POPULATION STUDIES OF THE CABBAGE APHID, *BREVICORYNE BRASSICAE* (L.), AND ITS PARASITES, WITH SPECIAL REFERENCE TO SYNCHRONISATION.

by

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ABSTRCT

The present study aimed to provide a better understanding of the population dynamics of Brevicoryne brassicae (L.), its sole primary parasite, Diaretiella rapae (McIntosh), and the main hyperparasites, Alloxysta brassicae (Ash.). Other less important hyperparasites namely Asaphes vulgaris Walker, A. suspensus (Nees), Pachyneuron minutissimum (Förster) and Dendrocerus carpenterii (Curtis) were also briefly considered. Special emphasis was placed on the problem of synchronisation between D. rapae and B. brassicae, and between A. brassicae and D. rapae, in an attempt to explain the failure of D. rapae to check the aphid populations throughout the season, and the high rate of hyperparasitism of D. rapae by A. brassicae.

The field work was done at 2 sites, namely Silwood Bottom and Ashurst Lodge from 1973 - 75, using Brussels sprouts as the aphids' host plant. Different methods including actual counting in the field, sticky and water traps, and mummy collection were used a) to estimate the populations and activities of the aphid and parasites, and b) to determine whether synchrony occurred. A study was also made of the spring emergence of parasites, their sex ratios and the factors governing their emergence rates.

In the laboratory, the responses of D. rapae and A. brassicae to variations in host and parasite densities were investigated. The effects of synchronisation between D. rapae and B. brassicae (with respect to age and number of aphids) on the ability of D. rapae to eliminate aphid populations were also studied.

Computer simulations were conducted in 3 stages. A model was first built for the population growth of B. brassicae. A subroutine for D. rapae was then incorporated to simulate the experiments on synchronisation, and finally to investigate the effects of A. brassicae on the efficiency of D. rapae, a hyperparasite subroutine was added.

Finally the possibilities of improving the control of B. brassicae in the field by increasing the efficiency of D. rapae are discussed.

SECTION I. GENERAL INTRODUCTION.

Brevicoryne brassicae (L.) is a cosmopolitan aphid, feeding mainly on Crucifers (Bonnemaison, 1966). It normally overwinters as eggs, but small colonies may survive mild winters (Petherbridge & Wright, 1938). In the spring, freshly planted Cruciferous crops are colonised by fundatrices (which hatch from the overwintering eggs) and or. immigrant alates. Throughout spring, summer and autumn, B. brassicae reproduces parthenogenetically. Later in the season, however, owing to low temperatures and shorter photoperiods sexual forms begin to appear and overwintering eggs are laid on the Cruciferous hosts. In the Netherlands, Hafez (1961) has shown that the number of generations per year to be between 6 and 11. In the laboratory, the aphids thrive best at 20°C, taking about 10 days to grow from a newly born nymph to an adult (Akinlosotu, 1973). The average fecundity and adult longevity at 20°C for apterous adults are 28.5 $\pm$ 1.55 nymphs/adult and 23.5 $\pm$ 1.47 days respectively; and for alates: 16.1 $\pm$ 0.59 nymphs/adult and 21.1 $\pm$ 0.96 days respectively (Hafez, 1961).

In the field, the aphid can increase to high numbers, causing damage to Cruciferous crops such as Brussels sprouts, cabbage, cauliflower etc. by a) causing mechanical damage to crop plants, weakening and stunting them, b) making the products unsaleable, and c) transmitting plant viruses (Essig, 1948). In Great Britain, the aphid has always been considered a serious pest of cabbage and related plants (Petherbridge & Wright, 1938) and outbreaks were recorded as early as 1929 (Barnes, 1931). Strickland (1957) estimated that B. brassicae costs England and Wales about £1 million per annum through damage to the sprouts crop.

The Braconid, Diaretiella rapae (McIntosh) is usually recorded as the only primary parasite of B. brassicae in the field. It is an arrhenotokous internal parasite, attacking all aphid stages, although half-grown nymphs are much preferred. The females locate their aphid hosts by first responding to the mustard oils produced by the Cruciferous plants, and then by visual search. The males, on the other hand, are probably attracted to females by a pheromone

(Read et al., 1970). Mating may occur a few minutes after emergence from the pupa (found within the dead aphid host - the so called "mummy"), but the female will start ovipositing whether it has mated or not. In oviposition, the female bends its abdomen forward and probes the aphid with its ovipositor; the ovipositing act takes less than one second. Only one egg is deposited per insertion of the ovipositor, and the egg is laid into the haemocoel of the aphid. Superparasitism may occur, but only one adult parasite will emerge from each parasitised host. The developmental period from egg to pupa which normally takes about 10 days at 20°C is affected by the stage of the host (Akinlosotu, 1973). The pupal development takes 5 days. At the time of pupation, the aphid host is already dead and has become a "mummy". The sex ratio of parasites that emerge from mummies collected from the field is 2♂♂ : 3♀♀. The average fecundity and longevity at room temperature of such females is 83 eggs per adult (range: 25 to 175) and 9 days respectively (Hafez, 1961). In England, however, Akinlosotu (1973) found that adult females and males have shorter life spans of 5 and 4 days respectively (at 20°C). The fecundity of females is affected by age, mating, photoperiod and ovipositing intensity (Stary, 1970). Mated females are more fecund, and longer photoperiods tend to increase fecundity. The parasite overwinters as a final instar larva or pupa within the mummy.

However, the parasite does not appear to excercise much control on aphid populations in the field (Hafez, 1961; Sedlag, 1964; Paetzold & Vater, 1966; Way et al., 1969). This might in part be due to known hyperparasites, namely Alloxysta brassicae (Ash.) (Charipidae), Asaphes vulgaris Walker, A. suspensus (Nees), Pachyneuron minutissimum (Förster) (all Pteromalidae), and Dendrocerus carpenterii (Curtis) (Megaspilidae). These hyperparasites, which are not well studied, appear to be responsible for high levels of parasitism of D. rapae particularly towards the end of the growing season (Hafez, 1961; Paetzold & Vater, 1966).

The bionomics of the aphid and parasites, and possible control of the aphid by biological, chemical or integrated means have been investigated in some detail (George, 1957; Hafez, 1961; Shorey, 1963; Sedlag, 1964; Way & Murdie, 1965; Paetzold & Vater, 1967; Godfrey & Root, 1968; Way et al., 1969;

Akinlosotu, 1973). It is hoped that this thesis might contribute towards this end.

The main objectives of this work (which included field, laboratory and computer simulation studies) where i) to study the population trends of B. brassicae and its parasites, and ii) to determine whether these changes are affected by synchronisation between D. rapae and the aphid, and between A. brassicae and D. rapae.

SECTION II. POPULATION STUDIES OF BREVICORYNE BRASSICAE (L.) AND ITS PARASITES AND PREDATORS IN THE FIELD IN 1973 - 1975.

PART I. MATERIALS AND METHODS.

Studies on the field population of the cabbage aphid, Brevicoryne brassicae (L.) and its hymenopterous parasites, and predators were carried out at Silwood Park from 1973 to 1975.

The Brussels sprouts variety Irish Elegance were planted one metre apart at two sites, Silwood Bottom (1973-1975) and Ashurst Field, (1974). The areas were, at Silwood Bottom 20 x 20 metres and Ashurst Field 10 x 10 metres, containing 400 and 100 plants respectively.

1. Sampling and counting.

At Silwood Bottom, 50 sprout plants were sampled weekly. The plants were chosen randomly with the restriction that at least 2, but not more than 3 plants were selected from each row or column of the plot. Thus, every plant would be sampled once every 8 weeks. In Ashurst Field however, only 20 plants were sampled weekly, taking 2 plants from each row or column and sampling every plant once in every 5 weeks. The choice of the plants was based on a set of random numbers generated on the CDC 6600 computer.

In the early part of the 1973 season, every leaf of a chosen plant was examined for aphids, mummies, adult parasites and immature predator stages. The aphids were divided into the different instars as far as possible, and the mummies with emergence holes were removed. The number of live aphids, mummies, parasites and predators was recorded and summed for the whole plant. This method will be referred to as the "all-leaf" method.

However, later in the season, the aphid population increased to such an extent that the all-leaf method was obviously too time consuming and almost impossible. A different and more speedy method was then tried. For the new method, a plant was arbitrarily divided into 3 strata and only

6 leaves were examined, 2 from each stratum. Plainly this six-leaf method is very similar to the three-leaf method described by Church and Strickland (1954), and used by Strickland (1957), Hafez (1961), Akinlosotu (1973) and many others. The decision to sample 6 leaves instead of 3 was taken because it was thought that 6 leaves would provide a more accurate estimate of the aphid population.

Nevertheless, after comparison of the two methods (see below), it was concluded that the estimate was far from being accurate and henceforth all aphid counts were carried out by the all-leaf method.

2. Comparison of all-leaf and six-leaf methods.

On 19 September 1973, the aphid population and mummy number on 25 randomly chosen sprout plants were counted using the all-leaf method, while another 25 by the six-leaf method.

Both the geometric and arithmetic means of the counts of 2 leaves at each stratum have been calculated to show the differences (Table 1). From the results it is clear that the geometric mean of the 25 plants gave a very good estimate (=1053) of the aphid population (=1052). The mummy estimate however, was about 3 times as great (35 against 11).

A further test was carried out on 26 September 1973, when the aphids and mummies on 9 randomly selected plants were counted by the two different methods (Table 2). Whether the geometric or arithmetic mean of the plants is taken for comparison, the population estimated by the six-leaf method was 2 to 3 times as high as that by the all-leaf method. The χ^2 values, tested against the all-leaf method were all significant.

The main source of inaccuracy was the uneven distribution of aphids and mummies on the plants. Some leaves were not infested with aphids at all whereas others were heavily infested. Inclusion of heavily infested leaves would tend to overestimate the count, while omission would lead to underestimation.

Table 1. Comparison of all-leaf and six-leaf methods. Sampling was done at Silwood Bottom, 19 September 1973.

Method	Number of plants sampled	Mean of two leaves at each stratum	Number	Mean of 25 plants	
				Geometric	Arithmetic
six-leaf	25	geometric	Aphid	1053	4531
			Mummy	49	103
		arithmetic	Aphid	1592	6312
			Mummy	35	86
all-leaf	25	-	Aphid	1052	2799
			Mummy	11	21

Table 2. Comparison of all-leaf and six-leaf methods. Sampling was done at Silwood Bottom, 26 September 1973.

Method / Plant	Six - leaf				All - leaf	
	Mean of 2 leaves at each stratum geometric		arithmetic			
	aphid	mummy	aphid	mummy	aphid	mummy
1	10772	77	2521	48	5735	51
2	14700	95	9123	123	3260	9
3	4228	24	4148	62	745	15
4	4260	72	6066	78	8675	164
5	2333	35	1750	48	440	12
6	7	45	18	56	7	7
7	3648	46	2800	427	3260	31
8	3970	220	3759	202	1610	74
9	24820	357	24679	382	9460	108
χ^{2*}	99689***	2012***	60009***	8063***	-	-
geometric mean	2947	75	2561	111	1383	31
arithmetic mean	7637	108	6096	158	3688	52

* χ^2 is tested against all-leaf method.

*** value significant at $P<0.001$.

3. Determination of field parasitism.

After the 1973-74 season, it was concluded that the percentage of mummies in the aphid population did not give a good indication of the percentage parasitism. This was because many parasitised aphids had not yet become mummified at the time of counting. Therefore in the 1974-75 season, a varying number of live aphids (depending on the total aphid population on the sampled plants) was collected randomly from at least 10 sprout plants and brought back to the laboratory to be reared at 20°C. Subsequently it was found that removing leaf areas with aphids on them was not only more expedient, but it also caused less aphid mortality than brushing off and collecting individuals aphids. The pieces of leaf were placed on an uninfested potted sprout plant in 20°C control room and the aphids allowed to grow. The mummies that ensued from the rearing were collected and kept until the parasites emerged. The percentage of 'live parasitism' is calculated as the number of mummies formed divided by the total aphid number collected. The actual field parasitism is then calculated from the mummy number counted on 50 sprout plants and the percentage live parasitism as shown below.

On 12 June 1974, 1236 aphids and 10 mummies were recorded on 50 sprout plants. 105 aphids of all stages were collected of which 59 mummies were obtained after rearing. This gives a live parasitism of 56.19%. By extrapolation, it would be expected that 1236 aphids would yield 695 mummies. Hence the total parasitised aphids would be 705 which gives a percentage field parasitism of 56.58%, compared to a percentage of mummies of .80%

4. Collection of mummies for the study of parasite emergence.

During the aphid counts, mummies were collected randomly from each plant, the number of which depended on the total available on that plant.

Following collections during 1973-74 it was found that a lot of mortality occured due to fungal infection. To reduce this mortality, the procedure of drying mummies on filter paper was adopted later in the 1973-74 season and in 1974-75 season.

The mummies were kept in vials (2.5 cm by 7.5 cm) lined with filter paper, and stored at different temperatures viz. 20°C, 25°C and field temperature. They were checked daily and parasites that had emerged were removed to avoid hyperparasitism. The parasites were identified, sexed, counted and later in the day released near the crop. This was to ensure that the total number of parasites in the plot remained undepleted drastically over the season.

In 1974, some mummies were also collected from Brevicoryne brassicae on rape to compare the percentage of species of parasites emerging from these mummies. Again this was done at two sites, Silwood Bottom and Ashurst Field.

5. Determination of aerial population of alate aphids and adult parasites and predators.

Two types of traps were used to estimate the aerial populations i.e. sticky traps and water traps. The locations of both traps in the plots were initially selected randomly but were then retained for the whole season. Each trap was examined weekly and the alate aphids, adult parasites and predators were counted.

The designs of these traps are adequately described by Taylor & Palmer (1972).

A. Sticky traps.

Five each of flat horizontal, and vertical cylindrical traps were placed at a height of half to one metre above the ground. Grease-proof papers (37 x 45 cm.) were attached to the trap surfaces and painted with tree-banding grease. The papers were brought back to the laboratory for examination under the binocular microscope.

Since Broadbent (1948) and Heathcote (1957) reported that yellow traps caught more aphid species, it was decided to paint the traps yellow in the 1974-75 season.

B. Water traps.

These were used only in the 1974-75 season, 4 at Silwood Bottom and 2 at Ashurst Field. Yellow bowls of bottom diameter 26.5 cm were painted outside, and the upper inside brown so that only the inside base remained yellow. They were filled to a depth of about 7 cm with a solution made up of stergene (15%), formaldehyde (10%) and water.

