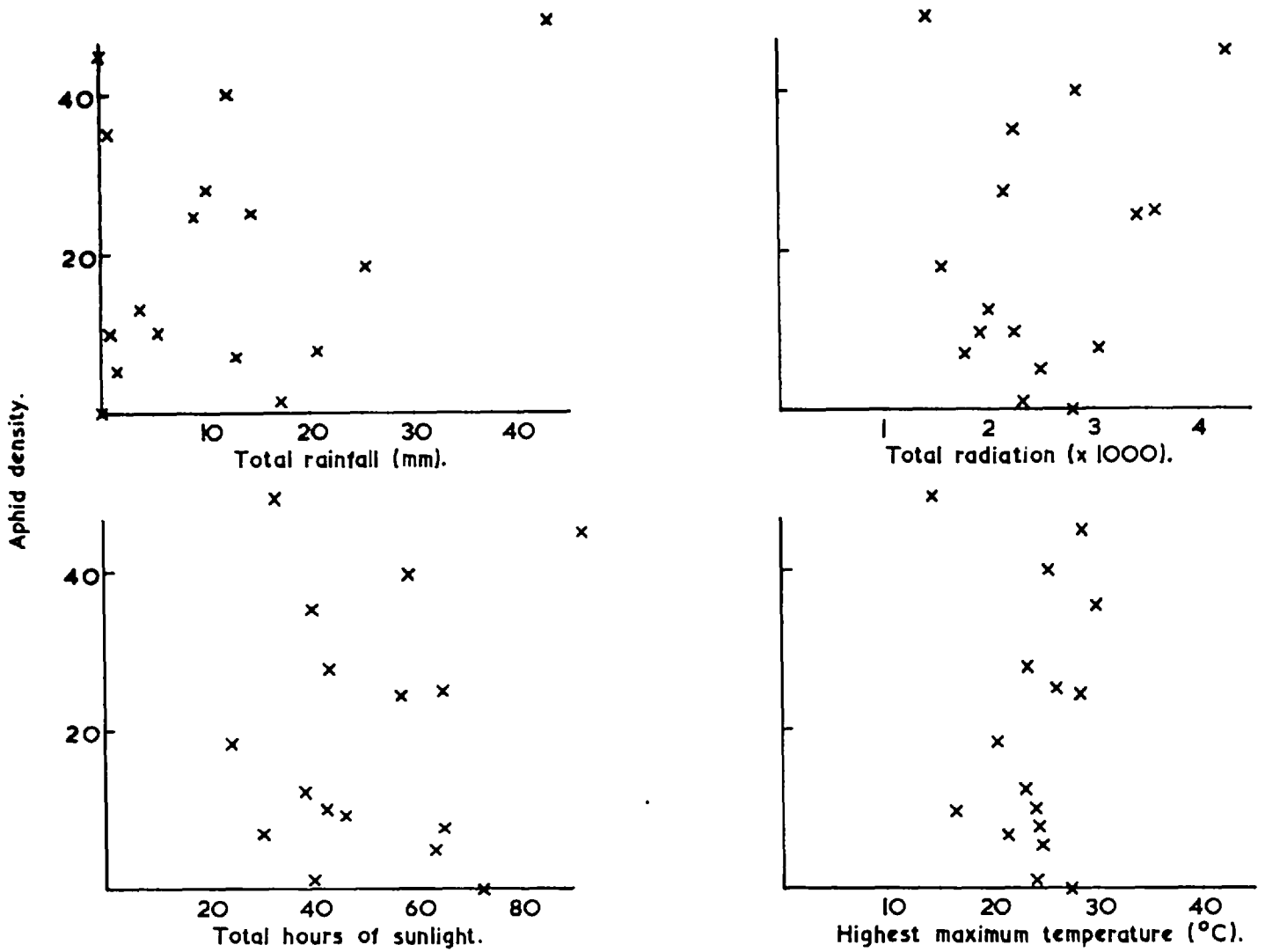
In Figure 28, the density of green A. pisum at the end of each week (from the 9th June onwards) is compared with total rainfall, total radiation, total hours of sunshine and maximum temperature recorded during the week in question. The method used to calculate aphid density was similar to that described on page 124 but, in this instance, plants on which no aphids were found were recorded as having a density of '0' instead of '1'.

There was no obvious correlation between any of the four factors considered and the density of the aphids. This does not eliminate the possibility that they may, at times, have contributed to the decline of the aphids, but it seems unlikely that weather conditions were of major importance.

(ii) Biotic factors

The decline in numbers may have been due to mortality as a result of predation or disease. The first possibility can be eliminated because the populations declined even when there were no active stages pf predators on the plants. Disease occasionally caused some mortality among populations of A. pisum but dead aphids remained attached to the plants so this factor

Figure 28 : Relationship between density of green A. pisum at the end of each week and weather factors during the week in question


Aphid density.
40
20
10
20
30
40
Total rainfall (mm).
1
2
3
4
Total radiation (x 1000).
40
20
20
40
60
80
Total hours of sunlight.
10
20
30
40
Highest maximum temperature (°C).

can also be discounted. In any case, it is unlikely that predation or disease would have caused such a high mortality over so short a period of time.

The only alternative explanation is that the aphids left the plants because they were disturbed, either by predators or by parasites.

Dixon (1958) observed that nettle aphids, Microlophium evansi, took avoiding action when approached by larvae or adults of the coccinellid Adalia bipunctata. 3rd and 4th instar nymphs and adults generally reacted to encounters with mature coccinellid larvae and adults by dropping from the plant. White (1958) reported that Acyrthosiphon spartii adults moved away if syrphid adults alighted near them, although they showed no response to hovering syrphid flies.

Similar escape reactions have been recorded for other aphid species, such as Drepanosiphum platanoides (Dixon, 1958) but the intensity of the response varies from species to species.

M. viciae and both biotypes of A. pisum exhibit escape responses when subjected to certain stimuli, and it therefore seemed possible that the aphids had left the plants as a result of disturbance by ovipositing syrphids. This theory was rejected, however, because the aphid populations declined each week in August when very few eggs were laid on any of the plants, but remained at a high level between the 9th and 16th September when the highest number of eggs was recorded.

The only alternative explanation is that the decline of the aphid populations was in some way related to the activity of adult parasites. In the case of green and pink A. pisum, there appeared to be an inverse correlation between the number of aphids retained for parasite studies, and the percentage parasitism. The size of the aphid sample was largely governed by the number of aphids remaining on the plants, which suggests

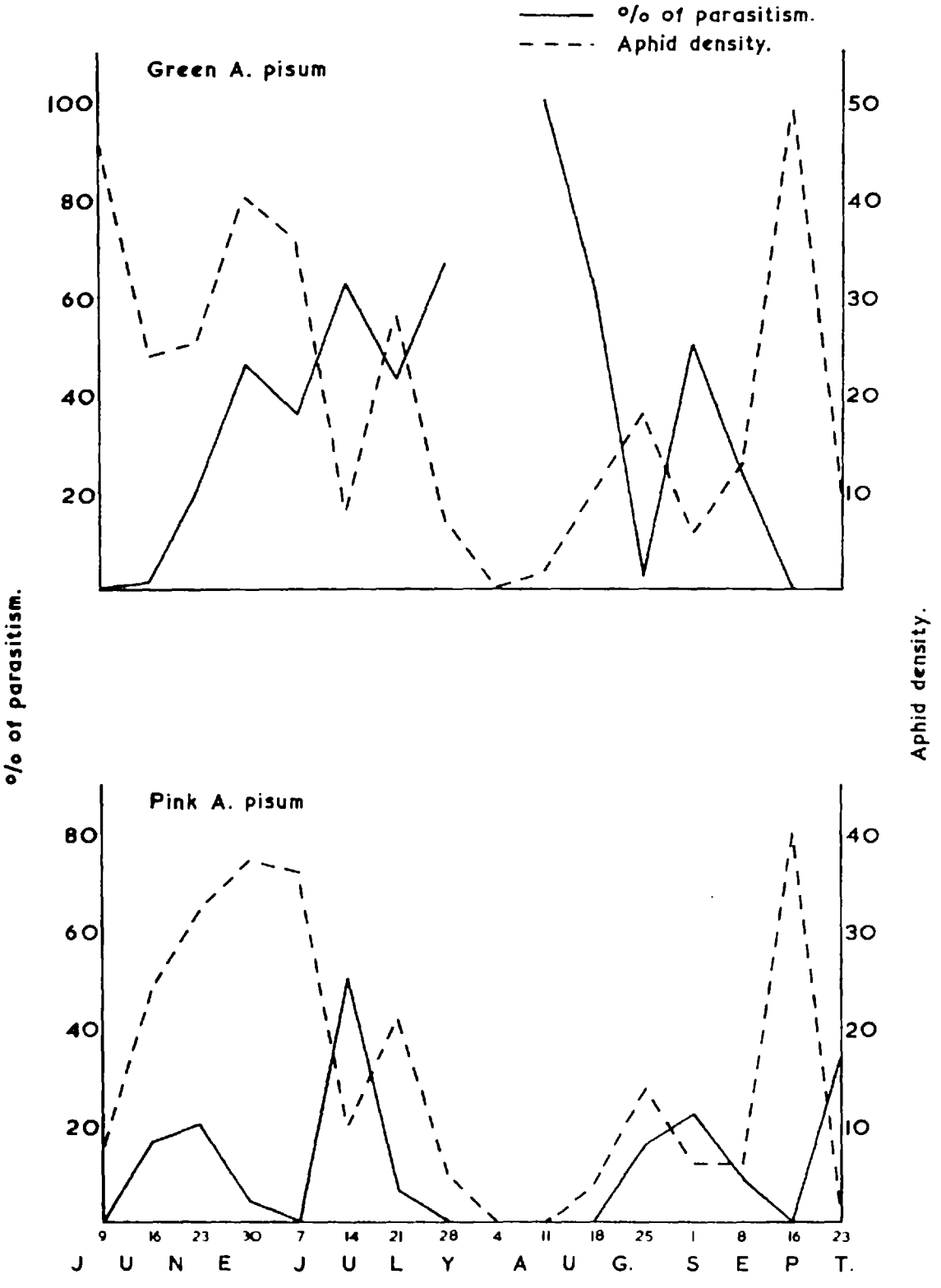
that there was also an inverse relationship between aphid density and percentage parasitism (Figure 29).

An inverse relationship between aphid density and percentage parasitism was also reported by Shiga (1968). He attributed it to the fact that the number of aphids which could be parasitised was limited therefore the percentage parasitism would depend on the extent to which the aphid population exceeded this level. This type of situation may well have occurred in 1970, and could partly have accounted for the fluctuation in the percentage parasitism from week to week but the question still remains as to why the aphid density did not remain at a consistently high level. Furthermore, although both biotypes of A. pisum were attacked by the same species of parasites, the percentage parasitism was almost invariably lower in the pink biotype, even when the aphid density was lower than that of the green biotype (Figure 29). It therefore seems likely that the decline in the aphid populations was due to harassment by the adult parasites which induced the aphids to leave the plants, and the increase in the percentage parasitism in certain weeks was due to the increased activity of adult parasites as well as to the smaller number of aphids available.

Tamaki et al. (1970) studied the behaviour of populations of A. pisum when exposed to the parasite, Aphidius smithi. They found that the aphid colonies were reduced by 50 - 60% within 24 hours of the adult parasites being released into the greenhouse and that the aphids dispersed randomly over the large seed trays used in the experiments. Subsequent experiments proved that the response of the aphids was due mainly to harassment by the parasites and not necessarily to oviposition. 27% of the aphids which left the plants were parasitised, as opposed to 13% of those which remained on the plants.

During an experiment on bird predation in 1970, pink A. pisum was

Figure 29 : Relationship between density of A. pisum and percentage parasitism at the end of each week


% of parasitism.
Aphid density.
Green A. pisum
100
80
60
40
20
50
40
30
20
10
% of parasitism.
Aphid density.
Pink A. pisum
80
60
40
20
40
30
20
10
9
16
23
30
7
14
21
28
4
11
18
25
1
8
16
23
J U N E J U L Y A U G. S E P T.

observed on one occasion to 'rain' from the plant when the colony was approached by an adult parasite. This biotype is known to be more sensitive to various external stimuli than the green biotype and to have a more strongly-developed escape response (Lowe and Taylor, 1964). This could account for the fact that parasitism was nearly always lower in the pink than in the green biotype, even when the aphid density of the pink biotype was lower.

Stary (1962, 1964 a, 1966) observed that 4th instar nymphs and adults of A. pisum generally dropped from the plant if attacked by parasites. The response was less marked in M. viciae, and A. fabae virtually ignored the parasites.

The fact that M. viciae populations declined in some weeks suggests that it may have been attacked by parasites. The low incidence of parasitism in this species may have been due to its relative unsuitability as a host. It is known to be toxic to certain invertebrate predators, and could conceivably be toxic to certain species of parasites as well.

These conclusions, particularly those concerning M. viciae, are largely based on circumstantial evidence and need to be proved by carefully controlled experiments in the laboratory and by observations on field populations. If the decline in the aphid populations were due to parasites, the importance of parasites has, in many cases, been greatly underestimated. There could be several important side-effects on A. pisum - and perhaps on other species of aphids - which are overlooked when only the percentage parasitism is taken into account.

(i) By inducing the aphids to leave the plants they promote aphid dispersal. This may be disadvantageous because uninfested plants are more likely to become infested. On the other hand, if parasites are specifically attracted to dense aphid colonies, the dispersive effect of

parasites might reduce the amount of economic injury to the plants.

(ii) The continual harassment of the aphids would have an adverse effect on the aphids themselves - by lowering the rate of development and reproduction (Tamaki et al. 1970).

(iii) Mortality among migrating aphids would probably be relatively high. Tamaki et al. reported that a high proportion of the aphids which left the plants crawled down into the vermiculite and died.

The 'knockdown' effect of birds was almost certainly underestimated in the experiment conducted with green A. pisum in 1970. The bean plants used in the experiment were small and even aphids feeding on the apices of the plants were generally within reach of birds perching on the wire mesh frame.

Dixon (1958) found that Drepanosiphum platanoides reacted to vibrations caused by birds by 'leaping' from the plants. A. pisum (particularly the pink biotype) and M. viciae reacted in a similar manner when the host plants were accidentally jarred during field counts in 1967 and 1968. It is therefore reasonable to suppose that vibration caused by birds hopping about on the plants would provoke a similar reaction.

Although this type of escape response might increase their chances of survival, frequent disturbance by birds would have an adverse effect on the rate of development and reproduction of the aphids.

The experiments conducted in 1970 confirmed that populations of pink and green A. pisum may suffer a high mortality due to bird predation but that A. fabae is not significantly affected by birds.

SECTION III: LABORATORY AND FIELD EXPERIMENTS TO DETERMINE THE EFFECT OF TEMPERATURE ON RATE OF DEVELOPMENT, FECUNDITY AND VARIOUS POPULATION GROWTH STATISTICS OF APHIDS ON BROAD BEANS

A. INTRODUCTION

Temperature is one of the most important factors affecting the rate of growth of aphid populations in that it determines the rate of development of the immature stages and the reproductive rate of the adults. In the field, the response to temperature is modified by other factors, such as the density of the aphids and the condition of the host plant. For this reason, most studies primarily concerned with temperature effects have been conducted under controlled conditions - usually at constant temperatures - in the laboratory.

One of the earliest investigations on the effect of temperature on the development of Acyrthosiphon pisum was that by Campbell (1926). He determined the approximate length of the nymphal instars in the field at different times of the year in relation to the mean daily temperature. A similar investigation was undertaken by Markkula (1963) who compared the rate of development of the red and green forms of A. pisum on red clover and peas in an insectary. He found the rate of development to be very similar in both biotypes and on both host plants.

Kenten (1955), Meier (1956) and Fox et al. (1967) determined the total nymphal period of A. pisum at constant temperatures, and Cartier (1960) determined the duration of individual instars on peas at 20°C.

The rate of development of Aphis fabae at a constant temperature of 20°C was ascertained by Banks and Macaulay (1964) in the course of their investigations on honeydew production. Müller (1966) determined the total nymphal period of the same species on leaf discs at seven different constant temperatures ranging from 8.8° - 28.2°C.

The theoretical threshold temperature of development has been estimated for certain aphid species. In most cases, calculations were

based on the assumption that the time-temperature curve approximates to a hyperbola (Lathrop, 1923) and that the relationship between rate of development and temperature is therefore linear (Bodenheimer and Swirski, 1957; Hughes, 1963; Müller, 1966).

Bodenheimer and Swirski stated that, in many aphid species, the rate of development is proportional to the amount by which the environmental temperature exceeds a threshold value. They expressed the relationship by the formula D (T-c) = K where D = development time, T = environmental temperature, c = threshold of development and K = thermal constant.