All the insects caught in the bowls were collected weekly and brought back to the laboratory for examination under the binocular microscope.

At the beginning of the season, the bowls were placed at ground level. As the plants grew, it was found necessary to raise the traps to about half a metre above the ground to prevent the traps being covered by the leaves.

6. Determination of ovipositional activity of parasites and test of synchronisation.

In essence, the method consisted of exposing a known number of unparasitised aphids to attack by parasites in the fields. Hence these experiments shall be referred to as 'aphid-exposure' experiments.

Ten sprout plants (15 - 18 cm. tall) grown singly in pots were infected with unparasitised B. brassicae of all instars except the alates and the 4th

alatiform nymphs. These instars had been excluded as their emigration might affect the results.

Ten sites were randomly selected in the Silwood experimental plot and the plants were left at their sites. Excessive loss of moisture from the plants was avoided by burying the pots in the soil.

To estimate the activty of the primary parasites 5 of the plants were removed after one week. The others were removed after another week in order to estimate the activity of the secondary parasites.

The plants were then brought back and kept in a 25°C constant temperature room to speed up the mummification of the parasitised aphids. The mummies were collected and kept at 20°C until the parasites emerged.

Before and after leaving the plants in the crop, the aphids on the plants were recorded. The percentage parasitism by primary parasites was calculated as the proportion of aphids (before being left in the field) which became mummified. Similarly the percentage parasitism by secondary parasites was calculated as the proportion of mummies from which secondary parasites emerged.

Analysis of the results for synchronisation is discussed later (p. 78).

7. Determination of parasitism among immigrant alates.

To determine the percentage parasitism among the immigrant B. brassicae alates during the early part of the season, the alates were collected weekly from the field and reared at 20°C for 2 weeks. The mummies resulted were kept until the adult parasite emerged.

PART II. RESULTS AND DISCUSSION.

1. Field populations of Brevicoryne brassicae.

It should be remarked here that although the different aphid instars were distinguished during the counting, this could not be done with great

accuracy as noted by Way (1968) especially when the aphid colonies were large. Hence in this discussion of the changes in the cabbage aphid population, instars have been ignored and only total numbers were used.

The total number of aphid generations for the whole season has not been acertained principally because the generations overlapped as soon as the population began to grow. Nevertheless, Hafez (1961) recorded the number of generations per year in the Netherlands as between 6 and 11.

The populations of B. brassicae in the field for the years 1973-1975 (Fig. 1-3) were calculated as the geometric mean of the 50 plants sampled. It should be emphasised here that the term "aphid population" used hereafter includes all live aphids whether parasitised or not.

The aphid populations in the experimental plots under study showed three different levels of infestations, from light (Ashurst Field, 1974) to medium (Silwood Bottom, 1974) and heavy (Silwood Bottom, 1973). Although the levels of infestations and rates of population growth might differ, the aphid populations on the whole followed a bimodal curve. Such a population growth curve has also been observed by Hafez (1961), Herakly & El Ezz (1970), Akinlosotu (1973) and many others.

In the present study, an initial rise of aphid population from zero to a smaller peak observed as the immigrants began to arrive. This early peak was recorded about 3 to 4 weeks (on 19 June 1974 at Silwood Bottom and on 18 July 1974 at Ashurst Field) or about 8 weeks (on 18 July 1973 at Silwood Bottom) after the sprouts were planted. The number per plant recorded at this peak varied from 5 (Ashurst Field, 1974) to 15 (Silwood Bottom, 1973) and 24 (Silwood Bottom, 1974). Strickland (1957) also mentioned a similar peak occurring in the middle of July, 6 to 8 weeks after the sprouts had been planted.

The aphid population then fell slightly which could be a result of the death or the mummification of some of the alates before they became settled and started reproducing. As the season progressed, the population increased

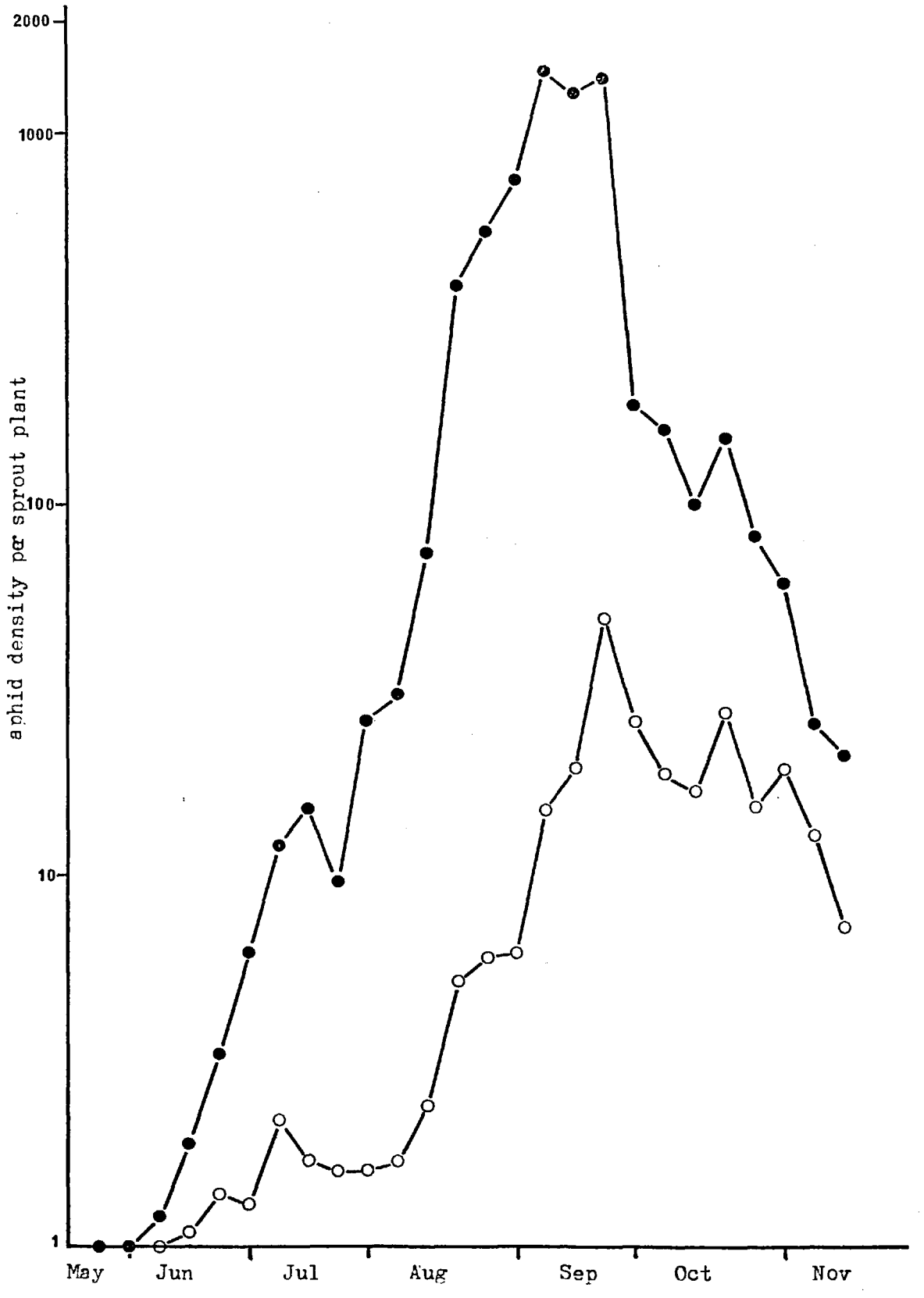
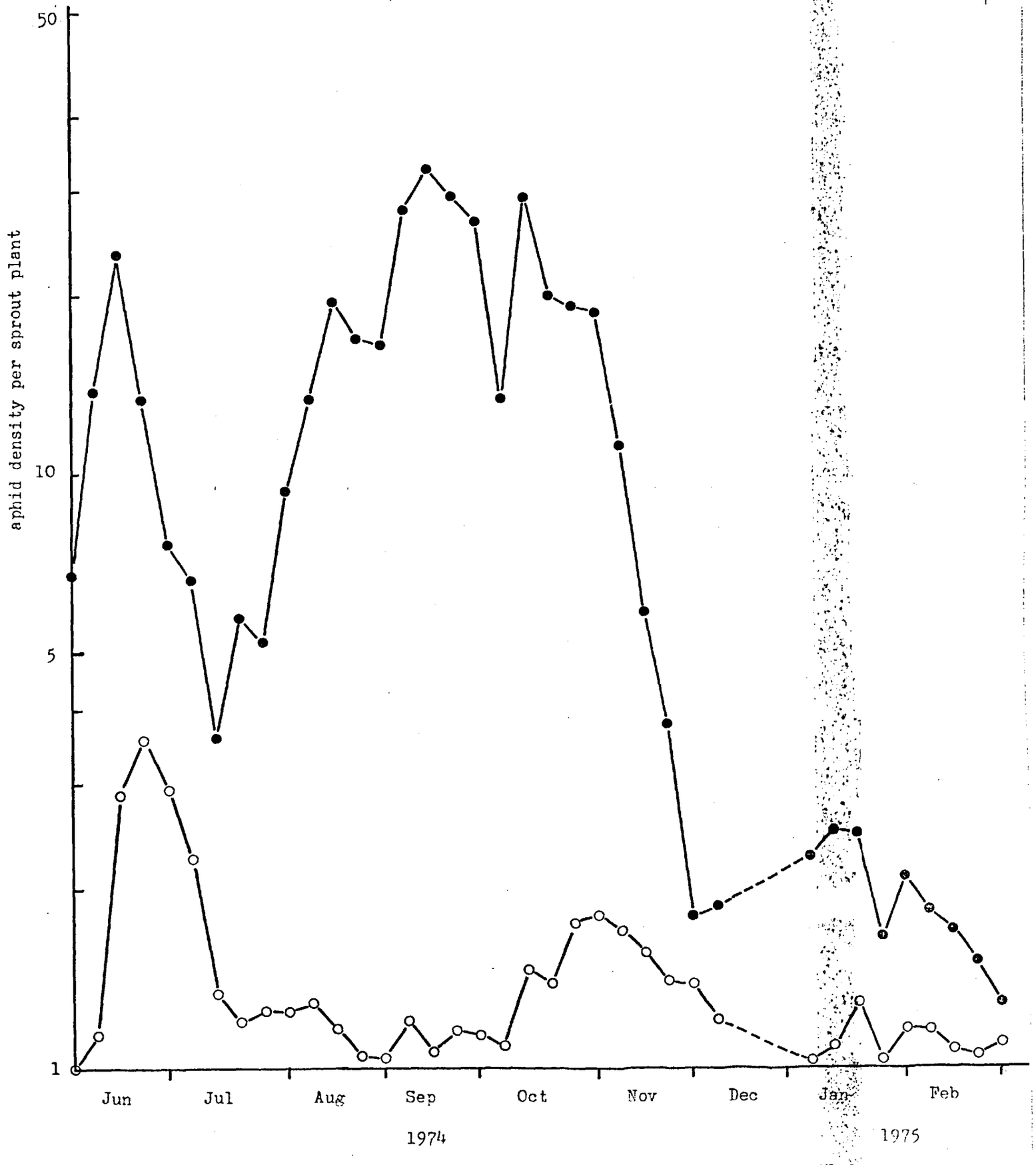


Fig. 1. The population of Brevicoryne brassicae on Brussels sprouts at Silwood Bottom, 1973. The graphs represent the geometric means of 50 plants sampled weekly. (•aphids; ○mummies).

Fig. 2. The population of Brevicoryne brassicae on Brussels sprouts at Silwood Bottom, 1974 - 75. The graphs represent the geometric means of 50 plants sampled weekly. (• aphids; o mummies)



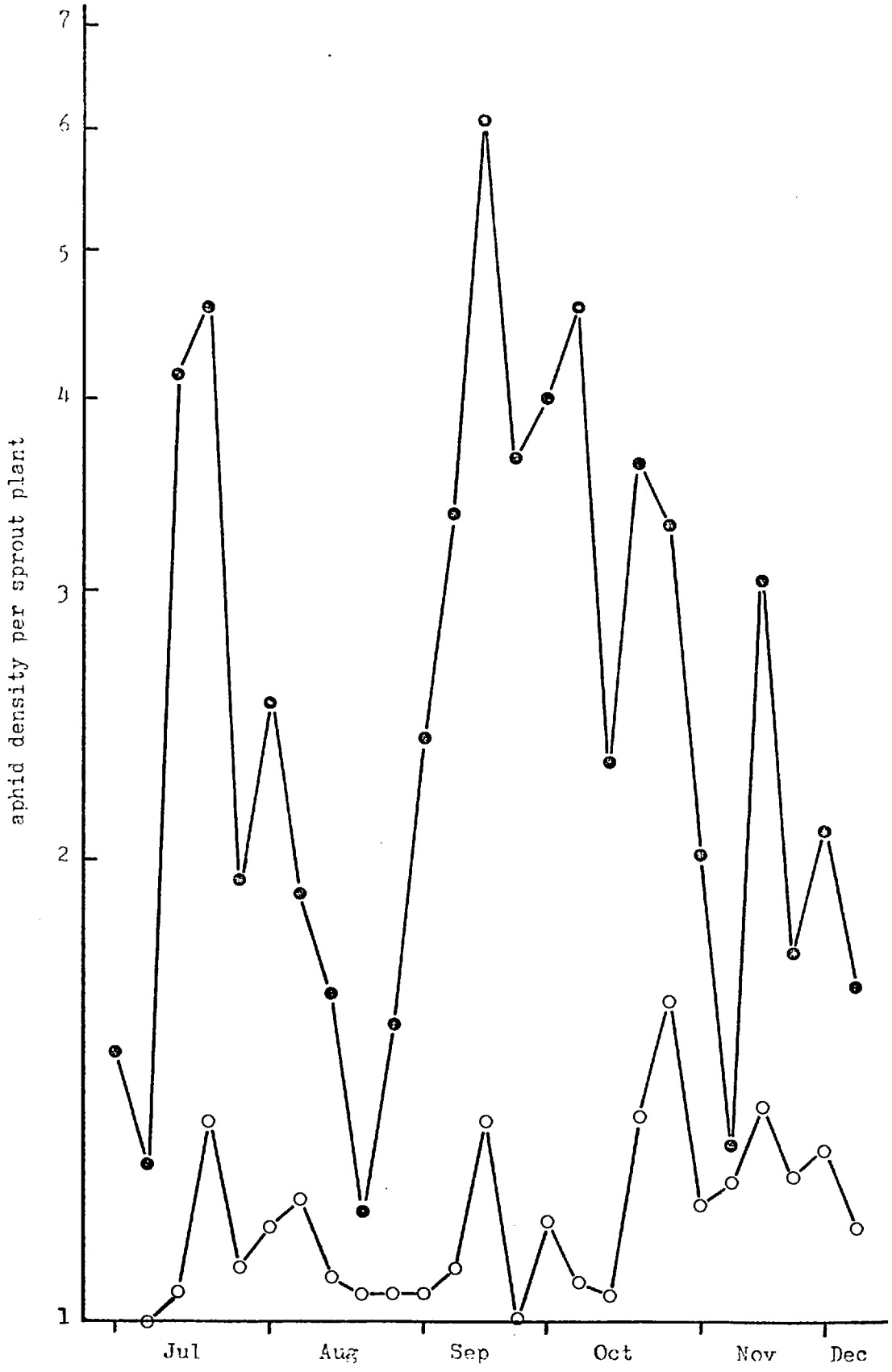


Fig. 3. The population of Brevicoryne brassicae on Brussels sprouts at Ashurst Field, 1974. The graphs represent the geometric means of 20 plants sampled weekly (• aphids; o mummies).

to a much higher maximum before declining once more. The second peaks occurred about the same time in these 3 plots despite the different times when the sprout plants were planted and when the infestation began. The dates of this maximum infestation were recorded about 13 to 16 weeks after the planting namely 12 September 1973, 18 September 1974 (Silwood Bottom) and 19 September 1974 (Ashurst Field). However, as expected the actual number per plant counted on these dates varied considerably from 6 (Ashurst Field, 1974) to 1,471 (Silwood Bottom, 1973). One interesting point which emerges is that although the early peak at Silwood Bottom was slightly higher in 1974 than in 1973, a higher second peak was recorded in 1973. This seems to indicate that the first peak was not a major factor , if at all, in determining the height of the second. Strickland (1957) called this second peak, the seasonal peak which he recorded in the middle of September, about 12 to 14 weeks after sprouts planting.

The decline in aphid population at the end of the season was largely due to the adverse weather conditions (Herrick, 1911; van Emden, 1963; Herakly & El Ezz, 1970; Daiber, 1971a). In fact Petherbridge & Mellor (1936) recorded that the rain in September reduced the aphid populations drastically.

Towards the end of the 1973 season, a great proportion of aphids appeared pink and were killed by an unidentified fungus. This was expecially noticeable in larger colonies in which honey dew accumulated. Hafez (1961), van Emden (1963) and Daiber (1971a) also recorded fungal attack on B. brassicae from September onwards and they attributed the decline in aphid population to the fungus.

The number of mummies followed closely that of the non-mummy aphids, There were also 2 main peaks. The earlier, and usually smaller, one was equivalent to the immigrant alate peak as some of these alates were no doubt parasitised (see p. 43). The later peak was equivalent to the main aphid peak. However, as expected, both the mummy peaks were usually later than

the aphid peaks. The early peak was usually one week after the aphid peak, while the later peak occurred 2 to 6 weeks after the corresponding aphid peak. As with the aphid population, the maximum mummy number also varied considerably. The highest was 76 per plant, recorded at Silwood Bottom in 1973, which could be a result of the higher aphid population in the same year.

The percentage of mummies indicates roughly the rate of parasitism in the field as only those parasites in the final larval or pupal stages are included. This leads of course to an underestimation of the actual percentage parasitism. The percentage parasitism (see p. 15 for method of calculation) is a more accurate estimate since both mummies and younger parasite stages are included in the calculations.

The percentage of mummies was high at the beginning and the end of the season with a period of low values in the middle (Fig. 4). The two-peak pattern was similar to the aphid population and mummy number. The first peaks were recorded around June to July, about 5 to 8 weeks after the sprouts were planted, while the second peaks occurred around mid-November to mid-December. Generally, however, the percentage of mummies was low with maximum values of 13.4 (Silwood Bottom, 1973), 27.8 (Silwood Bottom, 1974) and 54.5 (Ashurst Field, 1974). The exceptionally high percentage recorded at Ashurst Field could be a result of the low aphid population.

In 1974, during which the percentage parasitism was also studied, a clèarer picture of field parasitism can be seen. Generally both the percentage of mummies and percentage parasitism followed each other closely except in the beginning and the middle of the season. In the first 2 weeks, the percentage of mummies for Silwood Bottom were 0 and only 0.8 while the percentage parasitism were 50 and 56.6 respectively (Fig. 4C). In the ensuing weeks, however, percentage parasitism dropped while the percentage of mummies increased. The probable explanations are that in the early weeks

Fig. 4. The percentage of mummies and the percentage parasitism of Brevicoryne brassicae in the field.

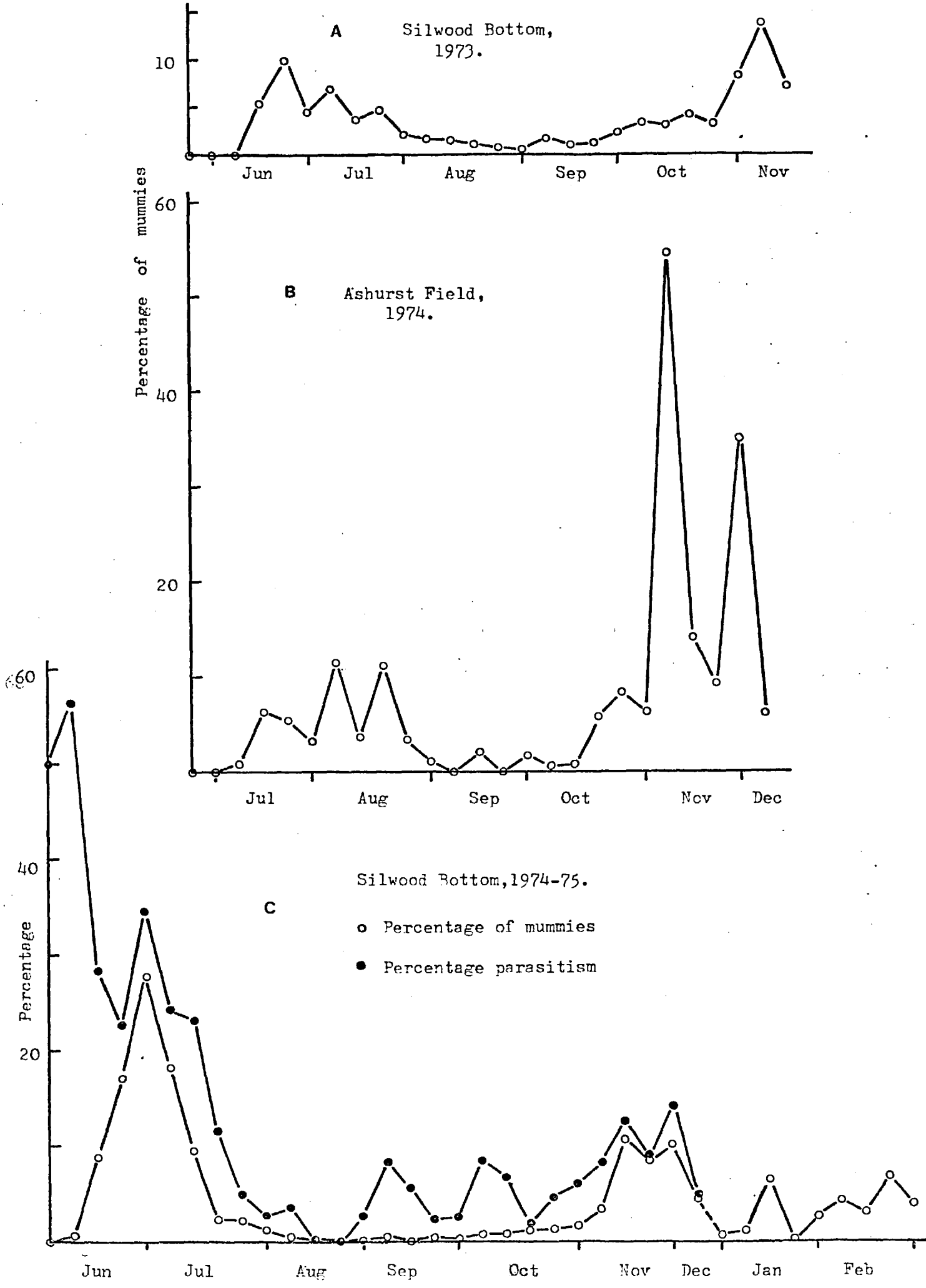

A
Silwood Bottom,
1973.
10
Jun
Jul
Aug
Sep
Oct
Nov
Percentage of mummies
60
40
20
B
Ashurst Field,
1974.
Jul
Aug
Sep
Oct
Nov
Dec
60
40
20
Percentage
C
Silwood Bottom, 1974-75.
o Percentage of mummies
● Percentage parasitism
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
1974
1975

Fig. 4.

some of the immigrant alates were already parasitised and the first generation of nymphs newly attacked by the immigrant parasites had not yet become mummified. As mummification proceeded within the next one to 2 weeks, there was an increase in the number of mummies recorded. Similarly, the second peak might be explained by the decline in aphid population later in the season, resulting in an apparent increase in mummy number. Van Emden (1963) also recorded a similar increase in mummy numbers at the end of the season.

The percentage field parasitism of B. brassicae had also been studied by George (1957), Hafez (1961), van Emden (1963) and Daiber (1971a,b). Hafez (1961) found parasitism in the first generation of the immigrants could be as high as 80 to 90%, but this was the only instance of high rates of parasitism observed. Generally he recorded low percentage and concluded that parasitism leads only to small fraction of the mortality of the aphid and is not the main factor causing the population changes. George (1957) and van Emden (1963) also recorded low field parasitism with the respective maximum of 14% and 30%. They and others (Petherbridge & Mellor, 1936; Otake ,1961; Oatman & Platner, 1973) concluded that the primary parasite could not control the aphid population. The unanimous reason given (George, 1957; Hafez 1961; Sedlag, 1964; Paetzold & Vater 1967; Oatman & Platner, 1973) is that the effectiveness of the primary parasites was reduced drastically by the secondary parasites. This will be dealt with in greater detail later.

However, a few workers reached a different conclusion. For example, Barnes (1931) stated heavy parasitism controlled the aphids' attack late in the season, while Herrick & Hungate (1911), Strickland (1916) claimed that the aphids never reached high densities because of the parasites.

The results of the sticky traps set up in 1974 show an increase in the number of syrphids caught during September (Fig. 6A). A concomitant decline of aphid population was noted. This decrease could be ascribed to predation by the syrphid larvae. The importance of syrphids in contributing to the

decline of aphids has also been echoed by other workers such as Petherbridge & Mellor (1936), George (1957), Hafez (1961) van Emden (1963), Way et al., (1969) and Pollard (1971).

It is interesting to note that during the three-year study, aphid eggs have never been recorded, although the other workers had encountered them as early as September (Hafez, 1961; Petherbridge & Mellor, 1936) or October (Herrick, 1911). Petherbridge & Wright (1938) also stated that egg laying commences in late September and terminates in mid-December. The absence of eggs was probably due to the mild winter during which the aphids could survive as virginoparae.

In conclusion, the B. brassicae population could be described as a bimodal curve with a small early peak and a larger one later in the season. The primary parasite Diaretiella rapae was found to be ineffective as a control agent of the aphids. Mortality of aphids due to syrphids, fungus and low temperature appear to be more important and these mortality factors caused the decline of aphid population later in the season.

2. Parasite species of B. brassicae.

In 1973 and 1974-5, 5074 and 1711 mummies respectively were collected from sprout plants at Silwood Bottom, and 147 were collected from Ashurst Field in 1974. In 1974, 574 and 66 mummies were collected from rape at Silwood Bottom and at Ashurst Field respectively.

From these mummies, 5 species of hymenopterous parasites belonging to 4 families emerged namely:

1) Aphidiidae: Diaretiella rapae (McIntosh)
2) Charipidae: Alloxysta brassicae (Ashmead)
3) Pteromalidae: a) Asaphes vulgaris Walker
   b) A. suspensus (Nees)
   c) Pachyneuron minutissimum (Förster)
4) Megaspilidae: Dendrocerus carpenterii (Curtis)

These 6 species have been recorded by many previous authors (Appendix 1).

Evenhuis (1972) on a taxonomic study of cynipidae Alloxystinae suggested that "all Alloxystinae hyperparasites of Brevicoryne brassicae through the primary parasite Diaretiella rapae, mentioned in literature from different parts of the world, belong in fact to the same species" viz. Alloxysta brassicae. This would in effect synonymise Xystus brassicae Ashmead (Herrick, 1911, Lowe, 1959), Charips longicornis (Hartig) (Barnes, 1931), Charips vitrix var infuscata (Kieffer) (Petherbridge & Mellor, 1936), Charips minuta (Hartig) (Bilanov'skll, 1938; Herakly & El Ezz, 1970), Charips ancylocerus (Cameron) (Hafez, 1961) and Charips vitrix Westw. (Way et al., 1969) with Alloxysta brassicae.

There are also 7 other species which have not been encountered in this work. These are Aphidius piceus (Cress.) (Herrick, 1911; Mellor & Yothers, 1915; 1917), Asaphes fletcheri (Crawford) (Godfrey & Root, 1968), Asaphes rufipes Brues (Herrick, 1911; Melander & Yothers, 1915; 1917), Lygocerus niger How. (Godfrey, 1930; Todd, 1957; Godfrey & Root, 1958), Pachyneuron micans How. (Herrick, 1911; Melander & Yothers, 1915; 1917), Tetrastictues rapo Walk. (Bilanovskell, 1938) and Aphidencyrtus africans Gahan (Daiber, 1971b). It is suspected, however, that at least some of these could be synonyms of species listed elsewhere.

3. Aerial population of alates, parasites and predators of B. brassicae.

A. Results.

i) Sticky traps.

The number of insects caught were much higher in 1974 (compare Fig. 5 & 6) despite the fact that in 1973 the population of B. brassicae and hence parasite or predator numbers were much greater. This was because the traps were painted yellow in 1974 and thus direct comparisons cannot be made.