Hughes (1963) and Müller (1966) calculated the regression of rate of development on temperature and determined the developmental threshold by extrapolating the regression line to the point at which it intercepted the X (temperature) axis.

The inherent disadvantage of this method is that the development - velocity/temperature curve departs from linearity towards the upper and lower extremes of the temperature range (Andrewartha and Birch, 1954). Lamb's (1961) investigations on the development of Brevicoryne brassicae at fluctuating temperatures revealed that the effects of temperature were exponential even at moderate temperatures.

Despite its limitations, temperature - summation has been widely used in ecological research and Hughes (1963) based his studies on the population dynamics of B. brassicae in the field on a physiological time scale i.e. day-degrees above the estimated threshold of development for the species.

The temperature to which aphids are exposed during the developmental period affects the size of the aphids and hence their fecundity (Murdie, 1965, 1969 a). Although rate of development is higher at temperatures of 25°C than at 15° or 20°C, such high temperatures are generally detrimental

to aphid populations. Murdie found that populations of green A. pisum maintained at a constant temperature of 25°C died out after 3 generations. He also observed that the aphids were progressively smaller in successive generations, with a corresponding decrease in fecundity. Fecundity did not, however, appear to be affected if aphids were exposed to unfavourable temperatures for short periods.

The fecundity of green A. pisum has been determined by a number of investigators. Host plants used in the experiments include beans (Kenten, 1955; Lowe and Taylor, 1964; Murdie, 1965, 1969 b; Müller, 1968), peas (Harrington, 1941; Cartier, 1960; Markkula, 1963), lucerne (Dahms and Painter, 1940) and red clover (Markkula, 1963). Markkula attributed the discrepancies between the results of different investigators largely to host-plant effects. He found the fecundity of A. pisum to be considerably lower on peas than on red clover. Harrington (1941) reported that aphids were significantly more fecund on a susceptible variety than on a resistant variety of peas.

Relatively little is known about the fecundity of the pink biotype of A. pisum. Lowe and Taylor (1964) found it to be significantly more fecund than the green biotype on beans at 20°C. This was contrary to the findings of Markkula who reported populations of the pink biotype to be less fecund than the green on both peas and red clover.

The fecundity of A. fabae was determined at a constant temperature of 20°C by Banks and Macaulay (1964, 1970) and Müller (1968). Müller found that fecundity was higher on one-leaved plants with the excised stems in water than on whole plants growing in pots. Banks and Macaulay (1970) observed that 'slow-developers' were less fecund than 'fast-developers'.

Kennedy and Booth (1951) found that the rate of reproduction in A. fabae was affected by the feeding site of the aphids. They reproduced more

slowly on mature leaves than on young or early senescent leaves. A. similar effect was reported by Dixon (1966) for Drepanosiphum platanoides.

Very little has been published concerning the fecundity of Megoura viciae. In the course of his investigations on factors affecting form determination in this species, Lees (1959) noted that fecundity was considerably lower at 25° than at 15° or 20°. Müller (1968) determined the fecundity of M. viciae on a susceptible variety of beans (Vicia faba, variety Schlanstedter) at 20°C. He found that fecundity was relatively higher on excised beans (92.4 ± 24.4) than on whole plants (70.8 ± 12.6).

The rate of increase of an aphid population in the field is determined by the intrinsic rate of increase of the species and by restrictions imposed on the intrinsic rate by the environment (Barlow, 1962). Birch (1948) determined the intrinsic rate of increase for the grain weevil, Calandra oryzae and his method has since been applied to the study of aphid populations (Lamb, 1961; Barlow, 1962; Messenger, 1964).

Barlow constructed life tables for populations of Macrosiphum euphorbiae and Myzus persicae at five different constant temperatures. At temperatures between 5° and 25°C, the finite rate of increase of M. persicae was greater than that of M. euphorbiae. In the latter species, the highest rate of increase occurred at 20°, whereas in M. persicae, the peak capacity for increase occurred at 25°C.

Messenger (1964) studied populations of Therioaphis maculata and its parasite, Praon palitans at fluctuating temperatures in the laboratory and constructed life tables for each species.

Experiments described in this section are concerned with the effect of temperature on the rate of development, fecundity and intrinsic rate of increase of A. fabae, M. viciaeand the pink and green biotypes of A. pisum.

B. MATERIALS AND METHODS

1. Rate of Development

The duration of the four nymphal instars of Aphis fabae, Megoura viciae and the pink and green biotypes of Acyrthosiphon pisum was determined at constant temperatures of 15°C, 20°C and 25°C, and at fluctuating temperatures in the field.

The experimental aphids were reared in clip-on leaf cages on seedlings of Vicia faba (variety: The Sutton) growing in 5 inch pots. The leaf cages were similar to those used by Murdie (1965). They consisted of rings of perspex 2 cm. in diameter and 1 cm. high and each cage was provided with a tightly-fitting removable lid covered with Terylene muslin.

Potted seedlings used in the field experiments were placed on a table 30 inches high in the centre of the bean plot. During the first field experiment, temperatures were initially measured by means of thermocouples inserted into two leaf cages so that the tips of the thermocouples were in contact with the ventral surface of the leaves. The temperature recorder broke down soon after the experiment was started and temperature records from the meteorological site at Silwood had to be used to analyse the rate of development. Field temperatures during the second experiment were measured by means of two thermistors and recorded at 15-minute intervals by a Grant recorder. The thermistors were too large to be inserted into leaf cages but were positioned so that each was in contact with the ventral surface of a bean leaf.

At the beginning of each experiment, apterous adults were taken from the stock aphid cultures maintained at a constant temperature of 20°C and 16-hour photoperiod and were placed in leaf cages on the bean plants. Each species was introduced into at least 20 leaf cages. The pots were

immediately transferred to the appropriate temperature. (In the case of the field experiment, the pots were placed in position before the experiment commenced and the aphids were transferred from the constant temperature room to the field in the leaf cages).

The cages were examined at 2-hourly intervals. When an adult had reproduced, the cage was numbered, the time of birth noted, and the adult discarded. Adults which had not reproduced within 8 hours of the start of the experiment were discarded and the cages removed. The new-born aphids were left undisturbed until a few hours before they were *expected to moult, when 2-hourly inspections were recommenced. When an aphid had moulted, the time was noted and the exuvia removed. This procedure was repeated for each moult.

In the experiments conducted in constant temperature rooms, 2-hourly inspections were continued throughout the night with the aid of an electric lamp. The lamp was provided with a red light-bulb so that the aphids were disturbed as little as possible. In the field experiment, inspections were discontinued shortly before midnight and recommenced at about 7 a.m. the following morning. After dark, the aphids were examined by torchlight.

Each of the experiments at constant temperatures was confined to only one temperature, but the four aphid species/biotypes were generally studied simultaneously.

2. Fecundity and Longevity

a) Aphids which had been used in studies on the rate of development at constant temperatures were also used to determine the reproductive rate, total fecundity and longevity at the same temperatures (15°C, 20°C and 25°C).

* Pilot experiments were conducted before the main experiments at constant temperatures to determine the approximate duration of the instars.

The leaf cages in which the aphids were confined were generally examined once a day (except in the case of A. fabae and green A. pisum at 20°C, when they were examined twice a week) and the total number of nymphs recorded. When the number of nymphs in a cage exceeded 14 in the case of green A. pisum, pink A. pisum and M. viciae, and 29 in the case of A. fabae, the parent aphid was transferred to another leaf.

The adults were transferred by means of a Shuco-vac electrically-operated suction apparatus. Before being transferred, the aphids were induced to withdraw their stylets from the leaf, either by blowing gently onto them or, in the case of A. fabae, by prodding them with a small squirrel-hair brush. The plants were changed once a week, and regular inspections were continued until the adults had died.

b) Three additional experiments were conducted with pink A. pisum to determine whether fecundity at constant temperatures (15°C, 20° and 25°C) was affected by the temperature at which the experimental aphids and/or previous generations were reared. Different temperature combinations were used in each experiment:-

(i) Parents of the experimental aphids were taken from stock cultures which had been maintained for at least two weeks at the relevant temperature.

(ii) Parents of the experimental aphids were taken from a stock culture maintained at 20°C, but the aphids themselves were reared at the experimental temperature.

(iii) The experimental aphids (and previous generations) were reared at 20°C and were transferred to the experimental temperatures only when they had reached adulthood and were about to start reproducing.

The various temperature combinations are given in Table XXIX.

Table XXIX : Temperature combinations used in fecundity experiments with pink A. pisum

Experiment	T° at which stock culture was maintained	T° at which experimental aphids were reared	Temperature at which fecundity was determined
(i)	15°	15°	15°
	20°	20°	20°
	25°	25°	25°
(ii)	20°	15°	15°
	20°	20°	20°
	20°	25°	25°
(iii)	20°	20°	15°
	20°	20°	20°
	20°	20°	25°

At the start of each experiment, apterous adults were taken from the stock culture and placed on bean seedlings (Vicia faba, variety : The Sutton) growing in 3-inch plastic pots. Each pot contained one seedling, and only one adult was introduced onto each plant. The plants were enclosed in lamp-glass cages, the open ends of which were covered with Terylene muslin.

After the adults had reproduced they were discarded and all but one of the nymphs were removed. There were 9 or 10 replicates in each experiment.

After the nymphs had reached adulthood, their weekly fecundity was recorded, and the adults were transferred to fresh plants.

C. RESULTS

1. Rate of Development

a) Duration of nymphal instars at constant temperatures

Except in the case of Megoura viciae, the number of individuals at the start of each experiment varied between 9 and 21. M. viciae adults were slow to settle down in the leaf cages and the number of nymphs born during the specified period at the start of each experiment was consequently low, particularly in the experiments at 20°C and 25°C. These two experiments were later repeated. It was also necessary to repeat the experiment with pink A. pisum at 25°C because only four of the 4th instar nymphs were apterous. The high proportion of alate nymphs was presumably due to crowded conditions in the stock culture before the start of the experiment.

The mean durations of the nymphal instars at each of the constant temperatures are given in Table XXX. In the case of Aphis fabae, the figures given as the duration of the 1st and 2nd instars at each temperature are approximate values. 1st instar exuviae were sometimes overlooked, particularly when the aphids were examined at night by lamplight. The duration of the 1st instar was therefore estimated from the time when 50% of the aphids were observed to have moulted. The estimates of the duration of the 2nd instar were also based on this figure. If a significant proportion of the 1st instar exuviae had been missed, this method would result in the length of the 1st instar being overestimated and consequent underestimation of the duration of the 2nd instars. However, the figures given for the 1st and 2nd instars at 20°C are very similar to those obtained by Banks and Macaulay (1964) which were based on honeydew production, and are therefore probably reasonably accurate.

The first three instars were of approximately equal duration, although

Table XXX : Mean durations in hours (with standard deviations) of nymphal instars at constant temperatures

Aphis fabae

Temperature	1st Instar	2nd Instar	3rd Instar	4th Instar	Total
15°C	* 63	* 60	62.4 ± 4.1	85.1 ± 4.4	270.5
20°C	* 46	* 39	42.8 ± 3.7	50.3 ± 2.7	178.1
25°C	* 31	* 30	28.7 ± 2.7	38.1 ± 4.6	127.8

* Approximate values - See text

Megoura viciae

Temperature	1st Instar	2nd Instar	3rd Instar	4th Instar	Total
15°C	63.5 ± 2.5	66.3 ± 3.5	68.9 ± 3.7	97.0 ± 4.2	290.7
20°C (i)	45.6 ± 2.7	43.5 ± 4.6	47.9 ± 2.9	65.3 ± 3.3	202.3
20°C (ii)	52.0 ± 4.6	50.7 ± 3.4	55.8 ± 3.8	73.0 ± 3.9	231.5
25°C (i)	34.6 ± 3.5	32.9 ± 2.7	33.8 ± 1.1	47.3 ± 2.0	148.6
25°C (ii)	31.9 ± 1.4	33.0 ± 2.3	32.2 ± 1.9	42.2 ± 1.3	139.3

Green Biotype of Acyrthosiphon pisum

Temperature	1st Instar	2nd Instar	3rd Instar	4th Instar	Total
15°C (i)	60.1 ± 2.3	59.5 ± 2.2	61.1 ± 5.1	92.1 ± 5.6	272.8
15°C (ii)	61.7 ± 2.1	63.5 ± 2.1	70.2 ± 3.1	-	-
20°C	38.7 ± 2.7	41.2 ± 2.1	43.4 ± 2.1	59.5 ± 1.6	173.8
25°C	31.0 ± 2.8	28.7 ± 1.8	32.1 ± 1.5	45.1 ± 1.4	136.9

Table XXX : Continued

Pink Biotype of A. pisum

Temperature	1st Instar	2nd Instar	3rd Instar	4th Instar	Total
15°C	64.8 ± 2.5	61.7 ± 2.7	72.0 ± 3.5	97.8 ± 4.3	296.3
20°C	47.6 ± 2.6	44.2 ± 2.3	51.0 ± 1.9	68.7 ± 1.8	211.5
25°C (i)	31.6 ± 2.0	30.3 ± 1.3	35.5 ± 1.2	48.0 ± 2.9	145.4
25°C (ii)	30.6 ± 1.2	29.9 ± 1.6	33.6 ± 1.3	43.9 ± 1.4	138.0

the 3rd instar tended to be slightly longer, particularly in pink A. pisum. The 4th instar was considerably longer than the earlier instars - by about 45% in green and pink A. pisum, 40% in M. viciae and 28% in A. fabae (averaged over the three temperatures).

Pink A. pisum occasionally underwent five moults.

When an experiment was repeated, the durations of each of the instars in the second experiment sometimes differed by several hours from those in the first experiment. 't' tests were applied to the data to determine whether the differences between the two sets of figures were significant. Calculated 't' values for the paired data are given in Table XXXI.

Differences between each pair of experiments were not significant in the 1st instar but tended to become significant in the 3rd and/or 4th instars which were relatively longer. In the case of green A. pisum the duration of the 2nd instar also differed significantly in the two experiments. In this instance the instars were prolonged - and the differences therefore exaggerated - by the low temperature.

Leaf cages could only be attached to expanded leaves which normally tend to be avoided by A. fabae. Development may have been adversely

Table XXXI : Differences between the duration of instars when experiments were repeated

Instar	*Megoura viciae* : 20°C 't'	Degrees of freedom	Probability	*Megoura viciae* : 25°C 't'	Degrees of freedom	Probability
1st	-2.76	4, 6	0.1 - 0.02	1.99	8, 6	0.1 - 0.05
2nd	-2.40	3, 6	0.1 - 0.05	-0.07	6, 6	> 0.5
3rd	* -3.36	3, 5	0.05 - 0.02	1.60	5, 5	0.2 - 0.1
4th	-2.50	2, 4	0.2 - 0.05	** 4.79	5, 5	0.01 - 0.001

Instar	Green *A. pisum* : 15°C 't'	Degrees of freedom	Probability	Pink *A. pisum* : 25°C 't'	Degrees of freedom	Probability
1st	-1.8	13, 10	0.1 - 0.05	1.63	15, 13	0.2 - 0.1
2nd	** -4.4	13, 10	< 0.001	0.72	15, 13	0.5 - 0.4
3rd	** -5.2	13, 9	< 0.001	** 4.02	13, 13	0.01 - 0.001
4th	-	-	-	* 2.40	3, 12	0.1 - 0.02

* and ** denote significant values of 't'.

affected by confining aphids to relatively unsuitable leaves. Subsidiary experiments were therefore conducted to determine the total nymphal period of unconfined aphids (*A. fabae* and green *A. pisum*) at 20°C and 25°C. The aphids used in these experiments were offspring of adults which had already reproduced in leaf cages at the same temperature within the previous 4 hours. The results are compared with those obtained for aphids confined in leaf cages in Table XXXII.

At 25°C, the nymphal period of aphids in leaf cages was similar to that on whole plants. At 20°C, aphids confined in leaf cages took considerably longer to complete their development than those on whole plants. The difference was most marked in the case of *A. fabae*, where the

Table XXXII : Total nymphal period in hours of *caged and uncaged aphids

Temperature	Aphis fabae		Green A. pisum	
	In leaf cages	On whole plants	In leaf cages	On whole plants
20°C	177	155	182	167
25°C	127	127	136	132

* Cages referred to are leaf cages.

total nymphal period was 22 hours longer in leaf cages. These results suggest that mature leaves are relatively unsuitable for aphid development, and that aphids are likely to develop much faster on younger leaves at the apex of the plant.

b) Threshold temperature of development

The method devised by Hughes (1963) was used to calculate the threshold temperature of development for each of the aphid species/biotypes, based on the first two instars. The rate of nymphal development (i.e. the reciprocal of the duration in hours of each instar) was plotted against temperature, and the regression line calculated from the available data. The threshold temperature of development was then calculated for each instar from the appropriate regression equation (substituting $y = 0$), although it may be estimated graphically from the point at which the regression line intercepts the X axis (Figures 30 and 31). The threshold temperature of development (k) was taken as the mean of the values obtained for the 1st and 2nd instars (Table XXXIII).

In subsequent calculations, the temperature threshold of development (k) of A. fabae and green A. pisum will be taken as 5, and of M. viciae and pink A. pisum as 6. A value of $k = 5$ for A. fabae agrees with that

Figure 30 : Graphical determination of temperature threshold for nymphal development in A. fabae and M. viciae

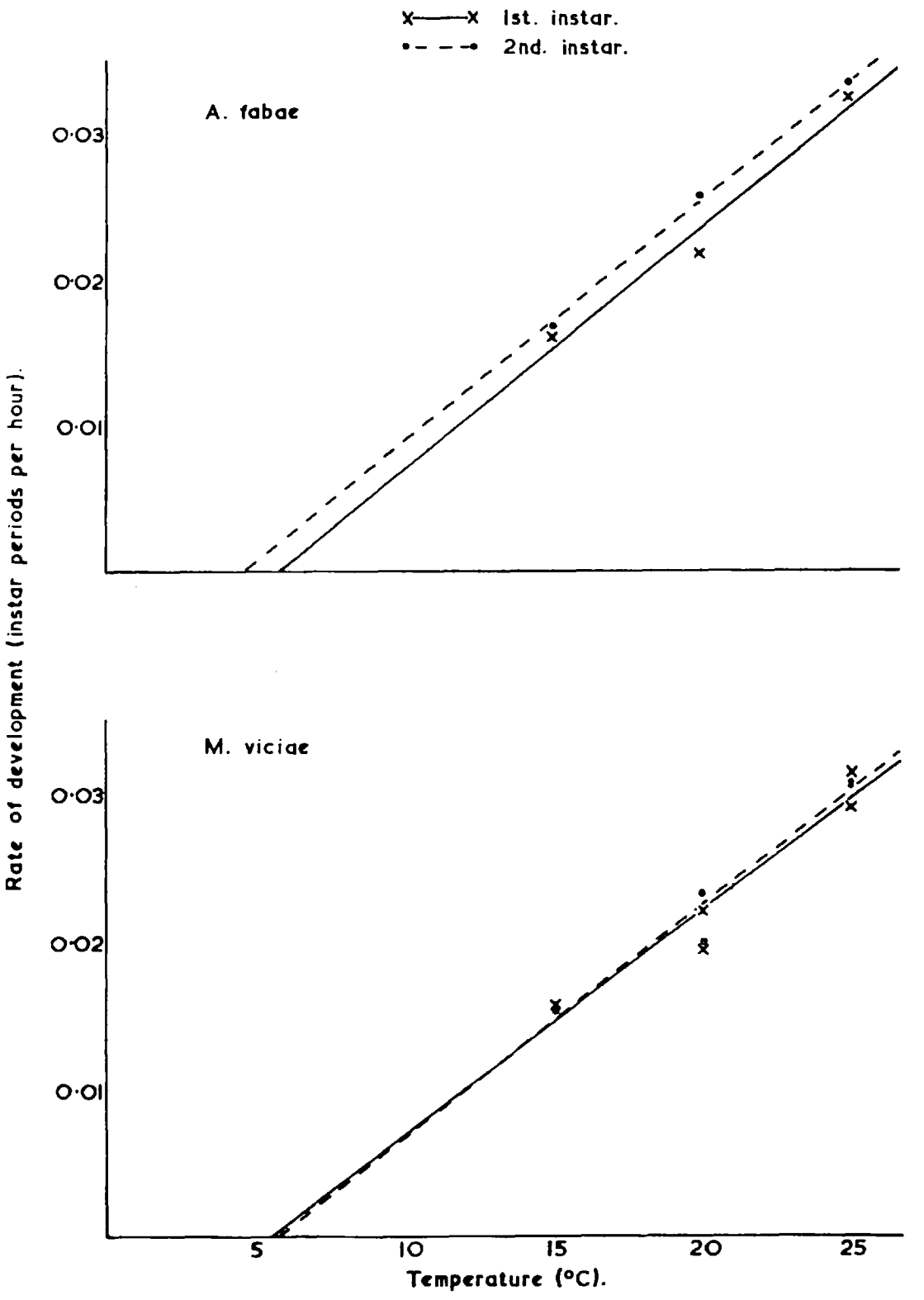

x——x 1st. instar.
•- - -• 2nd. instar.
A. fabae
0·03
0·02
0·01
M. viciae
0·03
0·02
0·01
5
10
15
20
25
Temperature (°C).
Rate of development (instar periods per hour).

Figure 31 : Graphical determination of the temperature threshold for nymphal development in the green and pink biotypes of A. pisum

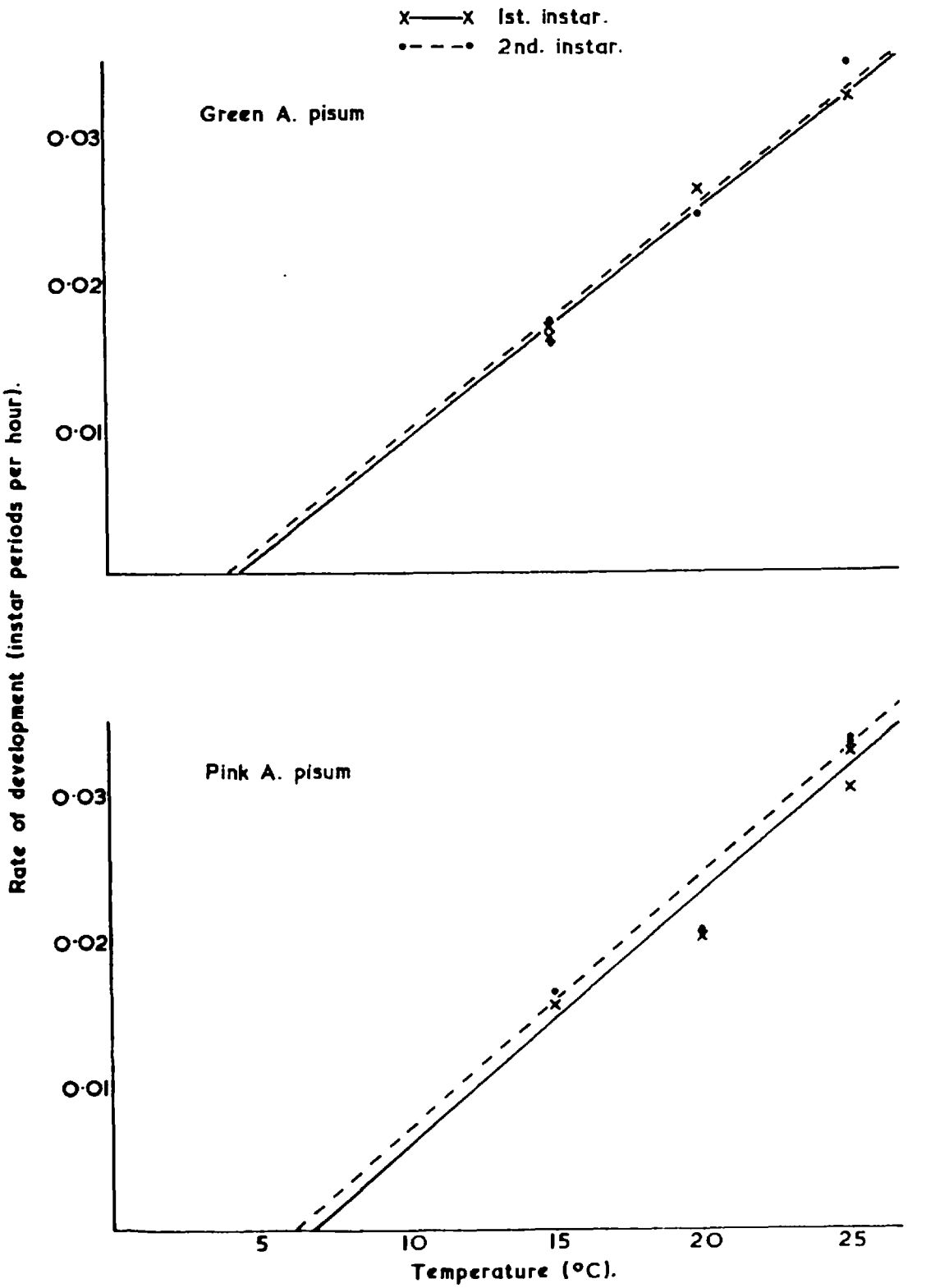

x——x 1st. instar.
•– – –• 2nd. instar.
Green A. pisum
0·03
0·02
0·01
Pink A. pisum
0·03
0·02
0·01
Rate of development (instar periods per hour).
5
10
15
20
25
Temperature (°C).

Table XXXIII : Regression equations and threshold temperature of development for each aphid species

Aphid species	1st Instar		2nd Instar		Mean Threshold T° for both instars
	Regression equation	Threshold T°	Regression equation	Threshold T°	
A. fabae	y= -0.0095+0.0016x	5.94	y= -0.0080+0.0017x	4.70	5.32
M. viciae	y= -0.0083+0.0015x	5.53	y= -0.0092+0.0016x	5.75	5.64
Green A. pisum	y= -0.0073+0.0016x	4.56	y= -0.0071+0.0016x	4.44	4.50
Pink A. pisum	y= -0.0115+0.0017x	6.76	y= -0.0106+0.0017x	6.24	6.50

determined by Müller (1966) for this species.

Thermal constants were calculated for each species (Table XXXIV) using the formula $K = D(\theta - k)$ where k = threshold temperature of development, θ = ambient temperature and D = time of development in hours or days (Bodenheimer and Swirski, 1957). Relative instar periods were also calculated taking the 1st instar as standard (Hughes, 1963).

The thermal constants were calculated separately for each experiment at each temperature. The figures given in Table XXXIV represent the mean values for each species over the three constant temperatures.

Differences between the species were most noticeable in the 4th instar. Whereas A. fabae required only about 789 hour - degrees to complete the 4th instar, M. viciae and the two biotypes of A. pisum each required approximately 900 hour - degrees.

Table XXXIV : Thermal constants for nymphal development of A. fabae, M. viciae, Green A. pisum and pink A. pisum at constant temperatures

Aphis fabae

	Thermal Constants				
	1st Instar	2nd Instar	3rd Instar	4th Instar	Total Nymphal Period
Hour-degrees above 5°C	647	595	613	789	2644
Day-degrees above 5°C	27.0	24.8	25.5	32.9	110.2
Instar periods	1.0	0.9	0.9	1.2	

Megoura viciae

	1st Instar	2nd Instar	3rd Instar	4th Instar	Total Nymphal Period
Hour-degrees above 6°C	640	634	665	902	2841
Day-degrees above 6°C	26.7	26.4	27.7	37.6	118.4
Instar periods	1.0	1.0	1.0	1.4	

Green A. pisum

	1st Instar	2nd Instar	3rd Instar	4th Instar	Total Nymphal Period
Hour-degrees above 5°C	605	606	652	905	2768
Day-degrees above 5°C	25.2	25.2	27.1	37.7	115.2
Instar periods	1.0	1.0	1.1	1.5	

Table XXXIV : Continued

Pink A. pisum

	1st Instar	2nd Instar	3rd Instar	4th Instar	Total Nymphal Period
Hour-degrees above 6°C	608	578	669	897	2752
Day-degrees above 6°C	25.3	24.1	27.9	37.4	114.7
Instar periods	1.0	1.0	1.1	1.5	

c) Rate of development at fluctuating temperatures in the field

Temperatures during the first field experiment were recorded by means of a thermograph in a Stevenson screen at the meteorological site at Silwood Park. During the second experiment, temperatures were measured by means of thermistors in contact with the ventral surface of bean leaves and were recorded at 15-minute intervals. The temperature records were used to calculate the mean temperature per hour throughout the experiments (26th August - 7th September for the first experiment, and 8th - 25th September for the second experiment). The effective temperature ($\theta - k$) was then determined, and the cumulative totals recorded, for each hour during the experiments. This involved two separate sets of calculations in each case, using $k = 5$ for A. fabae and green A. pisum, and $k = 6$ for M. viciae and pink A. pisum.

The duration of each instar (in hour-degrees) was then determined for each of the aphids by subtracting the accumulated hour-degrees at the estimated time of birth or of moulting from the value recorded for the subsequent moult. Mean durations and standard deviations were calculated from the individual observations for each species. The results are given in Table XXXV. As before, the duration of the 1st and 2nd instars of A.

Table XXXV : Mean durations (with standard deviations) of nymphal instars at fluctuating temperatures in the field

	EXPERIMENT I				
	1st Instar	2nd Instar	3rd Instar	4th Instar	Total
Aphis fabae					
Hour-degrees above 5°C	644	606	644.50 ± 62.04	681.75 ± 40.60	2576
Day- degrees " "	26.8	25.3	26.8	28.4	107.3
Instar periods	1.0	0.9	1.0	1.1	
Megoura viciae					
Hour-degrees above 6°C	601.50 ± 40.31	601.50 ± 43.13	628.00 ± 60.81	-	-
Day- degrees " "	25.1	25.1	26.2	-	-
Instar periods	1.0	1.0	1.0	-	
Green *A. pisum*					
Hour-degrees above 5°C	632.00 ± 26.60	567.63 ± 32.24	618.75 ± 21.75	775.25 ± 43.09	2594
Day- degrees " "	26.3	23.7	25.8	32.3	108.2
Instar periods	1.0	0.9	0.9	1.2	
Pink *A. pisum*					
Hour-degrees above 6°C	583.64 ± 24.19	559.18 ± 41.35	588.00 ± 74.02	760.80 ± 39.13	2492
Day- degrees " "	24.3	23.3	24.5	31.7	103.8
Instar periods	1.0	1.0	1.0	1.3	

Table XXXV : Continued

	EXPERIMENT II				
	1st Instar	2nd Inster	3rd Instar	4th Instar	Total
Aphis fabae					
Hour-degrees above 5°C	703	508	608.50 ± 82.48	677.20 ± 53.51	2497
Day- degrees " "	29.3	21.2	25.4	28.2	104.1
Instar periods	1.0	0.7	0.9	1.0	
Megoura viciae					
Hour-degrees above 6°C	633.81 ± 47.62	541.81 ± 68.14	660.13 ± 30.48	753.69 ± 42.18	2589
Day- degrees " "	26.4	22.6	27.5	31.4	107.9
Instar periods	1.0	0.9	1.0	1.2	
Green A. pisum					
Hour-degrees above 5°C	568.57 ± 39.75	516.31 ± 34.83	608.38 ± 47.49	874.45 ± 45.01	2567
Day- degrees " "	23.7	21.5	25.3	36.4	106.9
Instar periods	1.0	0.9	1.1	1.5	
Pink A. pisum					
Hour-degrees above 6°C	555.00 ± 43.21	425.57 ± 16.47	537.36 ± 38.50	732.29 ± 46.40	2250
Day- degrees " "	23.1	17.8	22.4	30.5	93.8
Instar periods	1.0	0.9	1.0	1.2	

fabae was estimated from the time (physiological time in this instance) when 50% of the nymphs were observed to have moulted.

The total nymphal period, measured on a physiological time scale (in hour-degrees) was invariably shorter when the aphids were exposed to fluctuating temperatures in the field (particularly in Experiment II) than when they were reared at constant temperatures in the laboratory.

The most likely explanation is that, during the field experiments, night temperatures often fell to within a few degrees of - and occasionally even below - the theoretical threshold of development of the species. At these low temperatures, the development velocity/temperature curve would presumably have deviated from linearity to a marked degree. Consequently, the amount of development, based on the summation of hour-degrees, would be underestimated.

The relative lengths of individual instars (i.e. instar periods) in the field experiments frequently differed from those at constant temperatures. Instars which were of relatively shorter duration in the field, for example the 2nd instar of all four species/biotypes in Experiment II, almost invariably coincided with periods when night temperatures fell to a very low level (5°C in this instance) and remained low for several hours. Conversely, the 4th instar of green A. pisum in Experiment II coincided with a period when diurnal temperatures rose above 25°C on two consecutive days. Temperatures of this magnitude are towards the upper limit of the temperature range for A. pisum (Murdie, 1965; 1969 a) and development would consequently have been overestimated.

2. Fecundity

a) Fecundity of aphids which were reared in leaf cages at the temperature at which fecundity was determined

Aphids used in these experiments were the offspring of apterous adults taken from the stock culture maintained at 20°C. The results are summarised in Table XXXVI.