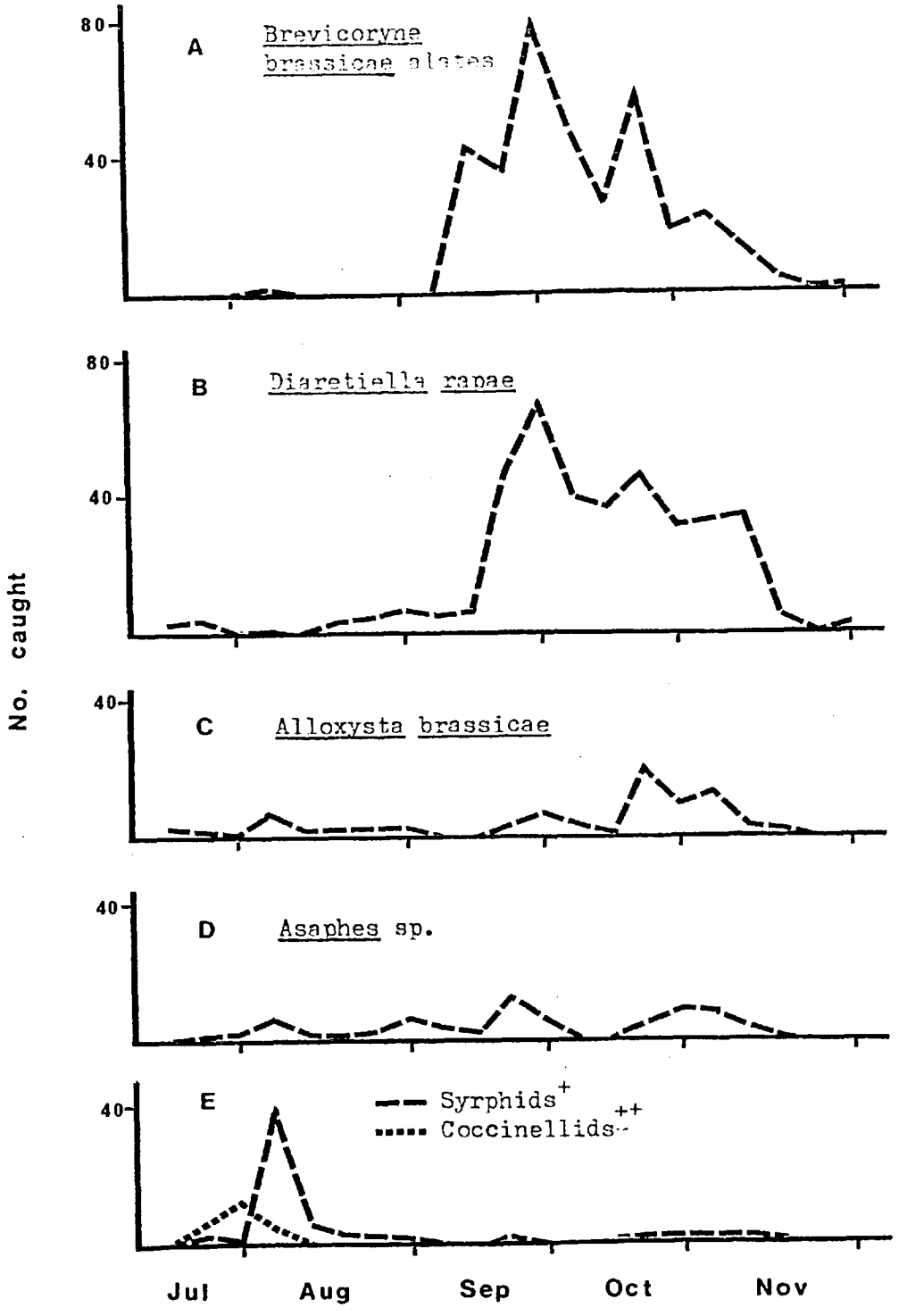


Fig. 5. The weekly total catch of 5 sticky traps (vertical cylindrical type) set up at Silwood Bottom, 1973.

+ Platycheirus peltatus, Syrphus balteatus, Sphaerophoria sp.

++ Adalia bipunctata, A. decempunctata.

Fig. 6. The weekly total catch of 5 sticky traps set up at Silwood Bottom, 1974.

Vertical, cylindrical traps ————

Horizontal, flat traps ....

A) Syrphids (*Platycheirus peltatus*, *Syrphus balteatus*, *Sphaerophoria* sp.)

B) Coccinellids (*Adalia bipuntata*, *A. decempunctata*)

C) *Dendrocerus carpenterii*.

D) *Asaphes* sp.

E) *Alloxysta brassicae*

F) *Diaretiella rapae*

G) *Brevicoryne brassicae* alates.

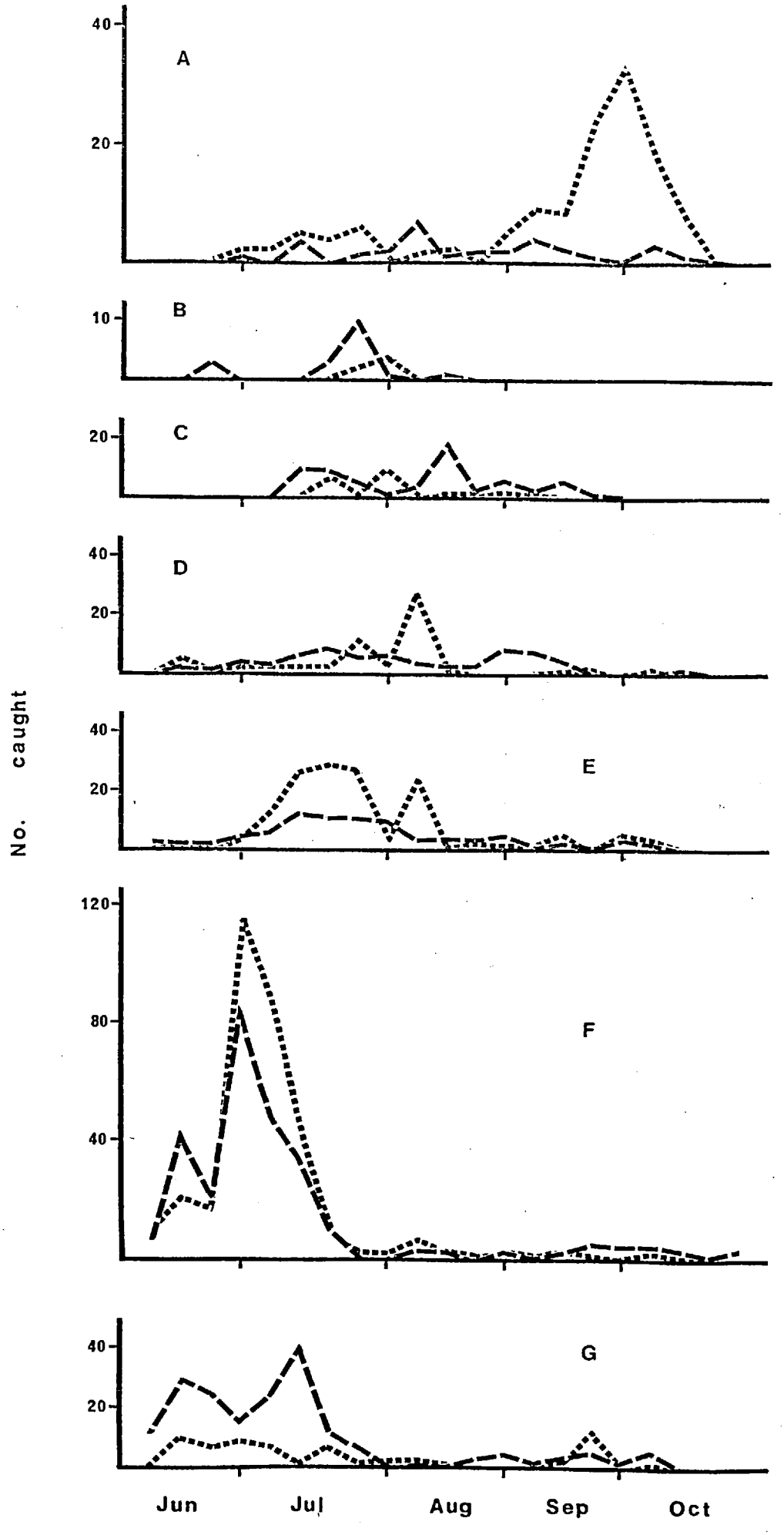


Fig. 6.

Comparisons of the number recorded in 1974 (Fig. 6) suggest that flat sticky traps are generally better for catching parasites and predators while the vertical ones are better for alate aphids.

Among the parasites, D. rapae was recorded in highest numbers, followed by A. brassicae and Asaphes sp. and finally 2 relatively uncommon species namely: P. minutissimum and D. carpenterii.

The parasites usually had one main peak, the timing of which depended on their biology. D. rapae being the primary parasite had the earliest peak and was followed by A. brassicae and then Asaphes sp. The peaks for D. rapae in 1973 was between 29 September and 5 October, whereas in 1974 it was much earlier at about the end of June. The earlier peaks in 1974 are also evident for A. brassicae, Asaphes sp. and B. brassicae alates. The reverse was true of the syrphids which had an earlier peak in 1973 (between 4 July and 11 August) than in 1974 (between 26 September and 2 October).

As it was uncertain till 1974 whether P. minutissimum and D. carpenterii are parasites of B. brassicae, they were omitted in the count for 1973. In 1974, they were recorded in very small numbers. For example, only 5 specimens of P. minutissimum were caught, one in the week between 8 and 15 August, 2 in the week between 5 and 12 September and one in the week between 12 and 19 September.

The wave of immigrant B. brassicae alates occurred only at the beginning of the sprouts season in 1974 (June to July), and by the end of July the immigrants dwindled to negligible numbers. However in 1973, almost none was caught until 8 September. From this date onwards, great numbers of B. brassicae were recorded reaching a peak number of 16 per trap at the end of September. The number then decreased falling to zero in November. This great increase in the number of B. brassicae alates caught so late in the season must have been due to the emigrating rather than immigrating alates. This view is substantiated by the fact that the number of alates counted on 50 sprout plants increased steadily from 46 on 3 August to 13,000 on

19 September.

ii) Water traps.

a) Silwood Bottom.

In 1974 the parasites recorded in greatest numbers were A. brassicae, followed by D. rapae and Asaphes sp. (Fig. 7). Almost twice as many A. brassicae as D. rapae were caught. D. carpenterii was recorded in very small numbers while only a female P. minutissimum was caught in the week between 10 and 17 July. Each parasite species had a single peak and as for sticky traps, the primary parasite D. rapae had the earlier peak (26 June to 3 July), followed simultaneously by the other three species: A. brassicae, Asaphes sp. and D. carpenterii (e.g. A. brassicae during 17 to 24 July).

Alates of B. brassicae were recorded in greatest numbers at the beginning of the season, when the sprouts were first planted. The immigrant alates began to decrease as the season progressed and only very small numbers were recorded after 3 July. The number of B. brassicae alates caught by the yellow water traps followed closely that counted on 50 sprout plants for at least the first 7 weeks, probably indicating that the alates found on the plants at the beginning of season were mostly immigrants. From the eighth week (24 to 31 July) onwards, the alates on the plants increased (as the total aphid population increased), while the number of alates caught remained low suggesting that few or no alates were emigrating at this time or being attracted to yellow water traps.

In 1975, water traps were set up about 8 weeks before the sprouts were planted, with the intention of determining the time of arrival of alates and parasites.

The results (Fig. 8) show that B. brassicae alates, adults of Diaretiella rapae and Dendrocerus carpenterii were already around the area during 14 to 21 May, 3 weeks before the sprouts plant were planted. The number of

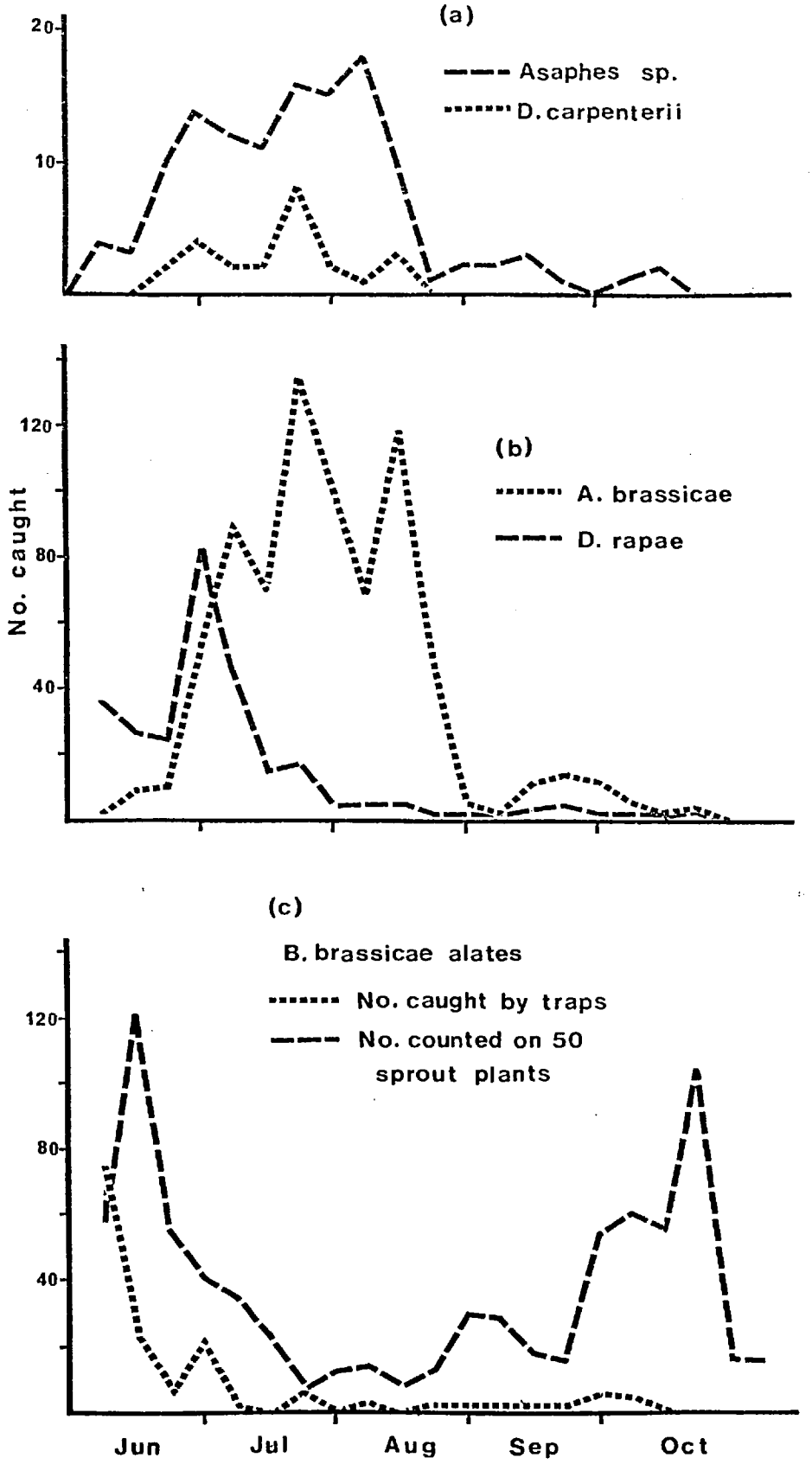


Fig. 7. The weekly total catch of 4 water traps set up at Silwood Bottom, 1974.

Fig. 8. The weekly total catch of 5 water traps set up at Silwood Bottom, 1975.

A) *Dendrocerus carpenterii* _____

Asaphes sp. --------

B) *Brevicoryne brassicae* alates _____

Diaretiella rapae -------

Alloxysta brassicae ------

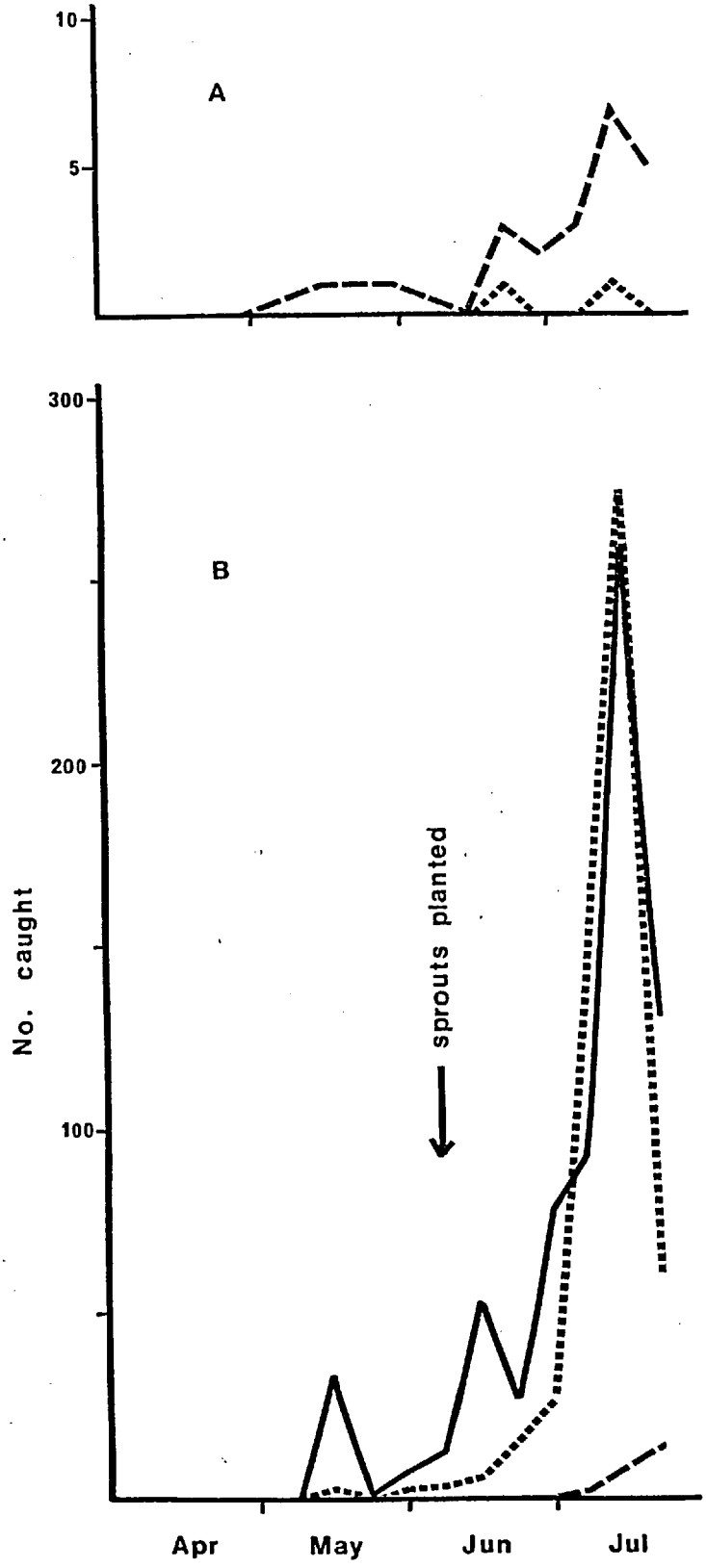


Fig. 8.

Table 3. The weekly total catch of 2 water traps set up at Ashurst Field, 1974.

Species / Week	B. brassicae (alates)	M. persicae (alates)	D. rapae	A. brassicae	Asaphes sp.	Others
11 - 18 July	-	1	1	13	-	1+
18 - 25 July	3	7	2	51	-	-
25 July - 1 August	-	2	-	47	1	-
1 - 8 August	3	2	-	4	1	-
8 - 15 August	-	-	-	6	-	-
15 - 22 August	1	-	-	4	1	-
22 - 29 August	-	-	-	2	-	-
29 - 5 September	-	-	-	5	-	-
5 - 12 September	-	1	-	1	-	-
12 - 19 September	-	4	-	1	-	-
19 - 26 September	-	-	-	1	-	1*
26 September - 3 October	-	1	-	4	-	-
3 - 10 October	1	-	-	-	1	-
10 - 17 October	-	-	-	2	-	-
17 - 24 October	-	-	-	-	-	-
24 - 31 October	-	1	-	-	-	-

\+ Dendrocerus carpenterii

* Melanostoma sp. (syrphidae).

alates and D. rapae generally fluctuated together, both reaching a peak during the week 9 to 16 July. A. brassicae, on the other hand was first recorded much later (2 to 9 July) when B. brassicae and D. rapae populations were already well established.

With respect to the other parasite species, the catches were similar to those in 1974 in that a) P. minutissimum was not caught at all, and b) D. carpenterii and Asaphes sp. were caught in low numbers.

b) Ashurst Field (Table 3).

The small experimental plot at Ashurst Field had only 100 plants and 2 traps. It is not surprising that except for A. brassicae, the numbers caught were very low. A. brassicae was recorded in peak number during the same week (18 to 25 July) as in Silwood Bottom.

B. Discussion.

When evaluating the results of the sticky and water traps for 1974, a few points need to be considered.

The numbers of traps and the trapping areas of each type were different. The sticky traps each offered a trapping area of 1665 sq. cm., while a water trap was only 1104 sq. cm. Therefore the total trapping area of both types of sticky traps = 1665 x 5 = 8325 sq. cm., which was almost twice that of water traps (= 1104 x 4 = 4416 sq. cm.). If the sticky and water traps were of equal trapping efficiency per unit area, one would expect the numbers caught per unit area by the 2 sticky trap types to be a) identical with each other, b) twice as many as that caught by the water traps. This however, was not the case showing that the trap types were not of equal efficiency.

The water traps were found to catch more alates and parasites that both types of sticky traps. For example, the respective maximum catches per 1000 sq. cm. trapping surface by water traps, vertical and horizontal sticky traps were for B. brassicae alates: 17, 5 and 1, for D. rapae: 19, 10 and 14,

and for A. brassicae: 30, 1 and 3.

With respect to sticky traps, the higher catch of parasites by flat traps could be a result of greater attraction of flat traps as surfaces for alighting by the parasites. On the other hand, the vertical traps caught more alates than flat ones could only be a result of the poor flying ability of alates. The alates could fly independentaly of the wind only at very low wind speed ($1\frac{1}{2}$ miles per hour or less, as suggested by Heathcote, 1957). These results agree with Heathcote's (1957) findings when he concluded that water traps caught more aphids than flat sicky traps which in turn caught only half as many as the vertical cylindrical ones. He also suggested that the number of alates caught on vertical traps depends largely on air movements and therefore that wind increases the catch.

The results from these 3 types of traps not only agree substantially with, but also complement each other. For example, the peak numbers recorded by these 3 types for D. rapae, A. brassicae and Asaphes sp. all fall on the same week viz. 26 June to 3 July, 17 to 24 July and 7 14 August respectively. Such data also gives a clue as to the relation between these parasites since the timing of the peaks suggest that A. brassicae is parasitic on D. rapae while Asaphes sp. is parasitic on A. brassicae. However, it is not possible to infer if D. rapae is parasitised by Asaphes sp. or not.

The catches of water traps in 1975 indicate clearly B. brassicae alates and adult D. rapae were around the plot long before the Brussels sprouts were planted. It is not clear where these immigrated from, though D. rapae adults could have emerged from overwintering mummies left in the soil (Way et al., 1969). This seems to suggest that B. brassicae and D. rapae were not well synchronised with their respective hosts. A. brassicae however appears to have better synchronisation with its host as it was recorded only much later when D. rapae was already established.

4. Counts of parasites and predators in the field.

During the aphid count on 50 selected sprout plants, live adult parasites and immature syrphid (larvae and pupae) were also counted (Fig. 9 - 10).

The number of parasites recorded in the earlier part of 1973 season were less than those in 1974. For the second half of the season however, the parasite numbers in 1973 continued to increase while in 1974 they were recorded in very low numbers which was probably due to the much lower aphid populations throughout the season. Again, as shown by catches of the sticky traps, A. brassicae's first peak was later than D. rapae.

The syrphid number recorded in 1973 was higher than in 1974 although they appeared earlier in 1974. The peaks however, in both years were around the same time viz. 9 to 16 October.

Generally, the numbers of adult parasites recorded during aphid count provide a reasonable indication of their activity in the field. The numbers thus recorded also agree with those caught by sticky and water traps. In fact, the dates on which the peak parasite numbers were recorded by these three different methods agree in all except for A. brassicae and Asaphes sp. in 1973.

5. Ovipositional activity of parasites in the field.
(Fig.11, 12).

Since the plants were exposed in the field for one to 2 weeks, the actual number of aphids available for attack daily was intermediate between the number recorded before and after the experiments. The number counted after the exposure period would be expected to be higher, but this was not necessarily so, as predation by syrphid or coccinellid larvae and adverse climatic conditions could reduce the aphid density drastically.

In both years, high percentage parasitism (86% in 1974 and 99% in 1973) was recorded only once and then only in the early weeks. The percentage then

Fig. 9. The weekly counts of parasites and predators of *B. brassicae* on 50 sprout plants at Silwood Bottom, 1973.

A. *Diaretiella rapae* — — —
Alloxysta brassicae .....
Asaphes sp. ——

B. Syrphids (larvae and pupae)

Adult coccinellids were recorded on 3 occasions only: one each on 27 June, 18 July and 15 August.

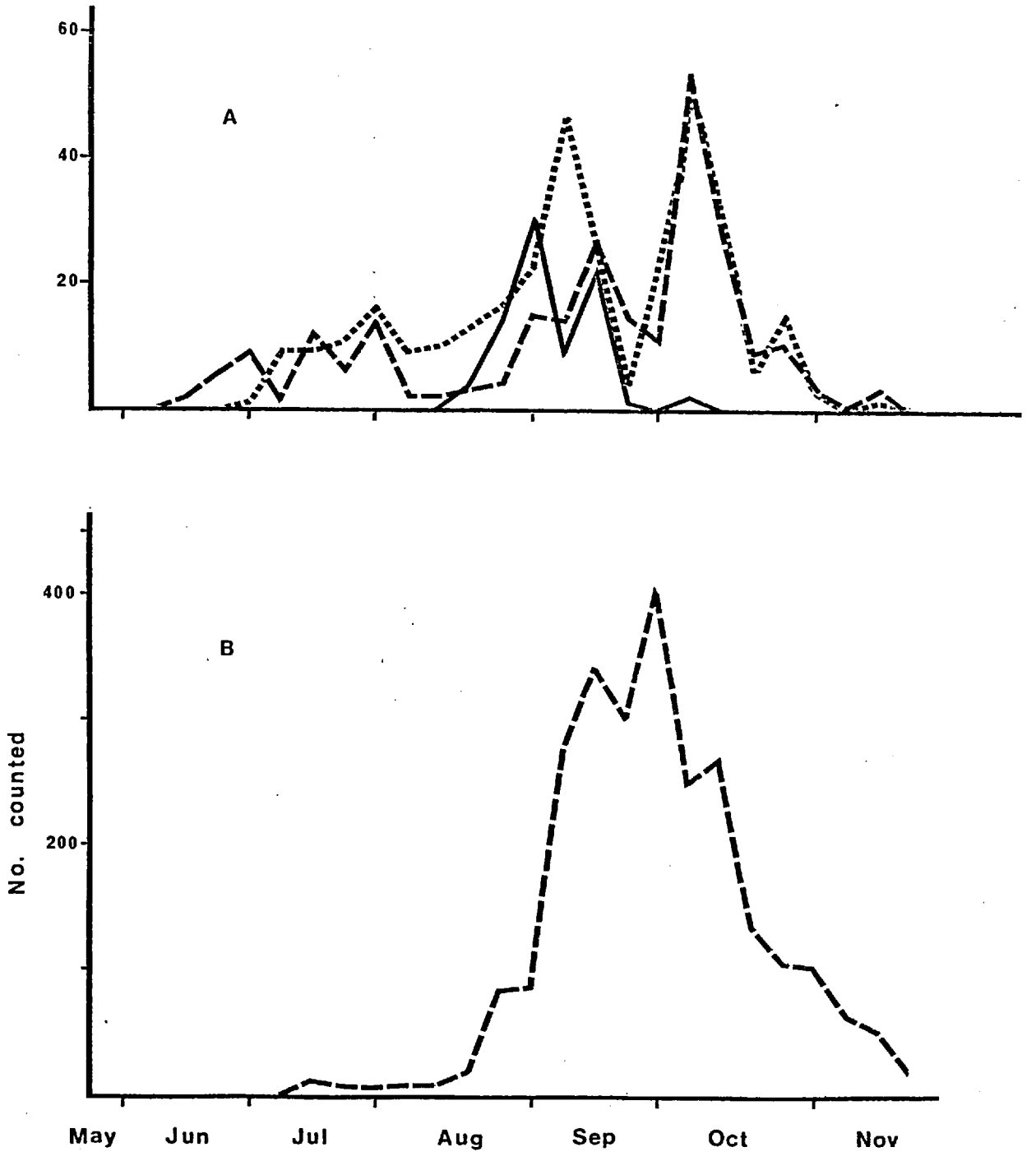


Fig. 9.