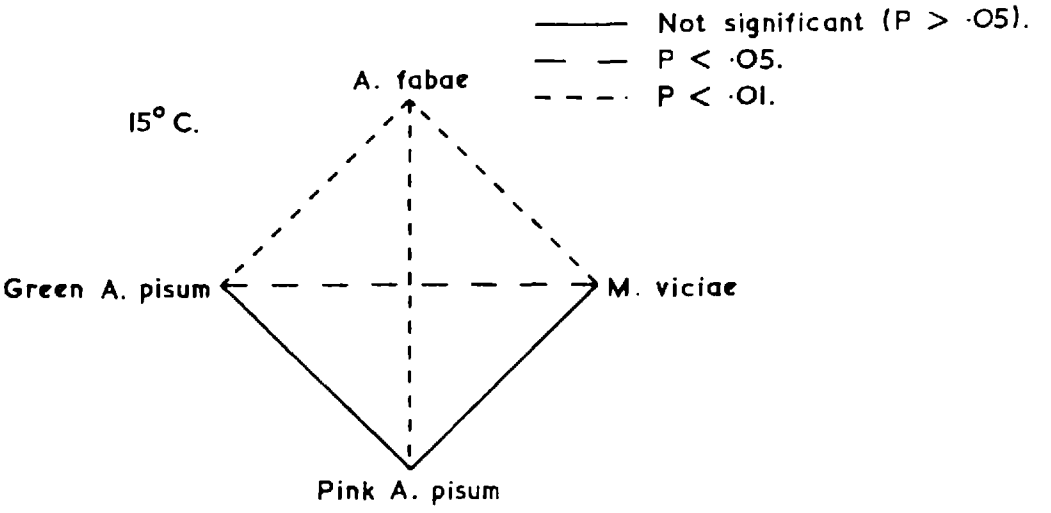
Table XXXVI : Mean fecundities (with standard deviations) of aphids in leaf cages at constant temperatures of 15°, 20° and 25°C.

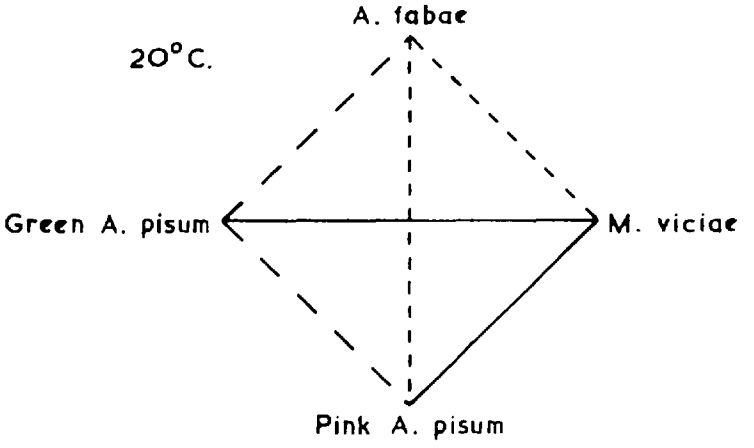
Species		Temperature 15°	20°	25°
A. fabae	Mean Range	50.75 ± 15.29 25 - 70	67.88 ± 23.72 13 - 88	72.13 ± 25.07 18 - 93
M. viciae	Mean Range	115.38 ± 11.17 94 - 131	101.09 ± 21.85 55 - 127	98.79 ± 23.33 27 - 119
Green A. pisum	Mean Range	91.50 ± 14.41 71 - 114	96.06 ± 17.81 38 - 115	85.69 ± 15.10 51 - 102
Pink A. pisum	Mean Range	94.14 ± 26.34 42 - 116	108.56 ± 5.78 97 - 115	100.94 ± 10.96 79 - 115

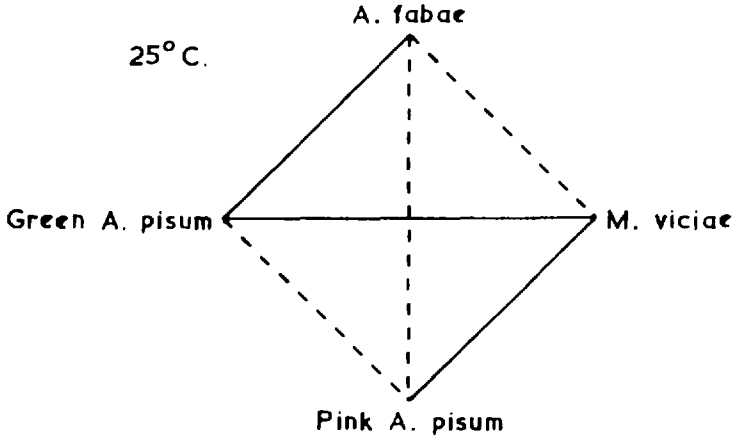
The fecundities were compared by Students 't'. Temperature did not significantly affect the fecundity of A. fabae, green A. pisum or pink A. pisum, but M. viciae was significantly less fecund at 25°C than at 15°C ($P < .05$). There was a general tendency for fecundity to be lower at 25°C than at 20°C, except in the case of A. fabae where it tended to increase with increasing temperature.

The fecundities of the four species/biotypes at each temperature were also compared by Student's 't'. The results are presented diagramatically in Figure 32. A. fabae was significantly less fecund than M. viciae and

Figure 32 : Significance of the differences between fecundities of the four species/biotypes at each temperature


Not significant (P > ·05).
P < ·05.
P < ·01.
15° C.
A. fabae
Green A. pisum
M. viciae
Pink A. pisum


20° C.
A. fabae
Green A. pisum
M. viciae
Pink A. pisum


25° C.
A. fabae
Green A. pisum
M. viciae
Pink A. pisum

pink A. pisum at all three temperatures ($P < .01$). The differences between A. fabae and green A. pisum tended to become less significant with increasing temperature, and those between green A. pisum and pink A. pisum to become more significant with increasing temperature. The fecundity of M. viciae did not differ significantly from that of pink A. pisum at any of the three temperatures.

At 25°C, the nymphs sometimes died soon after birth with their appendages still adhering to the sides of their bodies. Mortality was highest in green A. pisum where 6.2% of the nymphs died in this manner. The other species/biotypes were also affected but mortality was less than 1% in each case. Moribund nymphs were occasionally born at 15° and 20°C but usually towards the end of the reproductive period.

A supplementary experiment was conducted to determine the fecundity of A. fabae and green A. pisum at 20°C when the aphids were not confined in leaf cages. The fecundities are compared with those of aphids in leaf cages in Table XXXVII.

Table XXXVII : Fecundity of A. fabae and green A. pisum in leaf cages and on whole plants at 20°C

	In leaf cages	On whole plants
A. fabae	67.88 ± 23.72	89.50 ± 17.55
Green A. pisum	96.06 ± 17.81	97.00 ± 6.48

The fecundity of A. fabae was significantly lower in leaf cages than on whole plants ($P < .05$). In the case of green A. pisum, however, the fecundity of aphids in leaf cages was very similar to that of the aphids on whole plants.

b) The effect of rearing temperature on the fecundity of pink A. pisum ('Silwood Strain') at 15°, 20° and 25° Centigrade

The treatments and results are summarised in Table XXXVIII.

In all three experiments, fecundity was significantly lower at 25° than at 15° or 20°C ($P < .01$ in experiments I and II; $P < .05$ in experiment III). Differences between fecundity at 15° and 20° were not significant.

Fecundity at each temperature was significantly affected by the temperature at which the experimental aphids were reared, but not by the temperature to which they were exposed during the reproductive period.

At 15°, fecundity was significantly higher when the aphids were reared at 20° than when they were reared at 15° ($P < .05$).

Fecundity at 20° should have been virtually the same in all three experiments but in fact was significantly lower in experiment I than in experiment III ($P < .05$). Differences between I and II and II and III were not significant.

Fecundity at 25° was significantly higher when the aphids were reared at 20° than when they were reared at 25° ($P < .001$), but the temperature at which the previous generation had been reared did not significantly affect the results.

Temperature treatments to which the aphids were exposed in experiment II were identical to those to which aphids in leaf cages were subjected (See previous sub-section). The two sets of data are compared in Table XXXIX.

Fecundity at 15° and 20° was very similar in both cases but, at 25°, it was significantly higher in the leaf cage experiment ('Rothamsted strain'). The only conceivable explanation is that the 'Silwood strain' of

Table XXXVIII : Fecundity of pink A. pisum reared at various temperatures

Experiment	T° at which previous generation(s) reared	T° at which experimental aphids reared	T° at which fecundity was determined	Mean fecundity (with std. deviation)	Range
I	15°	15°	15°	104.44 ± 6.67	97 - 116
	20°	20°	20°	96.44 ± 11.94	76 - 110
	25°	25°	25°	27.11 ± 20.12	4 - 58
II	20°	15°	15°	9[illegible].20 ± 20.65	52 - 117
	20°	20°	20°	111.90 ± 15.06	81 - 128
	20°	25°	25°	[illegible]2.50 ± 19.48	1 - 54
III	20°	20°	15°	117.70 ± 6.88	111 - 132
	20°	20°	20°	112.00 ± 13.39	87 - 126
	20°	20°	25°	84.90 ± 10.02	68 - 101

Table XXXIX : Fecundity of pink A. pisum reared at the experimental temperature in leaf cages and on whole plants

Temperature	Fecundity	
	Leaf cages (Rothamsted strain)	Whole plants (Silwood strain)
15°	94.14 ± 26.34	99.20 ± 20.65
20°	108.56 ± 5.78	111.90 ± 15.06
25°	100.94 ± 10.96	22.50 ± 19.48

pink A. pisum was more sensitive to high temperatures than the 'Rothamsted strain'. The stock culture of the 'Silwood strain' in the greenhouse suffered a high mortality when temperatures rose to a high level and eventually died out completely. Under the same conditions, the 'Rothamsted strain' was affected to only a minor extent and appeared to be less susceptible to heat injury.

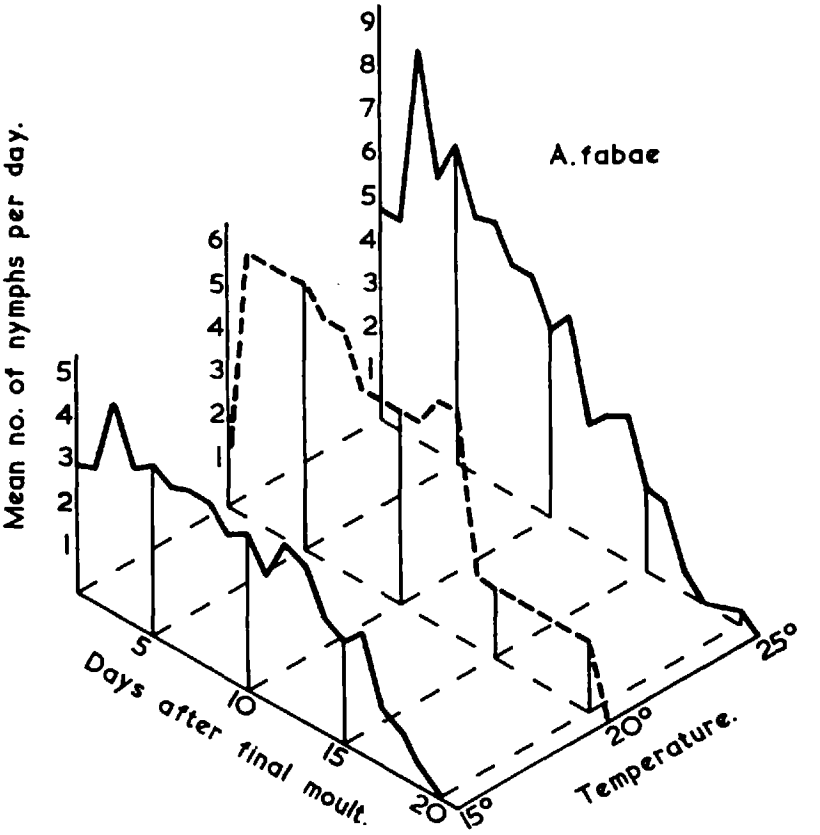
c) Reproductive rate of aphids in leaf cages

The period between the final moult and the commencement of reproduction (the pre-reproductive period) was invariably shorter in A. fabae than in the other species (Figure 33 and 34). In each species, an increase in temperature resulted in a decrease in the duration of the pre-reproductive period (Table XL).

The length of the reproductive period was similarly affected by temperature, except in the case of A. fabae where reproduction ceased about 20 days after the final moult at all three temperatures (Figure 33).

At 15°C, the daily reproductive rate was relatively low and there were no pronounced peaks. The reproductive rate decreased gradually towards the end of the reproductive period.

Figure 33 : Mean daily reproductive rate of A. fabae and M. viciae at constant temperatures of 15°, 20° and 25° Centigrade


A. fabae
Mean no. of nymphs per day.
Days after final moult.
Temperature.
15°
20°
25°

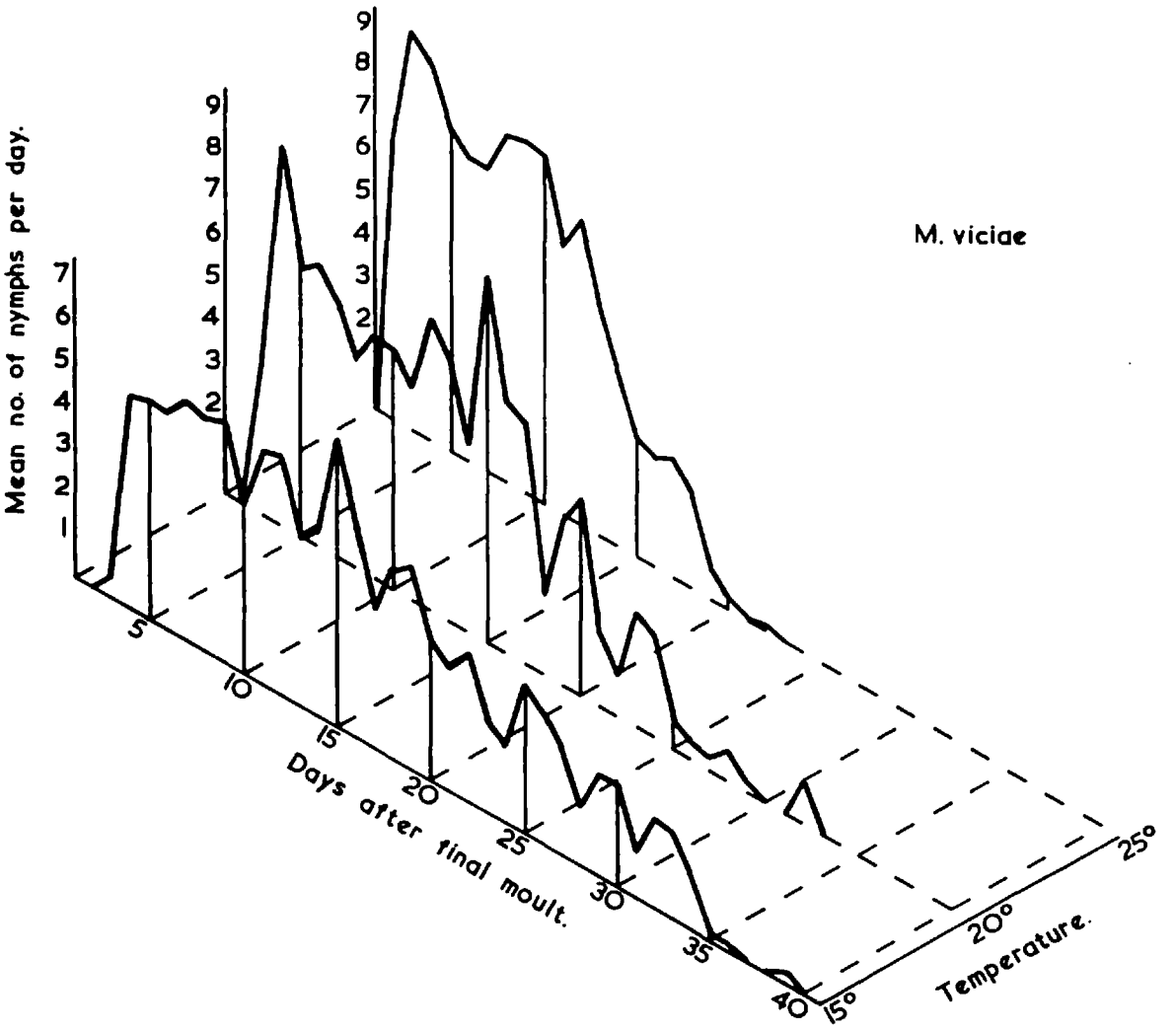
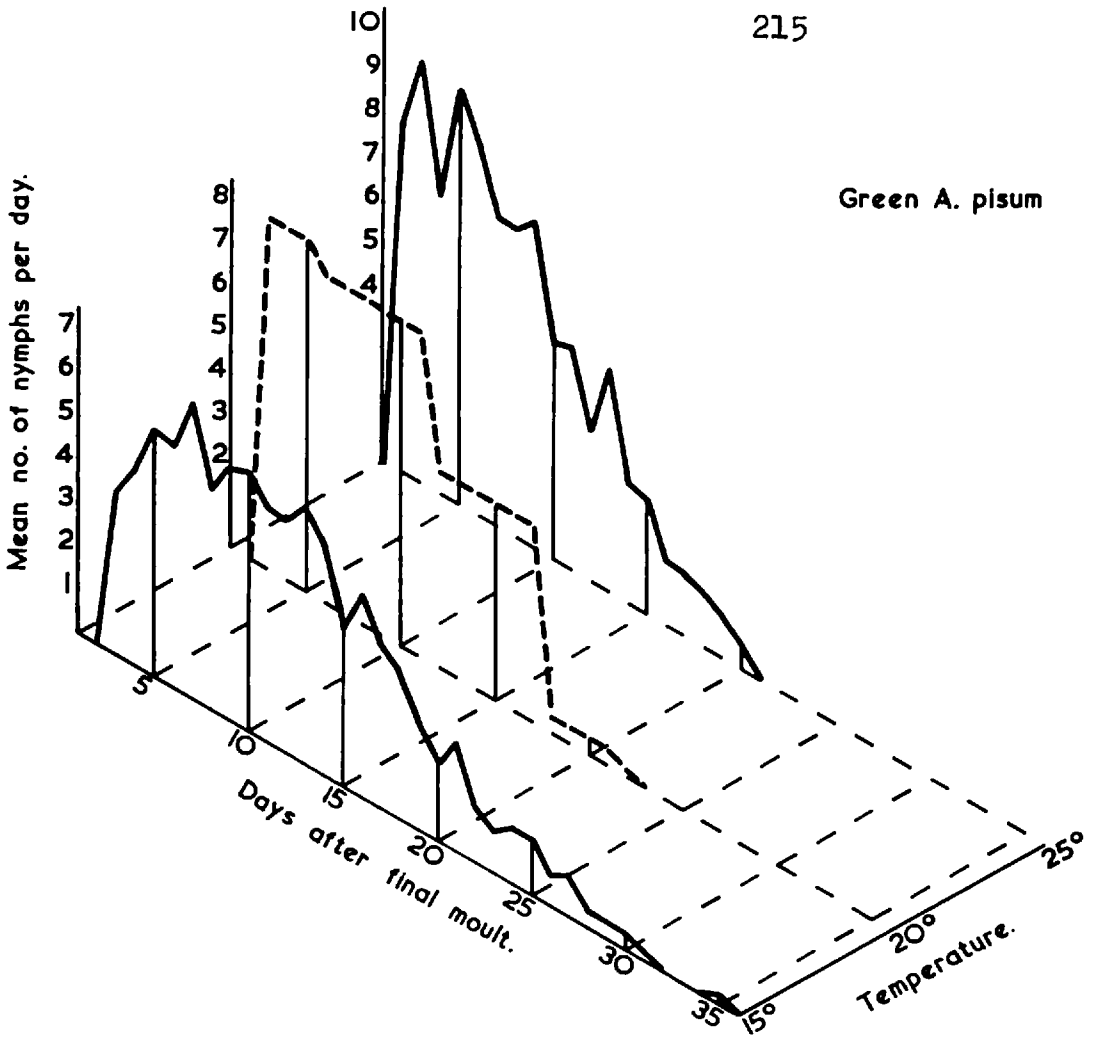

M. viciae
Mean no. of nymphs per day.
Days after final moult.
Temperature.
15°
20°
25°

Figure 34 : Mean daily reproductive rate of the green and pink biotypes of A. pisum at constant temperatures of 15°, 20° and 25° Centigrade


Green A. pisum
Mean no. of nymphs per day.
Days after final moult.
Temperature.
15°
20°
25°

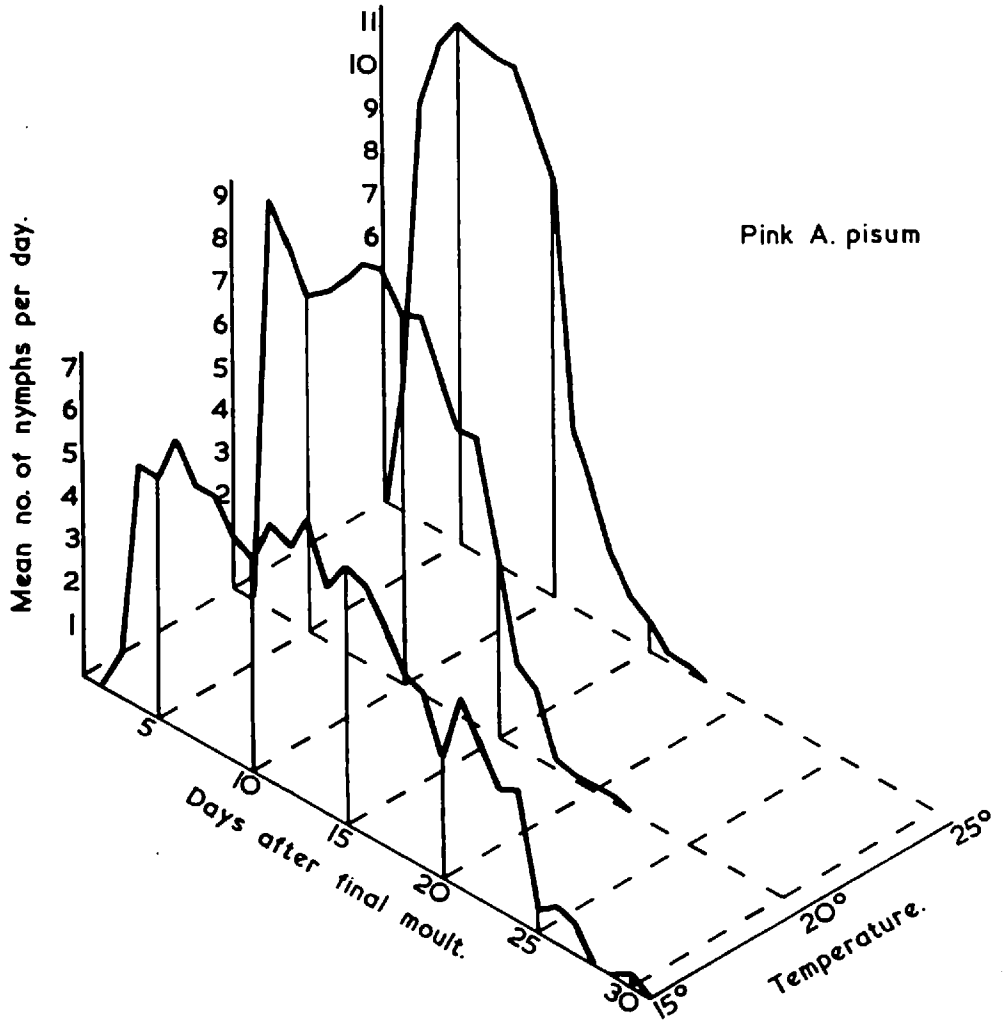

Pink A. pisum
Mean no. of nymphs per day.
Days after final moult.
Temperature.
15°
20°
25°

Table XL : Approximate length of the pre-reproductive period at 15°, 20° and 25°C

Species	Temperature		
	15°	20°	25°
A. fabae	20 - 24 hours	12 hours	8 hours
M. viciae	60 "	48 "	30 "
Green A. pisum	60 "	48 "	28 "
Pink A. pisum	60 "	48 "	25 "

At higher temperatures the peak reproductive rate occurred within five days of the final moult. The peak was more pronounced at 25° than at 20°, and the decline was correspondingly more rapid at the higher temperature.

The highest reproductive rate was recorded for pink A. pisum but the reproductive period was relatively shorter in this biotype than in M. viciae or the green biotype of A. pisum, particularly at 25°. At this temperature, there was a sharp decline in the reproductive rate after the 10th day, and reproduction had ceased by the 18th day after the final moult.

The transfer of adults to new leaves invariably resulted in a decline in reproduction during the following 24 hours. Most adults of a particular species were transferred on the same day and this largely accounted for fluctuations in the daily reproductive rate.

3. Determination of intrinsic and finite rates of increase and other population growth statistics

Life tables were constructed for each species at constant temperatures of 15°, 20° and 25°C by determining for each age interval (1 week):-

(i) The fraction of the initial number of aphids still alive at the mid-point of each age interval (lx);

(ii) The mean number of progeny produced per female during the week in question (mx). This value was computed by summing the daily reproductive rates for the relevant week.

The life tables are presented graphically in Figure 35.

For each life table, the following statistics were determined:-

a) The gross reproductive rate, G.R.R., calculated as Σ mx.

b) The net reproductive rate, R_o, measured as offspring per adult per generation. $R_o = \Sigma$ lx. mx.

c) The intrinsic rate of increase, r_m, measured as nymphs per adult per week. This value was calculated from the formula Σe^{7-rx} lx. mx = e^7 (Birch, 1948). Trial values for r were substituted in the equation and the true r_m was determined graphically by plotting the trial r_m's against the respective values for Σe^{7-rx} lx. mx (Southwood, 1966).

d) The finite rate of natural increase, λ, which is the number of times the population increases per week $\lambda = e^{r_m}$.

e) The generation time, T, calculated as $T = \frac{\log_e R_o}{r_m}$

The various population growth statistics for each species/biotype at each temperature are given in Table XLI.

Figure 35 : Survival rates and age-specific fecundity rates at constant temperatures of 15°, 20° and 25° Centigrade

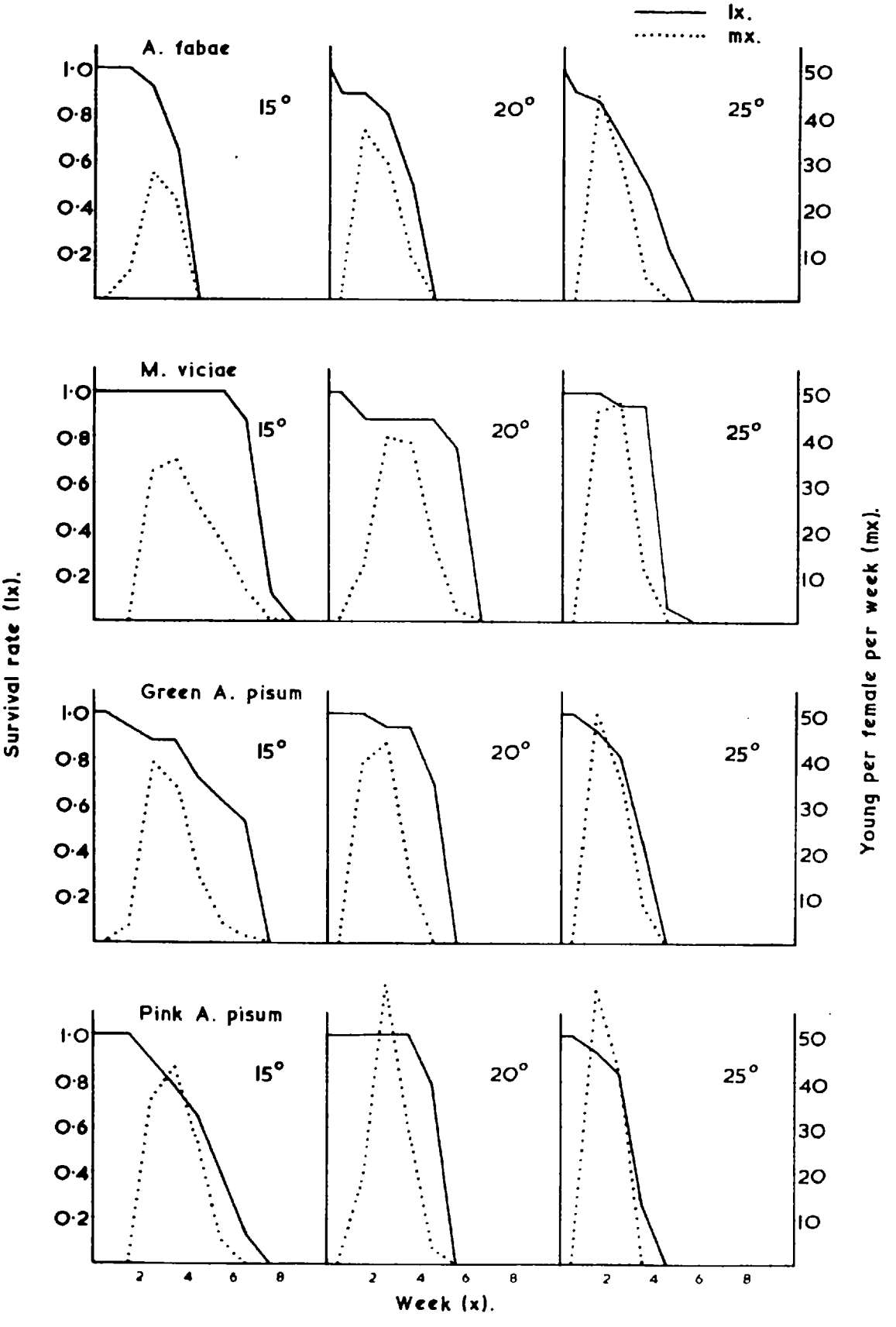

lx.
mx.
A. fabae
M. viciae
Green A. pisum
Pink A. pisum
15°
20°
25°
1·0
0·8
0·6
0·4
0·2
50
40
30
20
10
2
4
6
8
Survival rate (lx).
Young per female per week (mx).
Week (x).

Table XLI : Population growth statistics as affected by rearing temperature

	Aphis fabae			Megoura viciae			Green A. pisum			Pink A. pisum		
	15°C	20°	25°	15°	20°	25°	15°	20°	25°	15°	20°	25°
G.R.R. (♀/♀)	57.56	75.74	76.82	115.93	111.18	105.84	95.37	97.45	95.06	108.09	108.25	102.33
R_o (♀/♀)	44.97	61.06	59.97	114.82	97.50	102.20	80.63	93.94	78.63	82.02	108.17	90.91
r_m (♀/♀/week)	1.62	2.37	2.45	1.49	1.89	2.61	1.63	2.51	2.59	1.47	2.16	2.71
λ (♀/♀/week)	5.05	10.72	11.62	4.44	6.62	13.63	5.10	12.34	13.37	4.35	8.67	15.07
T (weeks)	2.36	1.73	1.67	3.18	2.42	1.77	2.69	1.81	1.69	3.00	2.17	1.66

a) Gross reproductive rate (G.R.R.)

In the case of A. fabae, the gross reproductive rate increased with increasing temperature, the highest value being obtained at 25°. In the other species, however, G.R.R. was lower at 25° than at 15° or 20°.

b) Net reproductive rate (R_o)

This value will only approximate to G.R.R. if the survival rate remains high throughout most of the reproductive period. In A. fabae and both biotypes of A. pisum, the highest values for R_o occurred at 20°. In M. viciae, R_o was highest at 15° because the survival rate was maximal (1.00) throughout most of the reproductive period.

c) Intrinsic rate of increase (r_m)

In all four species/biotypes, the value of r_m increased with increasing temperature between 15° and 25°C. At 15° and 20°, r_m was greater in A. fabae and green A. pisum than in the pink biotype and M. viciae. In the case of A. fabae, the relatively high rate of increase at these temperatures was mainly due to the short duration of the 4th instar and of the pre-reproductive period. Although the duration of the 4th instar and pre-reproductive period was relatively longer in green A. pisum, this was compensated for by a higher reproductive rate than that of A. fabae (Figures 33 and 34).

At 25°, r_m was highest in pink A. pisum and M. viciae. In the case of pink A. pisum, the high value of r_m was due to a high survival rate, coupled with a very high reproductive rate, during the first two weeks of larviposition. The reproductive rate was initially slightly lower in M. viciae than in green A. pisum, but this was offset by a higher survival rate in the former species.

d) Finite rate of increase (λ)

This value is derived from the intrinsic rate of increase and

followed a similar trend to that already described for r_m.

e) Generation time (T)

This represents the mean time (in weeks) elapsing between birth of the experimental aphids and the birth of their offspring. It is largely dependent on the rate of development and on the length of the pre-reproductive period of the adults, but is also affected by the rate of reproduction and the length of the reproductive period. The value of T for each species decreased with increasing temperature between 15° and 25°. At all temperatures, T was greatest in M. viciae > pink A. pisum > green A. pisum > A. fabae.

f) Longevity

The longevity of each species at each temperature is depicted as the survival rate (lx) in Figure 35. Survival rates were determined by expressing the number of females alive at the mid-point of each week as a fraction of the original number of aphids in each experiment.

The longevity of A. fabae did not appear to be greatly affected by temperature. In the other species, however, longevity decreased with increasing temperature. M. viciae had the highest survival rate at all three temperatures.