Fig. 10. The weekly counts of parasites and predators of *B. brassicae* on 50 sprout plants at Silwood Bottom, 1974 - 75.

A. *Diaretiella rapae* .....

Alloxysta brassicae — — —

Asaphes sp. ——

B. Syrphids -— — (larvae and pupae of *Platycheirus peltatus*, *Syrphus balteatus*)

Coccinellids ..... (adults of *Adalia bipunctata* and *A. decempunctata*.)

Fig. 10

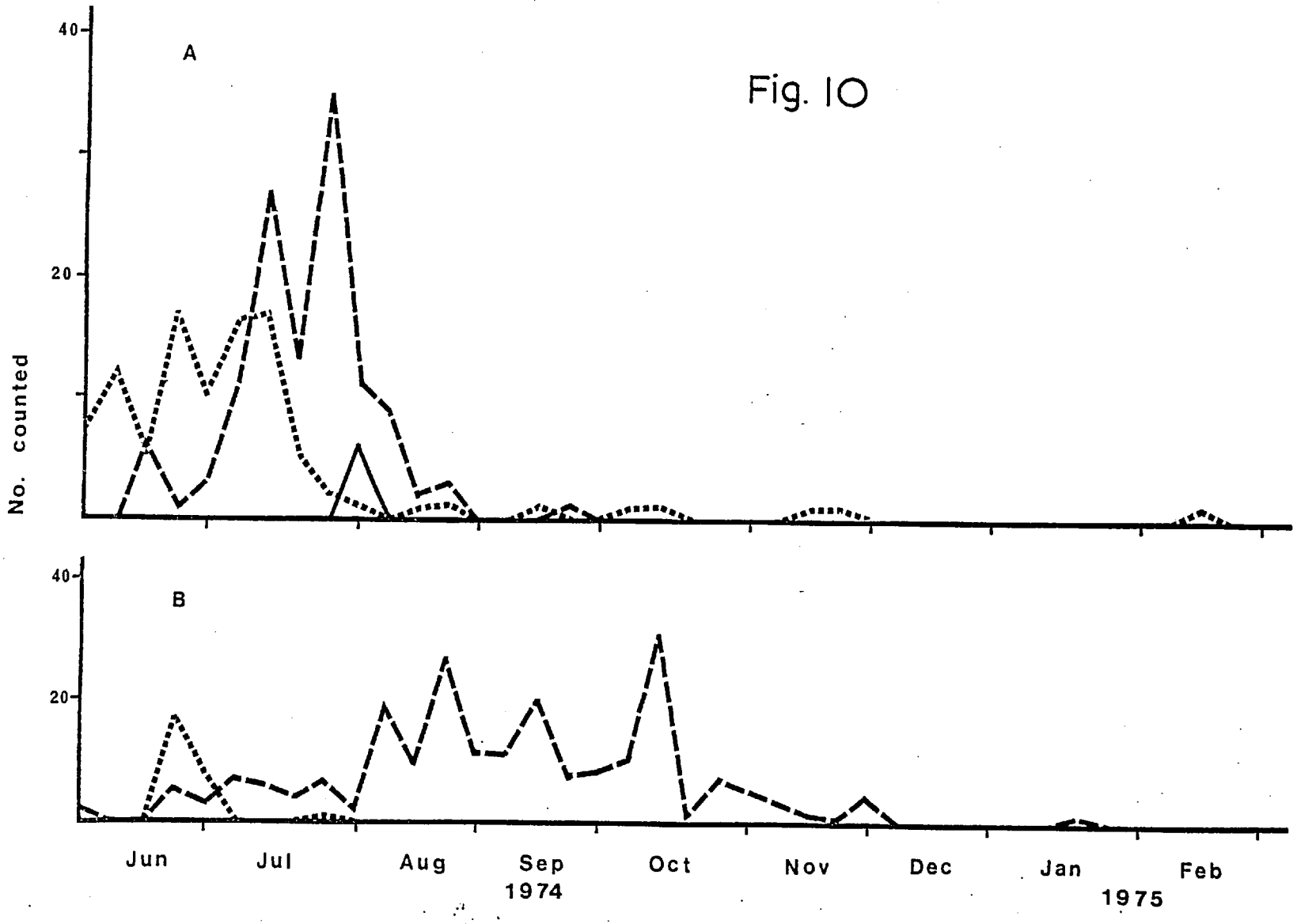

A
B
40
20
No. counted
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
1974
1975

Fig. 11. The results of aphid-exposure experiments carried out at Silwood Bottom, 1973. The aphids were exposed to attack by parasites in the field for 1 week (o) and 2 weeks (•).

Fig. 12. The results of aphid-exposure experiments carried out at Silwood Bottom, 1974. The aphids were exposed to attack by parasites in the field for 1 week (o) and 2 weeks (•).

Fig. 11.

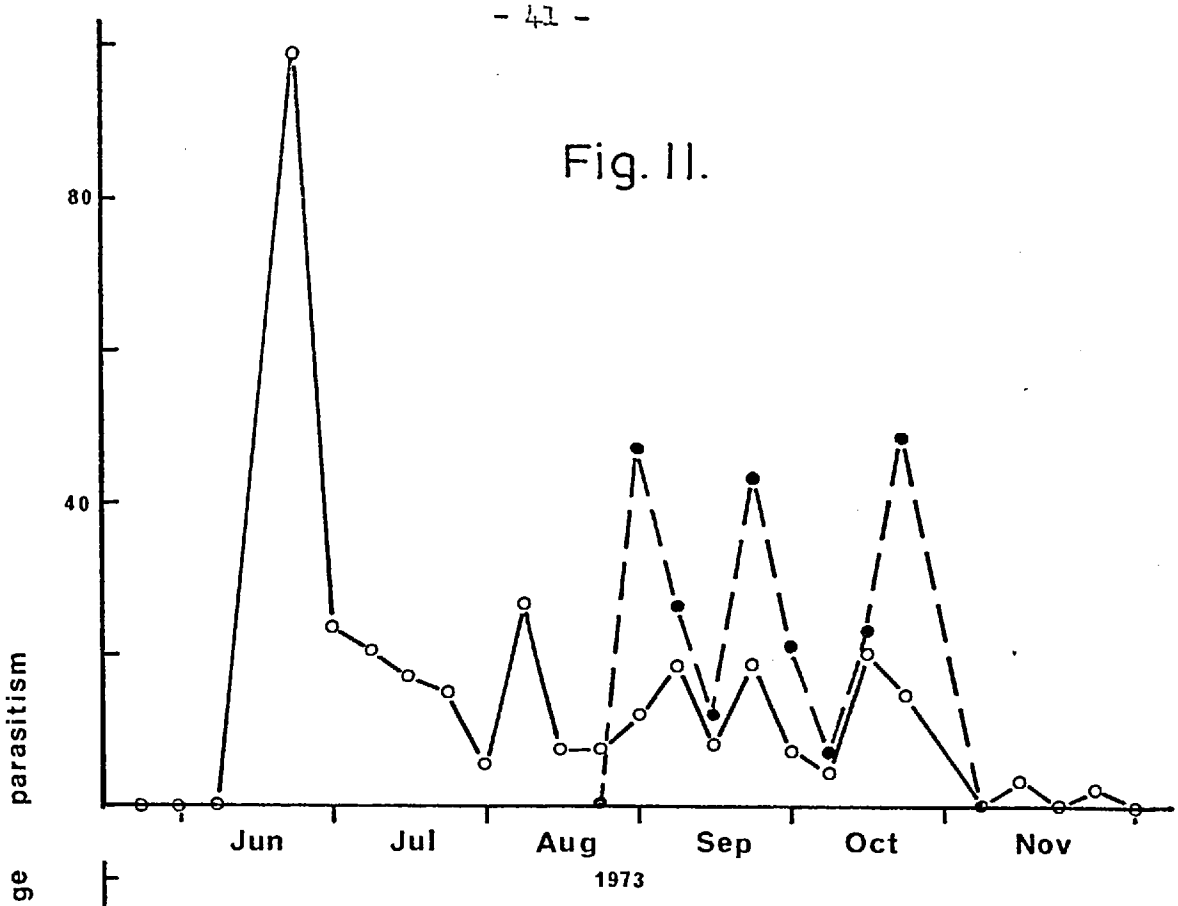
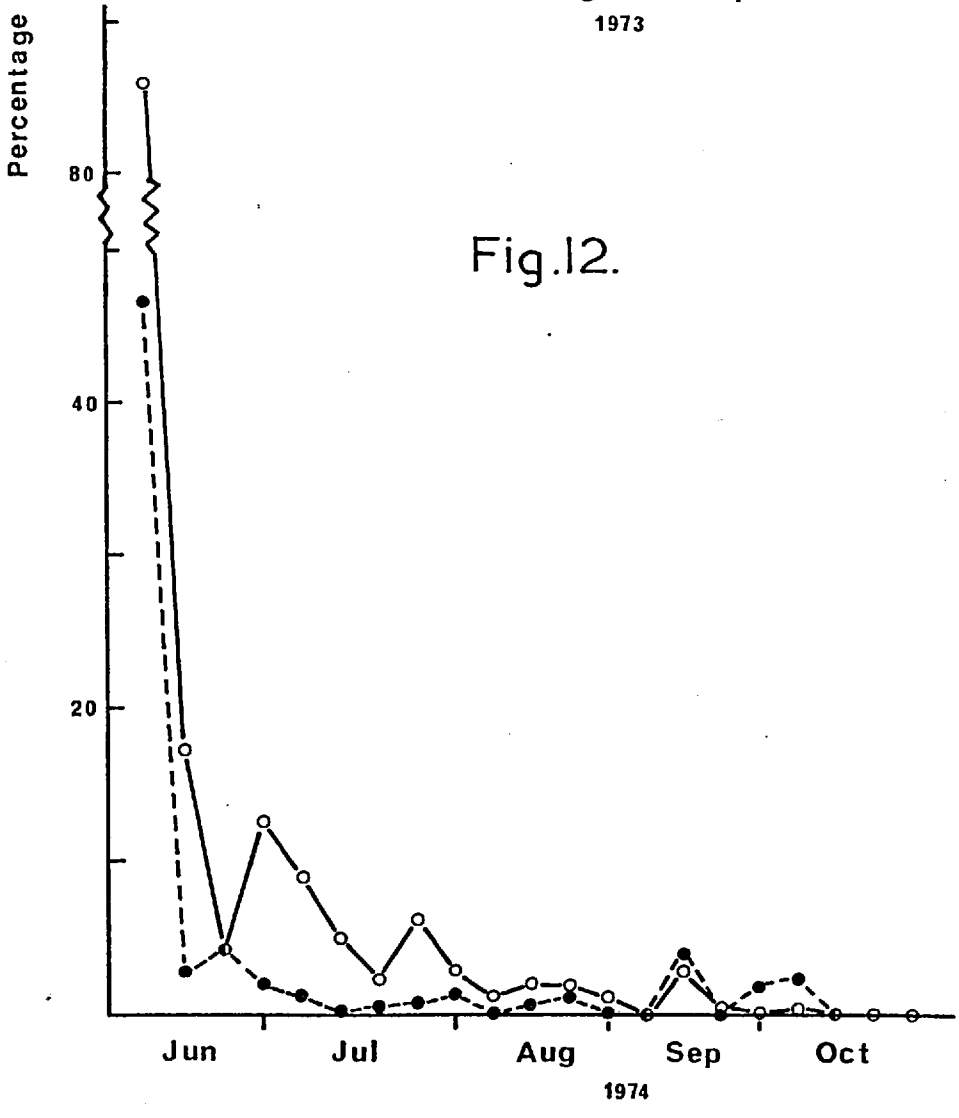

80
40
parasitism
Jun
Jul
Aug
Sep
Oct
Nov
1973

Fig.12.


Percentage
80
40
20
Jun
Jul
Aug
Sep
Oct
1974

decreased and fluctuated between 5-30% (1973) and 1-15% (1974), before it finally declined to zero at the end of the experimental period. The early high percentage was due mainly to the low field aphid population (Fig. 1-2), which resulted in the attraction of parasites to the relatively higher aphid density available on the experimental plants.

No apparent relation was observed in 1973 between the percentage parasitism of aphids exposed to attack and the numbers of D. rapae caught by sticky traps or recorded during the aphid counts on 50 sprout plants. In 1974, however, a definite correlation was noted. Excluding the result of the first weeks when the aphids on the experimental plants were much higher than the field plants, the peak percentage parasitism was recorded during the week when peak D. rapae numbers were caught by both the sticky and water traps, and also noted on the 50 sampled sprout plants.

Comparing the percentage of mummies, the percentage field parasitism and the results of aphid-exposure experiments, the following points may be made. Close correlation between these various estimates of parasite activity was observed especially in the early part of the season. The early peak percentage parasitism recorded from the experiments in 1973 coincided with the early peak percentage of mummies while the same in 1974 coincided with the maximum percentage field parasitism.

These observations also concur with studies on aphid field populations and results of sticky and water traps. All these support the view that the increase in percentage of mummies recorded later in the season (Fig. 4) was not due to the increase in parasite activity or parasite number but actually due to a decrease in the aphid number.

In 1973, mummies were not recorded until 20 June (Fig. 1) while parasitism of aphids exposed in the field was not observed until 19 to 27 June. Similarly in 1974, mummies first appeared on 12 June (Fig. 2), the second week after the sprouts were planted, while parasitism in the aphid-exposure experiments was first recorded during 6 to 12 June. This is

further confirmed by the percentage field parasitism (Fig. 4) which shows 50% of aphids in the field were parasitised on 5 June. These results seem to indicate that in 1974 the primary parasite, D. rapae was active much earlier in the field (5 June) than in 1973 (20 June).

On the other hand, if percentage parasitism could be taken as an indication of parasite activity, it might be interpreted that the activity of primary parasites (including emergence from mummies) in the field appeared to have been reduced earlier in 1974 (9 October) than in 1973 (2 November). This inference is supported by the records of percentage emergence of D. rapae from mummies collected from the field (Fig. 13, 16). The mummies collected on 31 October 1973 and 16 October 1974 contained more than 90% of overwintering parasites.