D. DISCUSSION

The duration of the total nymphal period, on a physiological time-scale, was generally very much shorter in the two field experiments (Table XXXV) than at constant temperatures in the laboratory (Table XXXIV). This was mainly due to the fact that temperatures at the lower end of the developmental range accounted for an appreciable proportion of the summation of hour-degrees, and rate of development was consequently underestimated.

Rate of development might also have been affected by the condition of the host plants. Although the bean seedlings were virtually identical at the start of the experiments, those in the field appeared to grow more vigorously than those in the constant environment rooms where light was provided by means of fluorescent tubes. The light intensity was undoubtedly lower under these conditions. Plants at 15° tended to become 'leathery'.

The relative lengths of individual instars were fairly consistent at the three constant temperatures but not at fluctuating temperatures in the field. This was mainly due to variation in temperature from day to day. Instars which were of relatively shorter duration in the field than at constant temperatures (on a physiological time-scale) invariably coincided with periods when night temperatures fell to a low level.

Another factor which may have influenced the relative lengths of individual instars in the field was the almost complete cessation of moulting between 11 p.m. at night and 7 a.m. the following morning, even when night temperatures remained several degrees above the theoretical threshold for development. When moulting resumed, a high proportion of aphids frequently moulted within a period of two hours. This suggests that there is a moulting threshold which may be governed by temperature. In

this case, the threshold temperature for moulting must be higher than that for development. Light can be eliminated as a possible factor because moulting continued throughout the night at constant temperatures.

Discrepancies between results at constant and fluctuating temperatures raise considerable doubt as to the feasibility of using summation of hour-degrees to predict the rate of increase of aphid populations in the field. Closer agreement might have been obtained if the field experiments had been conducted in June or July when night temperatures were relatively mild. On the other hand, prolonged periods at high temperatures would result in the rate of development being overestimated. Even in September, the temperature rose above 25° on two consecutive days and remained high for several hours. The likelihood of the temperature remaining within the intermediate range for development, where the relationship between development-velocity and temperature is virtually linear, therefore seems remote. At widely fluctuating temperatures, estimates of population growth based on a logistic curve would probably be far more accurate than those based on the summation of hour-degrees.

The optimum temperature for fecundity varied in the different species - 15° for M. viciae, 20° for both biotypes of A. pisum and 25° for A. fabae. In the case of A. fabae, the increase in fecundity at higher temperatures may have been partly due to an indirect temperature effect through the host plant. At 20°, rate of development was retarded when the aphids were confined in leaf cages on mature leaves and fecundity was also lower. At 25°, however, the total nymphal period of aphids confined in leaf cages was similar to that of aphids on whole plants. High temperatures may possibly have caused premature senescence of the leaves and rendered them more suitable for aphid development and reproduction.

Although the fecundity of the other species in leaf cages was not significantly lower at 25° than at 20°, the higher temperature was

obviously less favourable and the aphids, especially green A. pisum showed some evidence of heat injury.

The 'Silwood strain' of pink A. pisum, which was used in experiments to determine the effect of rearing temperature on fecundity, appeared to be extremely sensitive to high temperatures. The fecundity of the aphids was significantly lower at 25° than at lower temperatures, even when the aphids were reared at 20° and exposed to a temperature of 25° only during the reproductive period.

The intrinsic rate of increase at the two lower temperatures (15° and 20°) was primarily determined by the length of the developmental and pre-reproductive periods of the aphids. At these temperatures, M. viciae and pink A. pisum underwent the final moult approximately one day later than A. fabae and green A. pisum and the values of r_m were consequently higher in the latter species even though their survival rate, reproductive rate and total fecundity were lower than those of M. viciae and pink A. pisum.

At 25°, the rate of development was relatively high in all four species/biotypes and the intrinsic rate of increase was significantly affected by the reproductive rate of the species, particularly during the first two weeks of the reproductive period. Values of r_m for A. fabae and green A. pisum at this temperature were therefore lower than those for M. viciae and pink A. pisum.

The intrinsic rate of increase was undoubtedly underestimated at 15° and 20° - at least in A. fabae and green A. pisum - because development was retarded by confining the aphids on leaves which were relatively unsuitable for development.

GENERAL DISCUSSION

The intrinsic rate of increase of an insect population is determined by the length of the developmental and pre-reproductive periods and the reproductive rate during the first few weeks of adult life. Aphids have a very short generation time and a high reproductive rate, and their intrinsic rate of increase is consequently considerably higher than in most other groups of insects.

The intrinsic and finite rates of increase of a particular aphid species are significantly affected by temperature. Within the temperature range for development of the species, an increase in temperature results in an increase in the rate of development and of reproduction, and hence in the intrinsic and finite rates of increase.

The finite rate of increase (λ) is, by definition, the factor by which a population which has attained a stable-instar distribution would be expected to increase per unit of time in an unlimited environment. Analysis of the instar distribution of aphid samples in 1967 and 1968 suggested that caged populations rarely attained a stable-instar distribution. However, most of the samples were taken when the populations were declining and stable-instar distributions may have been more common when the populations were increasing.

The mean daily temperature for the months of July and August, 1967, was just over 15°C. As this temperature is intermediate between the upper and lower limits for aphid development, there is some justification for using the finite rate of increase determined experimentally for the various aphid species at a constant temperature of 15°C to predict the approximate potential size of populations each week in the field.

The potential populations presented in Figure 36 were calculated as

$$P_t = \sum_{i=1}^{t} p_i \lambda$$

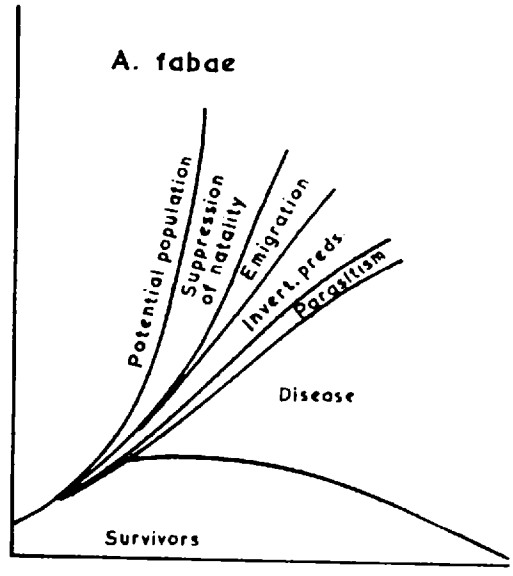
where p_i = potential population in week i (p_1 = 10) and λ = finite rate of increase at 15°C.

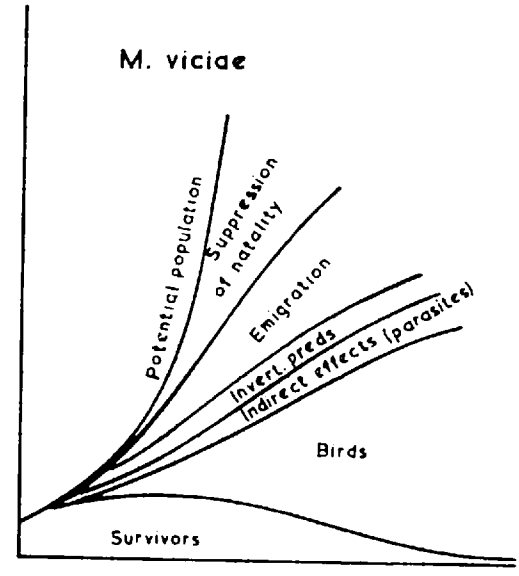
In the light of results obtained during the course of this investigation, particularly those from field experiments in 1967, it is possible to make certain predictions about the relative importance of major factors controlling populations of each of the four species/biotypes in the field. These factors are presented schematically in Figure 36. The diagrams indicate the possible fate of hypothetical populations resulting from a mass migration of aphids into the bean plot at Silwood Park in a year when conditions favour an outbreak of fungus disease. In order to equate the hypothetical populations with the caged populations in 1967, it will be assumed that the aphids are fairly evenly distributed throughout the plot and that the mean number of aphids per plant at the start of the infestation is 10.

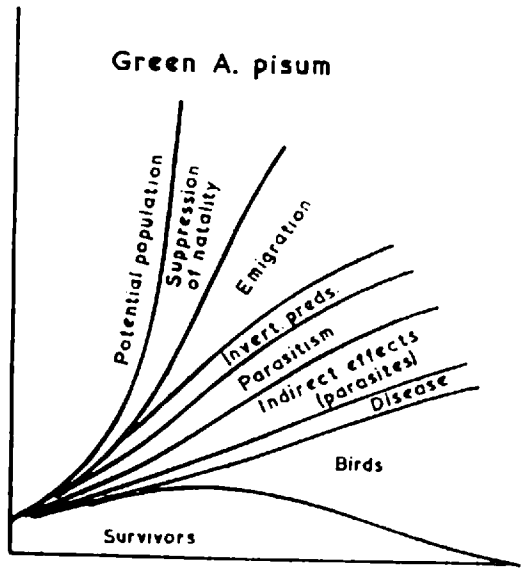
During the first week after the arrival of the aphids on the plants, the rate of increase of the populations would be expected to exceed the finite rate of increase because reproducing adults (the original migrants) would constitute a high proportion of the population at this stage i.e. the populations would not yet have attained a stable-instar distribution.

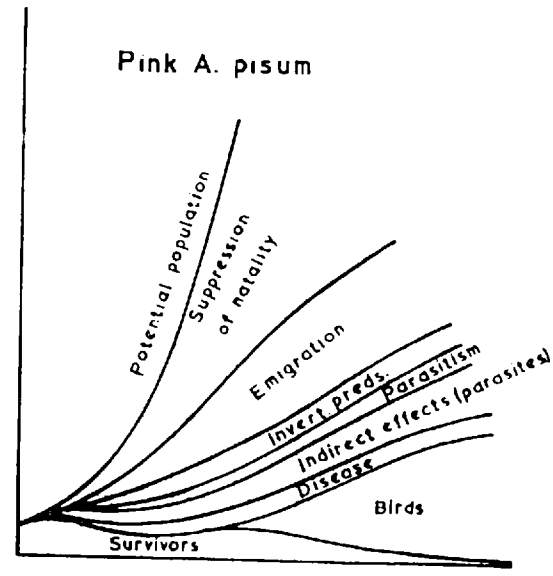
The rate of growth of the populations is affected even at low densities (fewer than 50 aphids per plant) by intra-specific competition. A. fabae and green A. pisum feed mainly on the young leaves at the apex of the plant and the preferred feeding sites become increasingly crowded as the population increases. M. viciae and pink A. pisum are more widely distributed over the host plant but are more sensitive to external stimuli than the other species and frequent encounters between individuals produce the same effects as crowding.

Figure 36 : Schematic representation of major factors affecting hypothetical aphid populations on broad beans in the field, based mainly on experiments conducted in 1967


A. fabae
Potential population
Suppression of natality
Emigration
Invert. preds
Parasitism
Disease
Survivors


M. viciae
Potential population
Suppression of natality
Emigration
Invert. preds
Indirect effects (parasites)
Birds
Survivors


Green A. pisum
Potential population
Suppression of natality
Emigration
Invert. preds.
Parasitism
Indirect effects (parasites)
Disease
Birds
Survivors


Pink A. pisum
Potential population
Suppression of natality
Emigration
Invert. preds.
Parasitism
Indirect effects (parasites)
Disease
Birds
Survivors

Intra-specific competition plays a major role in regulating the growth of aphid populations. It results firstly in suppression of natality and secondly in the production of alatae, most of which leave the plant. Pink A. pisum apparently has a lower crowding threshold than the other aphids studied. Its finite rate of increase at 15° is only slightly lower than that of M. viciae, but its actual rate of increase in the field is considerably lower. Sutherland (1969) found the pink biotype to be much more sensitive to crowding than the green biotype of A. pisum, as evidenced by the high proportion of alatae produced by the pink biotype even at low densities.

Populations of A. fabae were destroyed by disease before sampling commenced and it was therefore not possible to assess the effects of intra-specific competition on alate production. However, A. fabae is less active than the other species and probably has a higher density threshold for alate production.

It is virtually impossible to differentiate between crowding effects (competition for space) and host plant effects. The condition of the host plant is undoubtedly of considerable importance in regulating the size of aphid populations, particularly in the case of green A. pisum and A. fabae which often cause considerable damage to the host plants. Deterioration in the condition of the host plant will have an adverse effect on the aphids in that development will be slower and fecundity lower if the food supply is inadequate. It will also have an indirect effect because the aphids will become increasingly restless and crowding effects will consequently be intensified.

Host plant effects are probably less important in the case of M. viciae and pink A. pisum because the aphids themselves do not cause significant damage to plants on which they are feeding. Bean plants are

apparently able to support high populations (several thousands of aphids per plant) of M. viciae and populations of pink A. pisum are unlikely to have much effect because they remain at a very low level in the field.

A. fabae and both biotypes of A. pisum are subject to attack by fungus disease caused by Entomophthora spp. In 1967, this was by far the most important mortality factor in the case of A. fabae and the populations were completely destroyed within a few weeks of the plants being infested. The aphids form dense colonies and, if weather conditions are favourable, the fungus is able to spread rapidly through the population. Outbreaks of disease occur relatively infrequently, however, and in most years, the populations will increase to a high level and may cause considerable damage to the crop. A. pisum is affected to a relatively minor extent and M. viciae is apparently unaffected by disease.

M. viciae and both biotypes of A. pisum are extremely susceptible to bird predation. In 1967 and 1968, populations of these species almost invariably declined to a very low level within a few days of their being exposed to birds. However, these populations were restricted to only a small proportion of the total plants in the field; a widespread infestation would take longer to suppress. Nevertheless, bird predation would undoubtedly cause significant mortality among populations over a period of two or three weeks, except in the case of A. fabae which appears to be completely unaffected by bird predation.

Invertebrate predation would not be expected to have much effect on the aphid populations during the early stages of the infestation. The relatively small reduction in numbers resulting from invertebrate predation could easily be compensated for by increased reproduction by the aphids.

M. viciae is probably less affected by invertebrate predators than the other species because of its toxicity to certain species, particularly

coccinellids.

Parasitism may not, in itself, be a major mortality factor, except perhaps in the case of green A. pisum. However, the indirect effects, resulting from harassment of the aphids by adult parasites, may have a significant effect on populations of A. pisum. Harassment by parasites may cause a drastic reduction in populations on individual plants, but would only affect the total population if aphids which dropped from the plants were to suffer a high mortality and/or if the continual disturbance by parasites were to cause a significant reduction in the rate of development and reproduction. Tamaki et al (1970) found that aphids which left the plants did indeed suffer a high mortality. Their experiments were conducted in greenhouses and it is therefore likely that mortality would be at least as high - if not higher - in the field. There is also little doubt that the rate of increase would be adversely affected. The reproductive rate of adults which were transferred to new leaves during fecundity experiments invariably dropped during the following 24 hours. Thus the indirect effects of harassment by parasites may be of considerable importance in the regulation of populations of green and pink A. pisum. There is some evidence to suggest that M. viciae is also affected, even though the percentage parasitism is negligible in this species.

It can be concluded that the relative scarcity of M. viciae and A. pisum on broad beans in the field is due mainly to their susceptibility to bird predation, to their sensitivity to external stimuli, especially harassment by adult parasites and to their relatively low threshold for intra-specific competition, as compared to A. fabae. The latter species is unaffected by birds, nor is it disturbed by the presence of adult parasites. The only efficient mortality factor in the case of A. fabae is fungus disease.

SUMMARY

Exclusion techniques were used to determine the relative importance of some of the major factors affecting aphid populations on broad beans (Vicia faba) in the field.

Bird predation caused high mortality among populations of M. viciae and both biotypes of A. pisum but had no obvious effect on A. fabae.

Populations of A. fabae were destroyed in 1967 by an epizootic caused by a species of Entomophthora.

The continued build up of the population of M. viciae in the cage covered by Terylene net was due mainly to the retention of alatae and potential migrant apterae rather than to the exclusion of invertebrate predators.

M. viciae populations had no obviously adverse effect on the host plants except at very high densities (several thousands of aphids per plant).

Green A. pisum fed mainly on young leaves at the apex of the plant. Moderate infestations caused growth to be retarded and high infestations (approximately 700 or more aphids per plant) frequently resulted in the death of the host plant.

Populations of pink A. pisum remained at a low level, even in the cage covered by Terylene net.

Rain apparently had little, if any, effect on the aphid populations.

Invertebrate predation probably contributed to the decline of the aphid populations. Green A. pisum appeared to be more susceptible to parasitism than any of the other aphids included in the investigation.

Further studies concerning biotic factors affecting aphid populations

on broad beans in the field were undertaken in 1969 and 1970.

Syrphids were potentially the most abundant predators in both years. Eggs were laid almost continually from May to the third week in September, 1970. Coccinellid oviposition was restricted to a 3 week period during June.