6. Percentage parasitism among immigrant B. brassicae alates.

The results (Table 4) showed that many of the immigrant alates were parasitised, with percentage parasitism ranging from 3.3% to 46.2%. Hughes & Gilbert (1968) quoted a figure of 20%. It is noteworthy that only D. rapae emerged from the mummies.

It is clear then that many D. rapae individuals are carried into an aphid population by the immigrant alates themselves, although results of sticky and water traps also show that some adults immgrate on their own. Results of immigrant alate-rearing also show that some alates did not produce any nymphs before they became mummified, indicating not all alates arriving at a crop contribute to the growth of an aphid generation.

Table 4. The percentage parasitism among immigrant B. brassicae alates. Note that only D. rapae emerged from the mummies produced. Locality: Silwood Bottom. Dates of planting were 24 May 1974 and 3 June 1975.

Date (1974)	No. alates collected	% parasitised	Date (1975)	No. alates collected	% parasitised
5 June	19	15.8	11 June	30	3.3
12 June	20	30.0	18 June	51	46.2
19 June	6	33.3	25 June	76	17.1
26 June	5	0	2 July	152	29.6
3 July	2	0	9 July	38	26.3
10 July	-	-	16 July	36	13.9
18 July	2	0			
24 July	-	-			
31 July	2	0			
8 August	2	0			

SECTION III. STUDIES ON PARASITE EMERGENCE FROM MUMMIES COLLECTED FROM THE FIELD.

1. Percentage of individual species of parasites.

The disadvantage in collecting mummies on a weekly basis is that one cannot be sure how long the mummies have been formed. This is especially so during the colder weeks when the parasites begin to go into a quiescent state. This would no doubt lead to a percentage different from the actual one.

It should be remarked here that Asaphes vulgaris and A. suspensus have been grouped together under Asaphes sp. purely as a matter of convenience. These 2 species differ from each other in fine details only and had been in fact considered as a single species for a long time, until Graham (1969) separated them.

It is clear that the percentage varies with site, the aphids' host plant and with time (Table 5-9). This has been noted by George (1957), Sedlag (1959; 1964), Hafez (1961) and others.

Diaretiella rapae and Alloxysta brassicae were the 2 major species recorded, followed by Asaphes sp. A. brassicae usually accounted for about 70-80% of the total while D. rapae seldom attained more than 30%. Dendrocerus carpenterii and Pachyneuron minutissimum were found only occassionally and in very low numbers. They are clearly only incidental, since their main hosts are other aphid parasites (Graham, 1969; Dessart, 1972). As only a relatively small number of mummies were collected from Ashurst Field (Table 7), the following discussion is centred on the study carried out at Silwood Bottom during 1973-75.

The most obvious and significant variation in the percentage of each species is that related to time. This variation illustrates very clearly the great effect of A. brassicae on the number of and hence the efficiency of D. rapae as a biological control agent of Brevicoryne brassicae. For example, the percentage of D. rapae dropped from 42.8 to 14.6 within 5 weeks while

A. brassicae increased from 54.3 to 77.1% (Table 5). Similarly in 1974-75 (Table 6) D. rapae decreased from 27.7 to 0% while A. brassicae increased from 72.3 to 100% within the space of 3 weeks. The percentage of D. rapae usually then fluctuated at a low level of 30% or less while A. brassicae maintained its high level of 70% or more. Hafez (1961), Paetzold & Vater (1966, 1967) and Akinlosotu (1973) also reported similar temporal changes. In 1974-75 however, D. rapae somehow recovered and the percentage increased from 25.6 (16 December) to a high level of 80-100%. Concomitantly the percentage of A. brassicae gradually diminished and this species was absent in many mummy samples. The reason for this is not clear.

Asaphes sp. never occurred in large numbers and never exceeded 25% of the total parasites. In 1974, Asaphes sp. was absent from many samples.

On the whole, the hyperparasites were low in numbers in 1974-75. This could be linked indirectly to the relatively low aphid population or directly to the resultant few D. rapae mummies available for attack.

A review of previous work (Appendix 2) generally confirms the present findings. Some recalculations have been made using the total parasites emerged as a basis for comparison rather than the total mummies collected as done by the authors.

The percentage of D. rapae is generally low, and except for few instances usually less than 30% whereas A. brassicae attains much higher percentage and accounts for more than 40%. The other species are present occassionally and in small proportions.

2. Weekly emergence patterns of parasites.

The results of emergence of parasites from mummies collected from Silwood Bottom for 1973 and 1974 are shown in Fig. 13-18. The emergences of the less common species viz. D. carpenterii and P. minutissimum have

Table 5. The percentage of parasites that emerged from B. brassicae mummies collected from sprout plants in Silwood Bottom, 1973.

Date of collection	Number of mummies collected	Number of parasites that emerged	Percentage of parasites			
			D.rapae	A.brassicae	Asaphes[+] sp.	D.carpenterii
25 July	35	35	42.8	54.3	2.9	-
3 August	38	38	42.1	42.1	15.8	-
8 August	44	37	24.3	59.5	16.2	-
15 August	71	61	31.2	63.9	4.9	-
22 August	164	146	20.5	75.3	4.1	-
29 August	160	144	14.6	77.1	8.3	-
5 September	161	140	43.6	53.5	2.9	-
12 September	312	277	28.5	69.7	1.8	-
19 September	215	181	25.4	72.9	1.7	-
26 September	196	173	28.9	69.4	1.7	-
4 October	297	255	24.7	71.0	4.3	-
10 October	372	300	16.3	75.7	8.0	-
17 October	376	318	13.8	77.7	8.5	-
24 October	455	364	18.4	73.1	8.5	-
31 October	538	485	9.9	87.2	2.9	-
7 November	521	428	14.0	77.6	7.7	0.7
14 November	743	640	13.3	76.9	9.2	0.6
21 November	421	353	14.2	71.9	13.6	0.3
	Total=5074					
Mean	-	-	23.7	69.4	6.8	0.1

+ Asaphes vulgaris and A. suspensus.

Table 6. The percentage of parasites that emerged from B. brassicae mummies collected from sprout plants in Silwood Bottom, 1974 - 1975.

Date of collection	Number of mummies collected	Number of parasites that emerged	Percentage of parasites			
			D.rapae	A.brassicae	Asaphes** sp.	Others
19 June'74	105	94	27.7	72.3	-	-
26 June	121	102	27.5	72.5	-	-
3 July	104	95	6.3	93.7	-	-
10 July	45	33	-	100.0	-	-
17 July	18	14	21.4	64.3	14.3	-
24 July	6	6	33.3	66.7	-	-
31 July	17	11	36.4	45.4	18.2	-
7 August	13	13	30.8	61.5	7.7	-
14 August	15	14	14.3	78.6	7.1	-
21 August	27	26	76.9	23.1	-	-
28 August	15	15	33.3	66.7	-	-
4 September	4	4	25.0	75.0	-	-
11 September	11	9	11.1	88.9	-	-
18 September	14	7	28.6	71.4	-	-
25 September	18	9	22.2	77.8	-	-
2 October	24	18	16.7	83.3	-	-
9 October	7	6	16.7	83.3	-	-
16 October	49	43	25.6	69.8	2.3	2.3+
23 October	36	33	33.3	57.6	6.1	3.0*
30 October	79	62	59.7	30.6	8.1	1.6+
6 November	99	77	67.5	32.5	-	-
13 November	65	53	83.3	16.7	-	-
20 November	97	92	80.4	19.6	-	-
27 November	70	62	90.3	8.1	1.6	-
4 December	122	105	96.2	3.8	-	-
11 December	62	58	94.8	5.2	-	-
8 January'75	17	17	100.0	-	-	-
15 January	81	74	82.4	2.7	14.9	-
22 January	80	64	95.3	-	4.7	-
29 January	95	81	81.5	1.2	17.3	-
5 February	108	95	89.5	-	10.5	-
12 February	44	39	92.3	-	7.7	-
19 February	14	12	100.0	-	-	-
26 February	19	18	77.8	11.1	11.1	-
5 March	10	9	100.0	-	-	-
	Total=1711					
Mean	-	-	53.7	42.4	3.8	0.1+

+ D. carpenterii

* P. minutissimum

** Asaphes vulgaris and A. suspensus.

Table 7. The percentage of parasites emerging from B. brassicae mummies collected from sprout plants in Ashurst Field, 1974.

Date of collection	Total mummy collected	Total parasites emerged	Percentage of parasites		
			D. rapae	A. brassicae	Asaphes+sp.
18 July'74	5	5	-	100.0	-
25 July	2	1	-	-	100.0
1 August	4	4	75.0	25.0	-
29 August	2	2	50.0	50.0	-
12 September	2	2	100.0	-	-
19 September	7	6	66.7	33.3	-
3 October	4	4	50.0	50.0	-
10 October	1	-	-	100.0	-
24 October	10	8	50.0	50.0	-
31 October	27	19	15.8	84.2	-
7 November	20	17	23.5	64.7	11.8
14 November	16	9	33.3	22.2	44.4
21 November	12	10	80.0	-	20.0
28 November	16	11	72.7	27.3	-
5 December	13	9	22.2	-	77.8
13 December	8	8	100.0	-	-
	Total=147				
Mean	-	-	46.2	37.9	15.9

+ Asaphes vulgaris and A. suspensus.

Table 8. The percentage of parasites that emerged from B. brassicae mummies collected from winter rape in Silwood Bottom, 1974.

Date of collection	Total mummy collected	Total parasites emerged	Percentage of parasites				
			D. rapae	A. brassicae	Asaphes + sp.	D. carpenterii	P. minutissimum
28 May'74	26	23	13.0	82.6	4.3	-	-
12 June	113	90	43.3	50.0	2.2	4.4	-
21 June	148	126	34.9	63.5	1.6	-	-
28 June	109	91	15.4	74.7	4.4	5.5	-
5 July	120	102	4.9	49.0	42.2	3.9	-
12 July	58	43	-	34.9	51.1	7.0	7.0
	Total=574						
Mean	-	-	18.6	59.1	17.6	3.5	1.2

+ Asaphes vulgaris and A. suspensus.

Table 9. The percentage of parasites that emerged from B. brassicae mummies collected from summer rape in Ashurst Field, 1974.

Date of collection	Total mummy collected	Total parasites emerged	Percentage of parasites			
			D. rapae	A. brassicae	P. minutissimum	Asaphes+sp.
15 August'74	25	12	8.3	-	41.7	50.0
22 August	15	11	27.3	72.7	-	-
5 September	15	12	41.7	50.0	-	8.3
12 September	8	8	62.5	37.5	-	-
19 September	3	3	66.7	-	33.3	-
	Total=66					
Mean	-	-	41.3	32.0	15.0	11.7

+ include Asaphes vulgaris and A. suspensus.

been omitted since the numbers were very small.

A. Temperature records.

The mummies (in tubes) were stored just outside the main building. The ambient temperature of the mummies recorded by thermograph was compared with the official record for the Field Station and only a very small temperature difference was noted. The maximum Field Station temperature was about 0.2°C lower while the minimum temperature was about 0.6°C higher than the temperature recorded near the mummy storage area. In other words, the temperature experienced by the mummies fluctuated within wider limits (0.8°C wider) than the actual air temperature.

B. Results.

i) Diaretiella rapae (Fig. 13,16).

The emergence of D. rapae in summer was usually completed within one but sometimes 2 weeks after the mummy collection. From late September to early October onwards, one or 2 laggards were present, extending the completion of the emergence to about 5 weeks. Towards the middle of October some of the collected mummies entered into a quiescent phase and remained thus until the following May. From late October onwards, the proportion of mummies that emerged in the following year increased and reached a value of over 70% by late November in 1973 and early November in 1974.

In 1974, mummy collection was continued into the following year and stopped on 5 March 1975. It is clear that the later the mummy collection, the shorter quiescent period the mummies had to undergo (Fig. 16). This is to be expected as they were already in the quiescent state at the time of collection and the field temperature was rising.

Each collection had a peak emergence and considering the collections as a whole there was no distinctive single spring peak. However, the bulk

Fig. 13. The weekly emergences (expressed as percentage) of *Diaretiella rapae* from *B. brassicae* mummies collected from Silwood Bottom, 1973. Each set of histograms represents emergences from mummies collected on the indicated date.

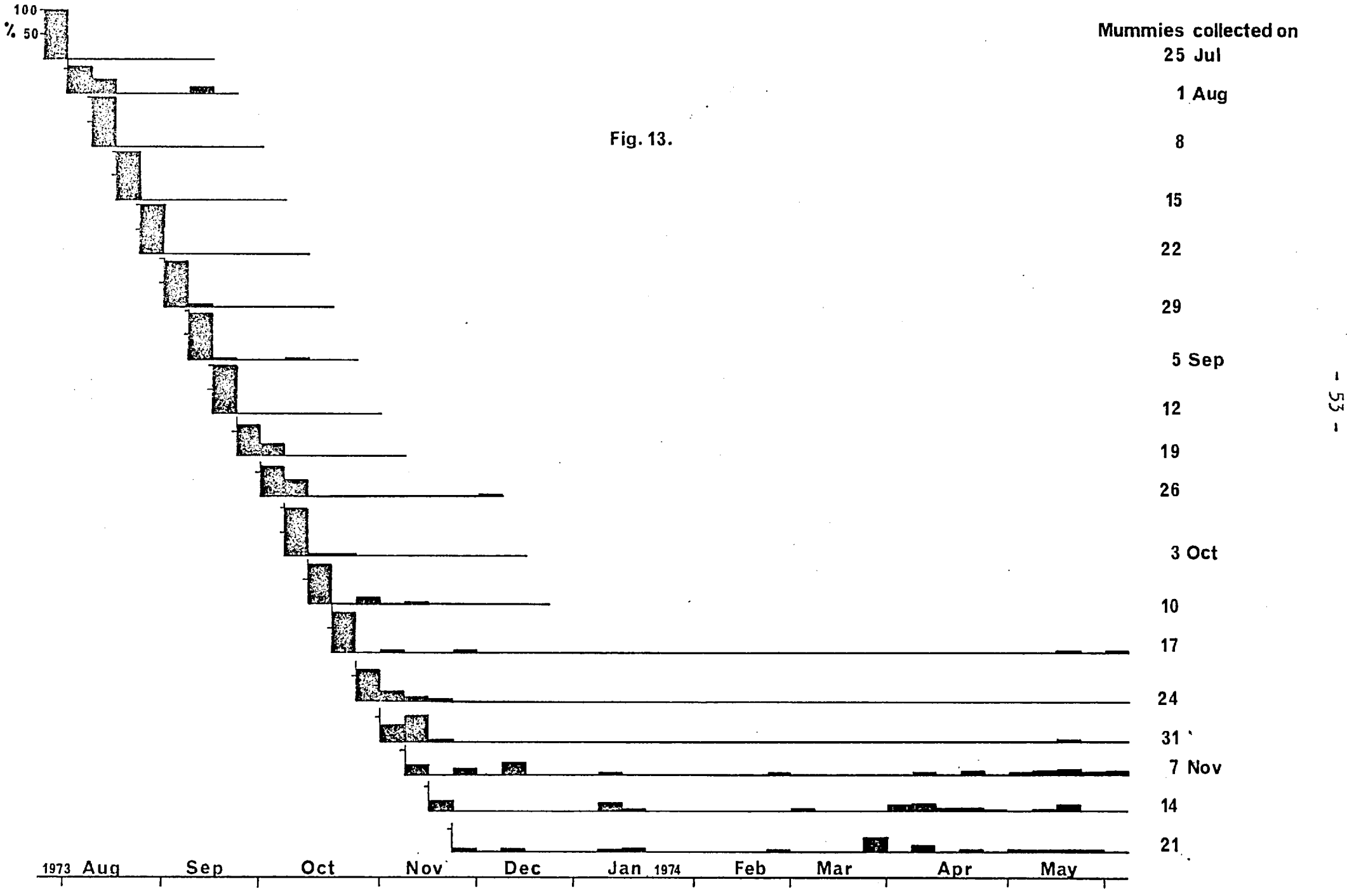

100
% 50
Mummies collected on
25 Jul
1 Aug
8
15
22
29
5 Sep
12
19
26
3 Oct
10
17
24
31
7 Nov
14
21
1973 Aug
Sep
Oct
Nov
Dec
Jan 1974
Feb
Mar
Apr
May

Fig. 13.