Syrphid species which were active only in spring (Syrphus eligens and S. nitidicollis) had a relatively restricted height range for oviposition. This was also true of Coccinella 7 - punctata which ignored the plants 30 inches above the ground but which accounted for the majority of coccinellid eggs on plants exposed at ground level.

Syrphid adults laid more eggs on plants with high aphid densities than on those with relatively few aphids.

There appeared to be a build up in the syrphid population towards the end of the season, as evidenced by the large oviposition peak in September.

A. fabae and both biotypes of A. pisum were parasitised by hymenopterous parasites throughout most of the season from May until August or September. In contrast, parasitism in M. viciae was negligible. In the case of green and pink A. pisum, the percentage parasitism appeared to be inversely correlated with aphid density.

The decline in populations of A. pisum, and possibly also M. viciae, on bean seedlings in 1970 was apparently due to dispersal resulting from harassment by adult parasites.

Further experiments were conducted to determine the effect of bird predation on populations of green and pink A. pisum and A. fabae over periods of 24 or 48 hours. Both biotypes of A. pisum suffered a high mortality on uncaged plants whereas populations on caged plants increased

over the same period. A. fabae was unaffected by bird predation; populations on caged and uncaged plants increased by a comparable amount over the 48 hour period during which the aphids were exposed in the field.

Rate of development and fecundity were determined for each species/biotype at constant temperatures of 15°, 20° and 25°C. An increase in temperature resulted in an increase in rate of development, but fecundity tended to be lower at 25° than at 20°, except in the case of A. fabae.

Additional experiments with the 'Silwood strain' of pink A. pisum revealed that fecundity was significantly affected by the temperature at which the aphids were reared.

The theoretical threshold temperature of development was calculated for each species. The feasibility of using summation of hour-degrees to predict the rate of growth of aphid populations was tested by determining the duration of instars, on a physiological time-scale, at fluctuating temperatures in the field in August and September. The total nymphal period was invariably shorter in field experiments than at constant temperatures in the laboratory.

Various population growth statistics, including intrinsic and finite rates of increase, were determined for each species at constant temperatures of 15°, 20° and 25°C.

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APPENDIX 1. Daily mean temperature, mean relative humidity and rainfall recorded at the Meteorological Site, Silwood Park, during July, August and September, 1967

DATE	JULY			AUGUST			SEPTEMBER		
	Mean T° (°C.)	Mean R.H. (%)	Rain (mm.)	Mean T° (°C.)	Mean R.H. (%)	Rain (mm)	Mean T° (°C.)	Mean R.H. (%)	Rain (mm)
1	15.9	76	0	19.2	84	1.0	17.2	87	2.7
2	16.5	76	0	15.1	86	6.4	16.0	74	0.4
3	14.0	71	0	13.7	76	0	14.2	79	2.9
4	13.5	82	0	12.0	68	0	13.9	76	0.4
5	16.0	78	0	13.7	69	0	13.6	78	6.0
6	15.6	77	0	15.0	80	0.7	12.3	73	0
7	17.5	73	0.3	16.8	67	0	11.2	80	0
8	15.8	70	1.8	16.9	79	1.2	9.5	81	0
9	14.8	71	0	17.2	79	0	10.5	77	0
10	18.1	75	0	16.1	83	0	12.5	81	0
11	19.7	72	0	14.3	83	2.5	13.1	87	0
12	19.7	76	0	13.0	77	0	13.1	74	0
13	19.4	81	0	14.0	75	0	12.9	85	1.0
14	18.7	73	0	15.0	87	12.3	13.4	90	1.9
15	17.0	76	0.3	13.2	90	5.2	14.2	88	0.7
16	18.8	76	0.2	14.4	82	3.7	13.3	90	0
17	21.2	71	0.4	14.8	76	0	14.3	83	0
18	19.1	84	1.5	16.2	83	0	13.2	84	4.7
19	17.3	83	0.5	15.6	92	25.3	12.5	81	4.5
20	16.1	74	0	14.6	74	0	11.2	83	0.2
21	15.1	71	0	15.2	76	0	9.6	85	0
22	17.3	77	*14.6	17.9	78	0	12.2	83	0
23	17.6	78	+35.2	17.8	83	0	11.2	90	2.3
24	17.9	71	0	15.9	90	0	14.4	90	1.3
25	17.1	86	0	17.4	83	0	15.5	89	26.8
26	19.1	71	0	17.6	78	0	16.8	86	0.8
27	17.5	86	1.4	19.4	78	0	14.6	86	0
28	17.2	79	6.7	17.5	81	0	16.0	87	1.5
29	15.2	82	4.3	16.1	76	0	15.4	91	3.6
30	18.1	88	0.2	14.7	77	0	13.4	80	0
31	19.4	83	0	16.3	82	0			

* In 2.0 hours

\+ In 2.9 hours

APPENDIX 2. Weekly estimates of populations of Aphis fabae on individual plants in each treatment (1967)

Treatment I : Roof and sides of Terylene net

PLANT	WEEK COMMENCING							
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
1	0	4	10	0	0	0	0	0
2	9	7	50	135	14	1	2	0
3	14	65	47	0	2	32	83	0
4	43	79	80	1	1	6	32	0
5	17	14	4	0	0	0	0	0
6	9	33	6	2	0	0	0	0
7	40	41	30	26	17	1	6	0
8	18	121	180	96	24	4	-	-
9	14	20	10	28	-	-	-	-
10	19	48	50	40	8	0	0	0
11	62	72	34	26	2	12	44	0
12	8	34	23	9	1	0	15	0

Treatment II : Roof and sides of chicken wire

PLANT	WEEK COMMENCING					
	11/7	18/7	25/7	31/7	7/8	14/8
1	25	15	6	21	0	0
2	0	18	35	18	0	0
3	32	140	280	45	-	-
4	49	117	149	44	0	0
5	41	132	152	11	0	0
6	24	108	235	28	3	0
7	44	33	100	77	1	0
8	20	55	87	15	0	0
9	28	140	250	100	0	0
10	41	182	260	50	0	0
11	31	101	201	67	1	0
12	43	93	186	69	0	0

APPENDIX 2. (Continued)

Treatment III : Cage removed

PLANT	WEEK COMMENCING						
	11/7	18/7	25/7	31/7	7/8	14/8	21/8
1	19	41	57	7	-	-	-
2	4	12	13	1	0	0	0
3	2	10	18	3	0	0	0
4	29	46	53	1	0	1	0
5	18	58	21	1	0	0	0
6	28	63	38	0	0	0	0
7	35	44	53	8	0	0	0
8	29	54	38	4	8	5	0
9	28	64	90	2	0	0	0
10	15	21	55	1	0	0	-
11	6	7	26	16	0	0	0
12	8	73	100	29	0	0	0

Treatment IV : Roof of Terylene + Polythene; no sides

PLANT	WEEK COMMENCING						
	11/7	18/7	25/7	31/7	7/8	14/8	21/8
1	6	16	20	5	10	8	0
2	6	29	150	6	0	0	0
3	3	39	90	18	-	-	-
4	6	89	220	12	0	0	0
5	26	78	105	2	1	0	0
6	50	552	130	1	0	0	0
7	7	33	7	6	0	0	0
8	17	54	100	35	1	0	0
9	1	63	90	23	0	0	0
10	39	133	43	2	0	0	-
11	5	87	120	5	0	0	0
12	10	12	90	3	0	1	0

APPENDIX 2. (Continued)

Treatment V : Sides of Terylene net; no roof

PLANT	WEEK COMMENCING							
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
1	8	82	100	120	0	0	0	0
2	5	3	9	0	0	0	0	0
3	24	32	17	0	0	0	-	-
4	20	120	110	170	3	0	0	0
5	2	44	40	35	0	0	0	0
6	45	200	230	49	0	0	0	0
7	5	120	80	100	3	1	1	0
8	38	80	40	70	-	-	-	-
9	10	70	30	11	8	0	0	0
10	34	69	80	60	2	0	0	0
11	14	64	80	140	30	3	1	0
12	44	130	100	65	1	1	0	0

Treatment VI : Terylene roof and sides + Polythene roof

PLANT	WEEK COMMENCING							
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
1	6	71	190	220	18	0	0	0
2	38	152	200	100	8	3	-	-
3	5	23	16	80	79	34	37	0
4	7	55	90	66	17	1	0	0
5	18	94	55	4	4	0	0	0
6	9	54	50	55	18	0	0	0
7	4	110	100	51	12	1	0	0
8	26	58	31	8	1	3	0	0
9	36	81	43	20	14	3	1	0
10	1	84	250	59	-	-	-	-
11	32	171	40	13	44	7	0	0
12	16	100	80	29	12	0	0	0

APPENDIX 3. Weekly estimates of populations of Megoura viciae on individual plants in each treatment (1967)

Treatment I : Roof and sides of Terylene net

PLANT	WEEK COMMENCING									
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8	4/9	11/9
1	22	84	440	1200	3200	4000	5000	2800	300	0
2	72	170	400	650	1050	1000	400	200	1	0*
3	26	125	580	2000	2830	3000	5800	470	2	0*
4	59	144	780	1900	4000	3000	5000	760	0	0*
5	42	250	600	1200	500	1000	0*	-	-	-
6	18	68	570	670	1000	1050	0*	-	-	-
7	47	185	390	1850	3290	3600	5000	900	3	0*
8	26	111	310	910	1700	4300	7500	2900	2300	1
9	32	56	150	750	1100	2000	3000	900	15	0
10	18	114	330	1400	1850	4300	4000	1400	-	-
11	15	97	280	1920	3300	3000	-	-	-	-
12	28	101	380	1280	-	-	-	-	-	-

* Plant dead

Treatment II : Roof and sides of chicken wire

PLANT	WEEK COMMENCING												
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8	4/9	11/9	18/9	25/9	2/10
1	22	212	340	760	580	1100	1140	500	530	170	30	1	0
2	22	141	300	300	150	650	900	300	100	60	0	0	0
3	24	109	450	700	1100	500	410	360	200	60	30	5	0
4	28	144	300	650	-	-	-	-	-	-	-	-	-
5	28	160	300	800	470	620	530	260	-	-	-	-	-
6	32	134	420	600	500	220	350	110	80	10	1	1	0
7	18	145	330	510	980	1300	1350	1300	1230	150	15	0	0
8	23	124	150	620	750	500	-	-	-	-	-	-	-
9	18	93	200	850	500	870	1030	750	500	50	5	0	0
10	56	148	370	650	50	20	70	170	410	300	220	6	-
11	33	97	400	1000	50	10	90	250	310	160	-	-	-
12	42	76	200	500	230	30	40	110	2	60	60	40	0

APPENDIX 3. (Continued)

Treatment III : Cage removed

PLANT	WEEK COMMENCING												
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8	4/9	11/9	18/9	25/9	2/10
1	25	56	70	4	0	0	0	1	-	-	-	-	-
2	50	108	147	19	1	2	1	0	0	0	0	0	0
3	28	150	100	31	0	0	0	0	5	32	110	0	0
4	42	150	25	4	1	0	-	-	-	-	-	-	-
5	40	120	14	4	0	0	0	0	0	0	1	0	0
6	67	310	84	26	4	0	0	0	2	20	0	1	-
7	63	111	16	0	8	1	0	0	0	0	0*	-	-
8	37	95	65	14	-	-	-	-	-	-	-	-	-
9	42	100	75	4	3	1	0	1	0	10	30	25	0
10	36	140	17	3	0	0	0	12	1	0	20	0	0
11	46	160	110	1	1	0	0	0	0	0	0	0	0
12	69	130	74	0	0	0	0	0	2	5	-	-	-

* Plant dead

Treatment IV : Roof of Terylene + Polythene; no sides

PLANT	WEEK COMMENCING									
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8	4/9	11/9
1	60	180	180	110	36	0	0	0	0	0
2	48	140	90	0	9	2	2	0	0	0
3	66	130	140	160	0	0	0	0	-	-
4	19	130	100	80	5	0	0	0	0	0
5	30	160	45	40	3	0	0	0	0	0
6	91	300	100	100	3	1	-	-	-	-
7	51	130	103	65	-	-	-	-	-	-
8	32	130	40	80	0	0	0	0	0	0
9	36	140	90	8	2	1	3	0	0	0
10	59	140	55	60	3	1	18	3	5	0
11	25	96	50	35	0	4	0	0	0	0
12	61	n.c.	53	45	0	0	0	0	0	0

n.c. = not counted

APPENDIX 3. (Continued)

Treatment V : Sides of Terylene net; no roof

PLANT	WEEK COMMENCING								
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8	4/9
1	36	108	260	970	700	4	2	0	0
2	22	75	280	800	250	2	0	0	0
3	25	73	380	1300	535	6	5	0	0
4	20	77	240	1000	410	1	1	0	0
5	11	68	240	740	-	-	-	-	-
6	12	76	170	600	380	9	-	-	-
7	30	76	222	1300	670	15	4	0	0
8	37	77	120	200	160	15	1	0	0
9	30	171	360	760	120	13	12	34	0
10	14	95	230	480	60	0	0	0	0
11	5	49	100	870	200	31	8	1	-
12	6	43	94	400	470	31	1	0	0

Treatment VI : Terylene roof and sides + Polythene roof

PLANT	WEEK COMMENCING													
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8	4/9	11/9	18/9	25/9	2/10	9/10
1	31	150	450	3110	7500	n.c.	3100	1800	0	*0	-	-	-	-
2	35	160	450	1200	2500	"	2600	1700	90	*0	-	-	-	-
3	46	156	550	920	3200	"	2600	0	0	*0	-	-	-	-
4	39	140	430	1360	3300	"	2000	2000	-	-	-	-	-	-
5	44	127	450	1180	-	"	-	-	-	-	-	-	-	-
6	47	44	130	790	1540	"	-	-	-	-	-	-	-	-
7	0	0	30	370	1170	"	1350	1970	2000	550	450	410	120	200
8	0	0	0	130	600	"	1300	700	280	250	75	20	30	0
9	2	0	6	70	220	"	900	1100	1000	550	-	-	-	-
10	7	34	120	1000	2770	"	900	40	0	*0	-	-	-	-
11	32	186	1000	1380	2650	"	1800	1800	1	*0	-	-	-	-
12	49	240	1100	2520	4250	"	4000	2650	2600	1550	800	120	-	-

PLANT	17/10	23/10	30/10
7	40	37	15
8	1	0	0

n.c. = not counted

* = plant dead

APPENDIX 4. Incidence of instars and morphs of Megoura viciae on sample plants, expressed as a percentage of the total population on the plant

Date	Treatment	No. of Aphids on Plant	APTERAE						ALATAE		
			1st Inst.	2nd Inst.	3rd Inst.	4th Inst.	ADULTS		4th Inst.	ADULTS	
							Viviparae	Oviparae		Females	Males
1/8	I	3,114	32.2%	23.8%	22.5%	11.7%	5.6%	-	3.3%	0.9%	-
	II	1,252	15.4	28.2	21.9	19.6	6.7	-	8.1	0.1	-
	III	28	25.9	7.4	11.1	11.1	40.8	-	3.7	-	-
	IV	106	17.8	38.3	12.2	5.6	25.2	-	0.9	-	-
	V	1,485	18.9	29.4	23.3	12.1	11.9	-	4.3	-	-
	VI	2,595	20.5	19.3	15.7	14.9	19.9	-	7.8	1.9	-
17/8	I	= 7000	21.1	27.2	22.2	14.6	4.5	-	8.2	2.2	-
	II	2002	22.3	30.5	23.9	14.1	6.0	-	2.7	0.4	-
	V	23	-	4.3	17.4	47.8	-	-	30.4	-	-
	VI	5206	40.7	22.4	13.1	7.2	6.1	-	3.2	7.3	-
30/8	I	3910	36.7	21.9	13.9	7.6	13.4	4.6	0.5	1.2	0.2
	II	688	52.6	17.0	8.4	8.1	10.0	2.7	0.7	0.5	-
	III	1	-	-	-	-	100.0	-	-	-	-
	V	1	-	-	-	-	100.0	-	-	-	-
	VI	4698	22.6	23.4	24.7	15.4	8.3	4.5	0.4	0.6	-
12/9	II	366	24.6	25.1	21.6	8.2	3.0	10.4	6.3	0.8	-
	III	9	77.8	11.1	-	-	11.1	-	-	-	-
	VI	547	21.8	34.9	31.4	1.8	3.7	0.9	4.2	0.8	0.5

APPENDIX 4. (Continued)

Date	Treatment	No. of Aphids on Plant	1st Inst.	2nd Inst.	3rd Inst.	APTERAE 4th Inst.	APTERAE ADULTS Viviparae	APTERAE ADULTS Oviparae	ALATAE 4th Inst.	ALATAE ADULTS Females	ALATAE ADULTS Males
25/9	II	18	-	22.2	11.1	50.0	-	5.6	-	11.1	-
	VI	106	10.4	2.8	6.6	34.9	1.0	31.1	9.4	3.8	-
5/10	III	1	-	-	-	-	-	100.0	-	-	-
9/10	VI	23	21.7	13.0	13.0	34.8	4.3	8.7	4.3	-	-
30/10	VI	15	-	13.3	20.0	6.7	6.7	26.6	13.3	-	13.3
21/11	VI	30	20.0	16.7	6.7	10.0	-	10.0	30.0	-	6.7

APPENDIX 5. Weekly estimates of populations of Acyrthosiphon pisum (Pink Biotype) on individual plants in each treatment (1967)

Treatment I : Roof and sides of Terylene net

PLANT	WEEK COMMENCING															
	11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8	4/9	11/9	18/9	25/9	2/10	9/10	17/10	23/10
1	2	50	143	152	108	14	9	1	0	1	0	0	1	0	0	0
2	6	9	39	98	59	42	6	0	0	-	-	-	-	-	-	-
3	2	39	89	114	119	90	0	1	0	0	0	0	0	0	1	0
4	13	43	222	599	280	105	4	8	0	0	0	0	0	-	-	-
5	1	63	73	92	96	6	2	0	0	0	0	0	0	0	0	0
6	8	46	75	54	106	-	-	-	-	-	-	-	-	-	-	-
7	21	11	21	17	26	33	8	0	0	0	0	-	-	-	-	-
8	1	15	28	11	28	20	3	0	1	0	0	1	0	0	0	0
9	0	50	50	50	31	16	4	0	0	0	0	0	0	0	0	0
10	5	50	183	266	147	92	7	0	3	3	1	1	0	0	0	0
11	14	73	130	115	109	24	0	0	0	0	1	1	0	4	0	-
12	8	19	58	150	145	60	4	-	-	-	-	-	-	-	-	-

APPENDIX 5. (Continued)

Treatment II : Roof and sides of chicken wire

PLANT	WEEK COMMENCING					
	11/7	18/7	25/7	31/7	7/8	14/8
1	15	19	48	1	0	0
2	19	10	10	0	0	0
3	25	40	26	2	0	0
4	27	36	18	0	1	0
5	23	64	66	14	3	0
6	35	54	38	5	0	0
7	21	37	18	2	0	0
8	19	98	19	1	0	0
9	76	69	50	1	0	0
10	22	44	27	0	0	-
11	36	171	47	0	0	0
12	26	63	44	0	0	0

Treatment III : Cage removed

PLANT	WEEK COMMENCING				
	11/7	18/7	25/7	31/7	7/8
1	19	48	9	0	0
2	2	39	3	1	0
3	12	78	5	0	0
4	8	95	7	0	0
5	14	40	5	0	0
6	8	20	7	0	0
7	30	50	17	0	0
8	11	87	10	0	0
9	22	46	7	0	0
10	8	79	7	0	0
11	8	86	4	1	0
12	18	36	1	0	0

APPENDIX 6. Weekly estimates of populations of Acyrthosiphon pisum (Green Biotype) on individual plants in each treatment (1967)

Treatment I : Roof and sides of Terylene net

PLANT	WEEK COMMENCING						
	11/7	18/7	25/7	31/7	7/8	14/8	21/8
1	85	128	335	36	5	1	0
2	92	303	279	19	0	1	0
3	39	339	255	108	4	0	0
4	73	186	590	39	5	-	-
5	76	165	470	25	1	0	0
6	50	402	520	34	1	0	0
7	91	240	480	142	8	0	0
8	12	131	240	200	40	0	0
9	69	306	850	95	0	0	0
10	84	189	500	45	0	0	0
11	62	289	425	9	0	0	0
12	65	130	260	36	1	0	0

Treatment II : Roof and sides of chicken wire

PLANT	WEEK COMMENCING				
	11/7	18/7	25/7	31/7	7/8
1	88	630	-	0	0
2	75	700	-	0	0
3	137	700	-	0	0
4	144	700	-	0	0
5	92	211	-	0	0
6	74	626	-	0	0
7	136	330	-	0	0
8	118	720	-	0	0
9	130	400	-	1	0
10	54	183	-	31	0
11	49	380	-	0	0
12	172	600	-	0	0

APPENDIX 6. (Continued)

Treatment III : Cage removed

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8
1	39	294	-	0	0
2	54	344	-	0	0
3	98	90	-	0	0
4	80	64	-	0	0
5	36	176	-	0	0
6	92	200	-	0	0
7	26	126	-	0	0
8	37	152	-	0	0
9	33	36	-	0	0
10	29	123	-	0	0
11	47	160	-	0	0
12	64	8	-	1	0

APPENDIX 7. Weekly estimates of the number of each aphid species on individual plants in 'Competition ' treatments (1967)

Treatment I : Roof and sides of Terylene net

a) Aphis fabae

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
* 1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0
4	0	0	0	2	20	65	30	0
* 5	23	97	150	350	450	900	1200	0
6	0	0	0	0	0	0	1	0
7	0	0	0	0	0	-	-	-
8	0	0	0	0	0	0	0	0
* 9	16	47	165	0	0	0	0	0
10	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0
12	0	3	0	0	0	0	0	0

b) Megoura viciae

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
1	0	0	2	1	90	80	250	700
* 2	3	0	0	45	40	70	350	380
3	0	1	0	3	70	200	340	800
4	0	0	8	45	80	170	600	300
5	0	1	22	130	400	450	1170	1020
* 6	23	125	170	900	840	1200	1150	4000
7	0	0	1	0	0	-	-	-
8	0	0	1	0	19	50	150	250
9	0	0	0	0	11	10	110	400
* 10	38	94	107	235	200	600	1000	2400
11	0	0	17	150	280	400	1000	1800
12	0	0	6	200	320	900	1100	2800

* Denotes plants initially infested with the species

APPENDIX 7. (Continued)

Treatment I

c) Acyrthosiphon pisum (Pink biotype)

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
1	0	0	0	0	0	0	1	8
2	0	0	0	0	0	0	0	0
* 3	8	0	0	0	0	0	0	9
4	0	0	0	3	1	2	0	3
5	0	1	0	7	7	3	2	3
6	0	1	0	3	7	9	8	4
* 7	0	0	0	0	0	-	-	-
8	0	0	0	0	0	1	4	1
9	0	0	0	0	0	0	0	1
10	0	3	0	3	5	3	2	10
* 11	1	3	2	7	20	3	20	4
12	6	21	44	13	1	26	13	33

d) Acyrthosiphon pisum (Green biotype)

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8	14/8
1	0	2	0	2	2	0
2	0	0	1	2	1	0
3	0	3	2	7	0	0
* 4	100	200	155	73	5	0
5	0	3	4	7	0	0
6	0	11	0	3	0	0
7	0	0	0	0	0	-
* 8	0	1	0	0	0	0
9	0	7	1	1	0	0
10	0	4	0	0	1	0
11	0	4	0	2	0	0
* 12	33	63	31	3	2	0

* Denotes plants initially infested with the species

APPENDIX 7. (Continued)

Treatment II : Roof and sides of chicken wire

a) Aphis fabae

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8
* 1	5	47	200	2	0
2	0	0	15	0	0
3	0	0	0	1	0
4	0	4	29	3	0
* 5	3	70	320	8	0
6	0	0	0	0	0
7	0	0	0	0	0
8	0	0	0	0	0
* 9	4	12	50	8	0
10	0	0	1	0	0
11	0	0	0	0	0
12	0	0	0	0	0

b) Megoura viciae

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
1	0	0	40	4	0	0	0	0
* 2	20	120	210	8	0	3	10	0
3	0	0	5	12	0	0	0	14
4	0	1	2	8	2	1	0	0
5	0	0	0	1	3	0	0	0
* 6	21	98	240	4	0	0	0	0
7	0	0	0	22	9	0	40	0
8	1	7	6	1	1	21	2	0
9	0	0	10	22	2	0	0	0
* 10	22	74	250	120	0	0	0	0
11	0	0	0	45	4	0	3	0
12	0	0	2	1	0	0	0	0

* Denotes plants initially infested with the species

APPENDIX 7. (Continued)

Treatment II

c) Acyrthosiphon pisum (Pink biotype)

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8	14/8
1	0	1	8	10	0	0
2	0	3	47	6	3	0
* 3	10	90	53	13	3	0
4	0	6	23	15	0	0
5	0	4	19	3	0	0
6	6	0	4	1	0	0
* 7	0	43	21	5	1	0
8	0	1	20	4	0	0
9	0	2	16	4	0	0
10	0	1	29	43	0	0
* 11	11	63	19	26	0	0
12	0	7	19	0	0	0

d) Acyrthosiphon pisum (Green biotype)

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8
1	0	2	1	2	0
2	0	1	1	4	0
3	0	17	75	12	0
* 4	25	114	31	7	0
5	1	23	16	4	0
6	0	7	1	0	0
7	0	0	10	2	0
* 8	50	150	450	1	0
9	0	17	90	4	0
10	0	0	40	9	0
11	1	13	22	16	0
* 12	50	252	550	0	0

* Denotes plants initially infested with the species

APPENDIX 7. (Continued)

Treatment III : Cage removed

a) Aphis fabae

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8
* 1	1	4	3	0	0
2	0	4	15	0	0
3	1	0	1	0	0
4	0	0	0	0	0
* 5	5	50	35	1	0
6	0	18	100	0	0
7	0	1	0	0	0
8	0	0	0	0	0
* 9	1	29	50	0	0
10	0	0	11	0	0
11	0	0	5	0	0
12	0	10	22	0	0

b) Megoura viciae

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7	7/8	14/8	21/8	29/8
1	0	0	0	1	0	3	0	0
* 2	30	0	1	0	0	0	1	0
3	0	0	1	7	4	13	17	0
4	0	0	0	0	0	0	32	0
5	0	9	9	0	0	0	0	0
* 6	35	91	45	0	0	0	0	0
7	0	0	0	0	0	0	0	1
8	0	1	0	0	3	0	0	0
9	0	0	0	1	0	0	0	3
* 10	29	47	60	0	3	3	0	0
11	2	0	0	0	1	3	0	0
12	14	4	2	0	0	0	8	0

* Denotes plants initially infested with the species

APPENDIX 7. (Continued)

Treatment III

c) Acyrthosiphon pisum (Pink biotype)

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7
1	1	0	0	0
2	0	2	0	0
* 3	13	13	2	0
4	0	7	6	0
5	0	1	3	0
6	0	0	0	0
* 7	0	0	0	0
8	0	0	2	0
9	0	0	0	0
10	0	1	0	0
* 11	0	0	0	0
12	0	1	0	0

d) Acyrthosiphon pisum (Green biotype)

PLANT	WEEK COMMENCING 11/7	18/7	25/7	31/7
1	1	5	0	0
2	0	2	1	0
3	5	34	7	0
* 4	33	70	3	0
5	0	0	1	0
6	0	2	0	0
7	0	0	0	0
* 8	6	5	0	0
9	0	5	1	0
10	0	4	1	0
11	1	8	0	0
* 12	47	49	2	0

* Denotes plants initially infested with the species

APPENDIX 8. Field counts of Acyrthosiphon pisum (Pink Biotype) on individual plants in each treatment (1968)

Treatment I : Roof and sides of Terylene net

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	69	47	-	-	-
2	50	34	18	n.c.	n.c.
3	13	67	68	5	1
4	30	45	54	n.c.	n.c.
5	18	32	42	n.c.	n.c.
6	53	95	97	11	8

n.c. = not counted

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	29	25	53	n.c.	n.c.
2	17	21	33	4	9
3	85	52	72	-	-
4	6	17	18	n.c.	n.c.
5	58	156	134	n.c.	n.c.
6	70	224	205	25	20

Treatment II : Terylene net sides; wire mesh roof

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	16	22	37	n.c.	n.c.
2	22	42	47	n.c.	n.c.
3	70	78	88	25	25
4	103	64	80	n.c.	n.c.
5	103	69	-	-	-
6	128	165	88	20	1

APPENDIX 8. (Continued)

Treatment II

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	112	71	112	n.c.	n.c.
2	87	41	26	15	0
3	159	97	150	-	-
4	59	61	47	n.c.	n.c.
5	214	82	56	n.c.	n.c.
6	174	230	196	33	3

Treatment III : Terylene net sides; no roof

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	39	12	-
2	110	17	2
3	45	3	1
4	95	16	7
5	45	5	1
6	50	4	1

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	128	9	2
2	25	6	0
3	69	15	3
4	46	22	5
5	87	15	1
6	55	22	5

n.c. = not counted

APPENDIX 8. (Continued)

Treatment IV : Wire mesh sides; Terylene net roof

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	256	201	122	n.c.	n.c.
2	100	214	-	-	-
3	196	273	322	2	10
4	179	71	139	n.c.	n.c.
5	107	236	435	n.c.	n.c.
6	137	319	505	4	0

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	275	153	-	-	-
2	178	249	10	n.c.	n.c.
3	113	85	5	4	1
4	99	54	12	n.c.	n.c.
5	326	358	5	n.c.	n.c.
6	80	96	6	1	0

Treatment V : Wire mesh sides; wire mesh roof

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	135	140	123	n.c.	n.c.
2	154	122	131	n.c.	n.c.
3	44	90	76	27	1
4	111	154	133	n.c.	n.c.
5	68	62	115	4	0
6	48	118	-	-	-

n.c. = not counted

APPENDIX 8. (Continued)

Treatment V

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7	25/7	22/8
1	52	60	72	-	-
2	40	17	16	n.c.	n.c.
3	93	102	28	1	0
4	74	129	53	n.c.	n.c.
5	53	121	21	n.c.	n.c.
6	60	41	29	3	0

Treatment VI : Wire mesh sides; no roof

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	12	23	1
2	141	37	3
3	86	73	4
4	93	41	4
5	126	60	-
6	295	71	3

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	115	10	0
2	68	4	6
3	58	1	0
4	183	0	0
5	126	2	0
6	126	4	3

n.c. = not counted

APPENDIX 8. (Continued)

Treatment VII : No sides; Terylene net roof

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	60	9	0
2	38	17	0
3	165	14	-
4	142	21	0
5	68	5	0
6	157	12	1

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	83	0	0
2	25	5	0
3	66	2	3
4	220	3	0
5	77	5	0
6	74	1	0

Treatment VIII : No sides; wire mesh roof

Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	77	15	-
2	60	10	0
3	99	24	2
4	69	6	0
5	112	18	0
6	75	11	1

APPENDIX 8. (Continued)

Treatment VIII

Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	191	5	0
2	94	5	0
3	34	1	1
4	321	5	1
5	58	0	0
6	85	2	0

Treatment IX : Cage removed

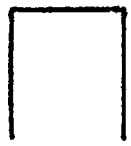
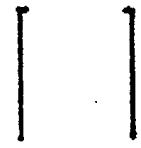
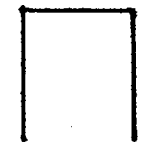
Block A

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	19	3	0
2	6	6	1
3	25	7	-
4	65	5	0
5	33	18	1
6	103	15	0

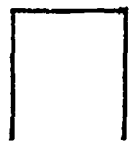
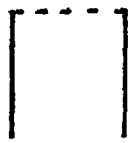
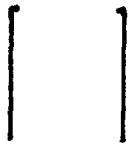
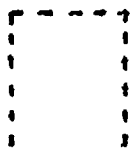
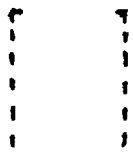
Block B

PLANT	WEEK COMMENCING 1/7	8/7	16/7
1	47	0	0
2	9	0	0
3	51	1	0
4	12	0	0
5	24	0	0
6	115	0	0

APPENDIX 9 : Summary of Treatments, 1967

TREATMENT		DESCRIPTION	PROBABLE EFFECT
I		Terylene net sides; terylene net roof	Excludes birds and most arthropod predators; minimises effect of rain and wind.
II		Wire mesh sides and roof	Excludes birds
III		Cage removed (control)	
IV		No sides; terylene net and polythene roof	Excludes rain
V		Terylene net sides; no roof	Delays effect of birds and arthropod predators; minimises effect of wind.
VI		Terylene net sides; terylene net and polythene roof	Excludes birds and most arthropod predators; excludes rain and minimises effect of wind.

APPENDIX 10 : Summary of Treatments, 1968

TREATMENT		DESCRIPTION	PROBABLE EFFECT
I		Terylene net sides; terylene net roof	Excludes birds and most arthropod predators; minimises effect of rain and wind.
II		Terylene net sides; wire mesh roof	Excludes birds and most arthropod predators minimises effect of wind.
III		Terylene net sides; no roof	Delays effect of birds and arthropod predators minimises effect of wind.
IV		Wire mesh sides; terylene net roof	Excludes birds minimises effect of rain.
V		Wire mesh sides; wire mesh roof	Excludes birds.
VI		Wire mesh sides; no roof	Delays effect of birds.
VII		No sides; terylene net roof	Minimises effect of rain.
VIII		No sides; wire roof	
IX		Cage removed (control)	