Fig. 14. The weekly emergences (expressed as percentage) of Alloxysta brassicae from B. brassicae mummies collected from Silwood Bottom, 1973. Each set of histograms represents emergences from mummies collected on a different date.

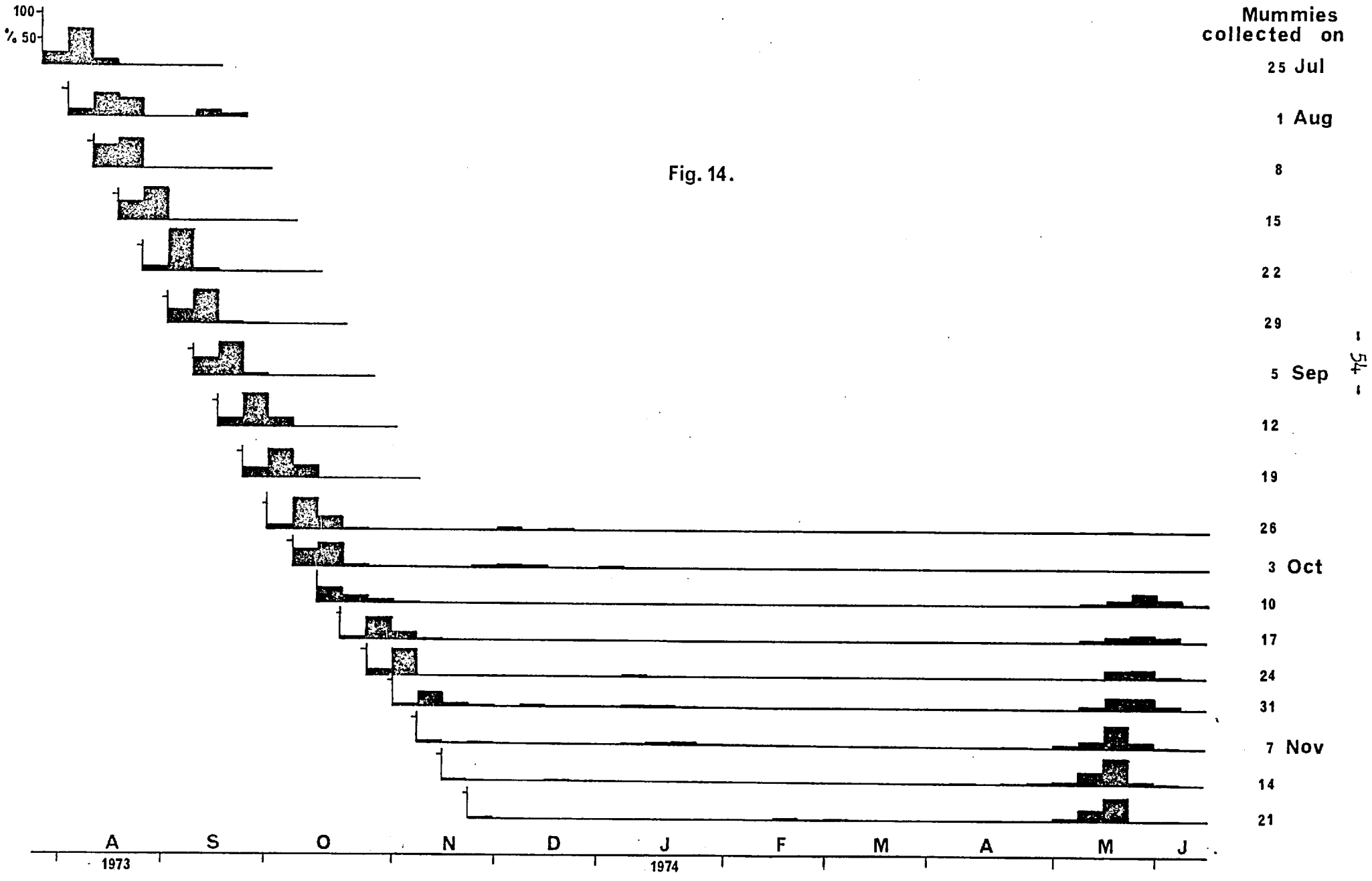

100
% 50
Mummies collected on
25 Jul
1 Aug
8
15
22
29
5 Sep
12
19
26
3 Oct
10
17
24
31
7 Nov
14
21
A
S
O
N
D
J
F
M
A
M
J
1973
1974

Fig. 14.

Fig. 15. The weekly emergences (expressed as percentage) of *Asaphes* sp. from *B. brassicae* mummies collected from Silwood Bottom, 1973. Each set of histograms represents emergences from mummies collected on a different date.

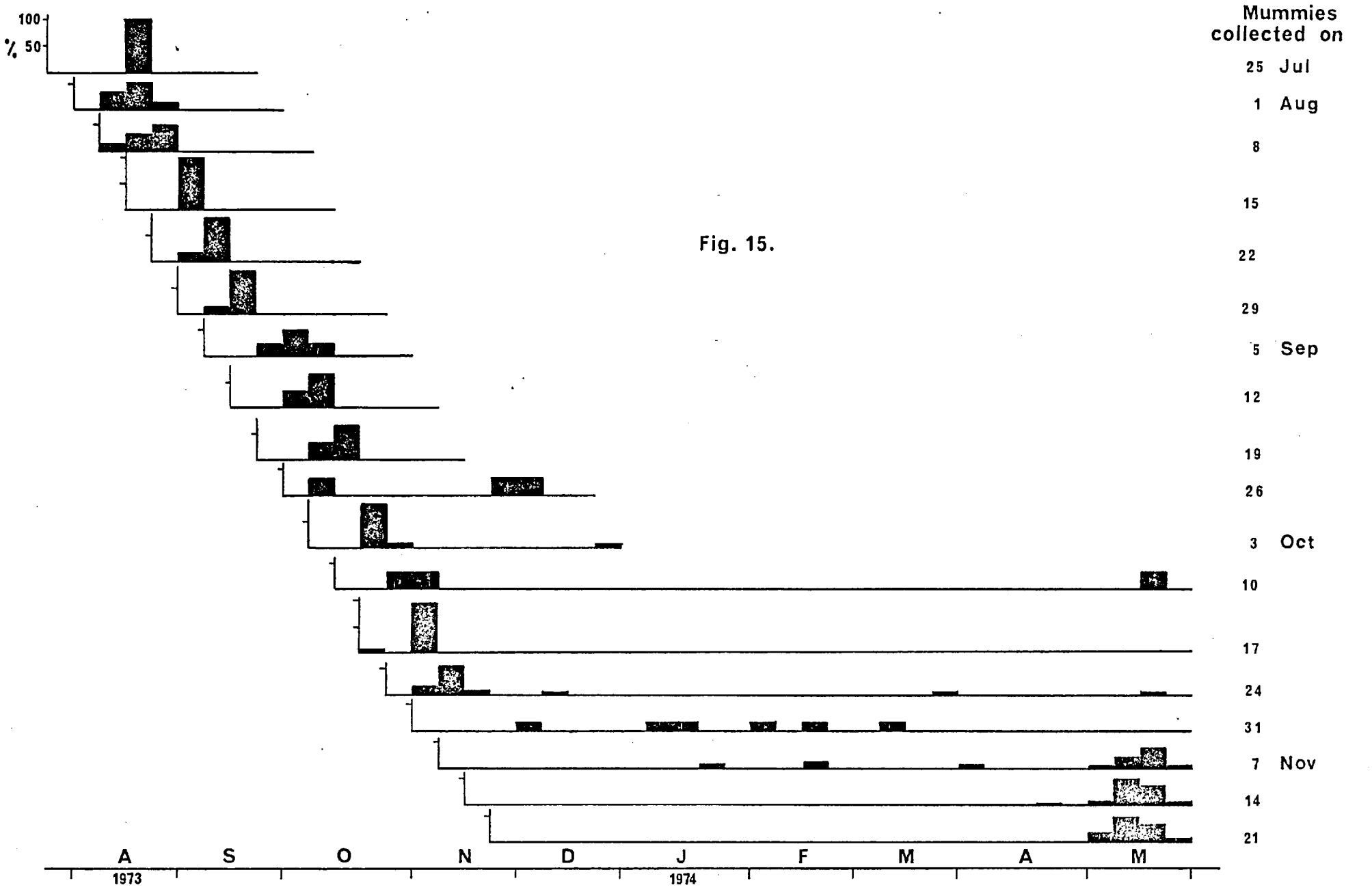

100
%, 50
Mummies collected on
25 Jul
1 Aug
8
15
22
29
5 Sep
12
19
26
3 Oct
10
17
24
31
7 Nov
14
21
A
S
O
N
D
J
F
M
A
M
1973
1974

Fig. 15.

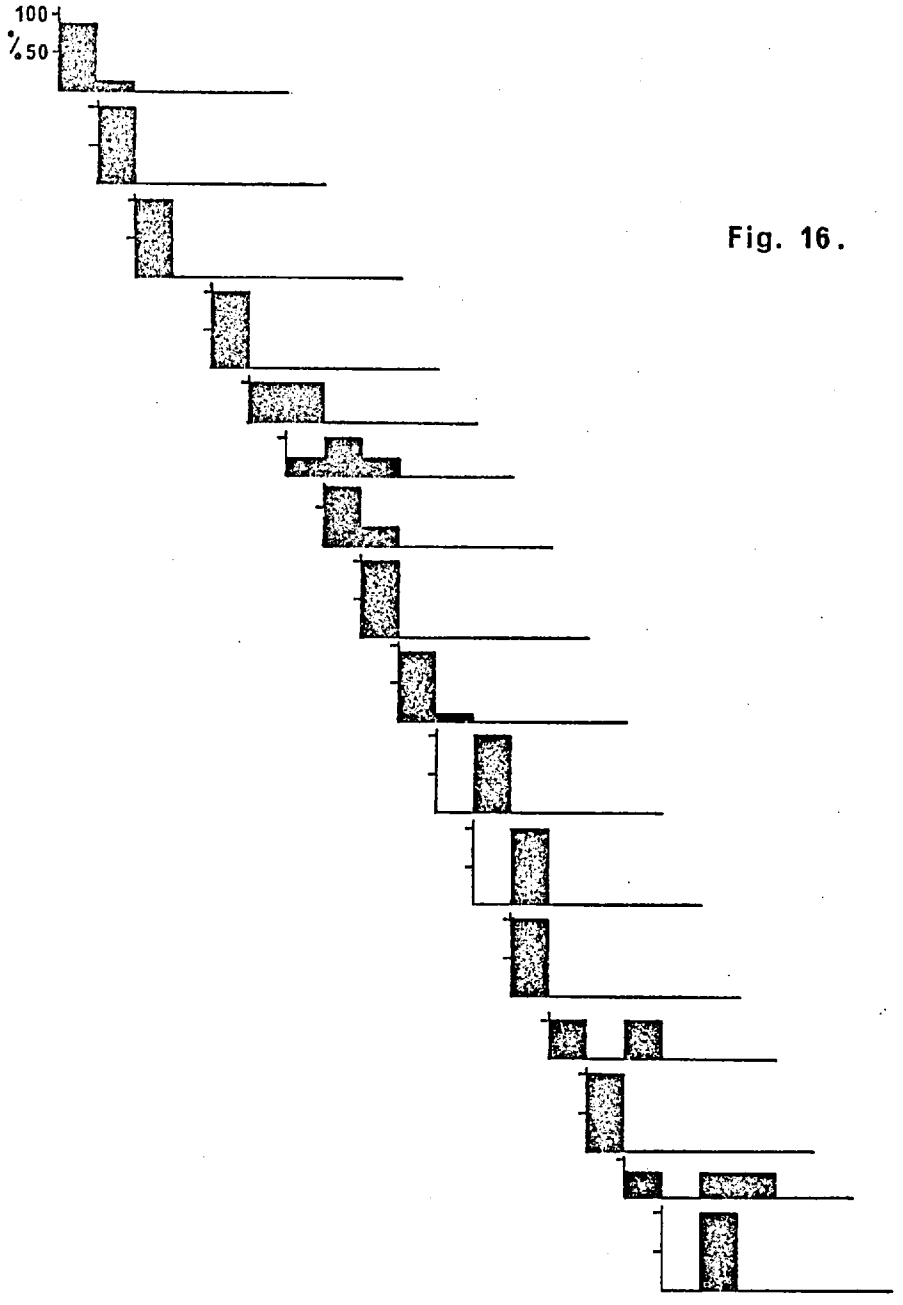


Fig. 16.

Mummies collected on

19 Jun

26

3 Jul

17

24

31

7 Aug

14

21

28

4 Sep

11

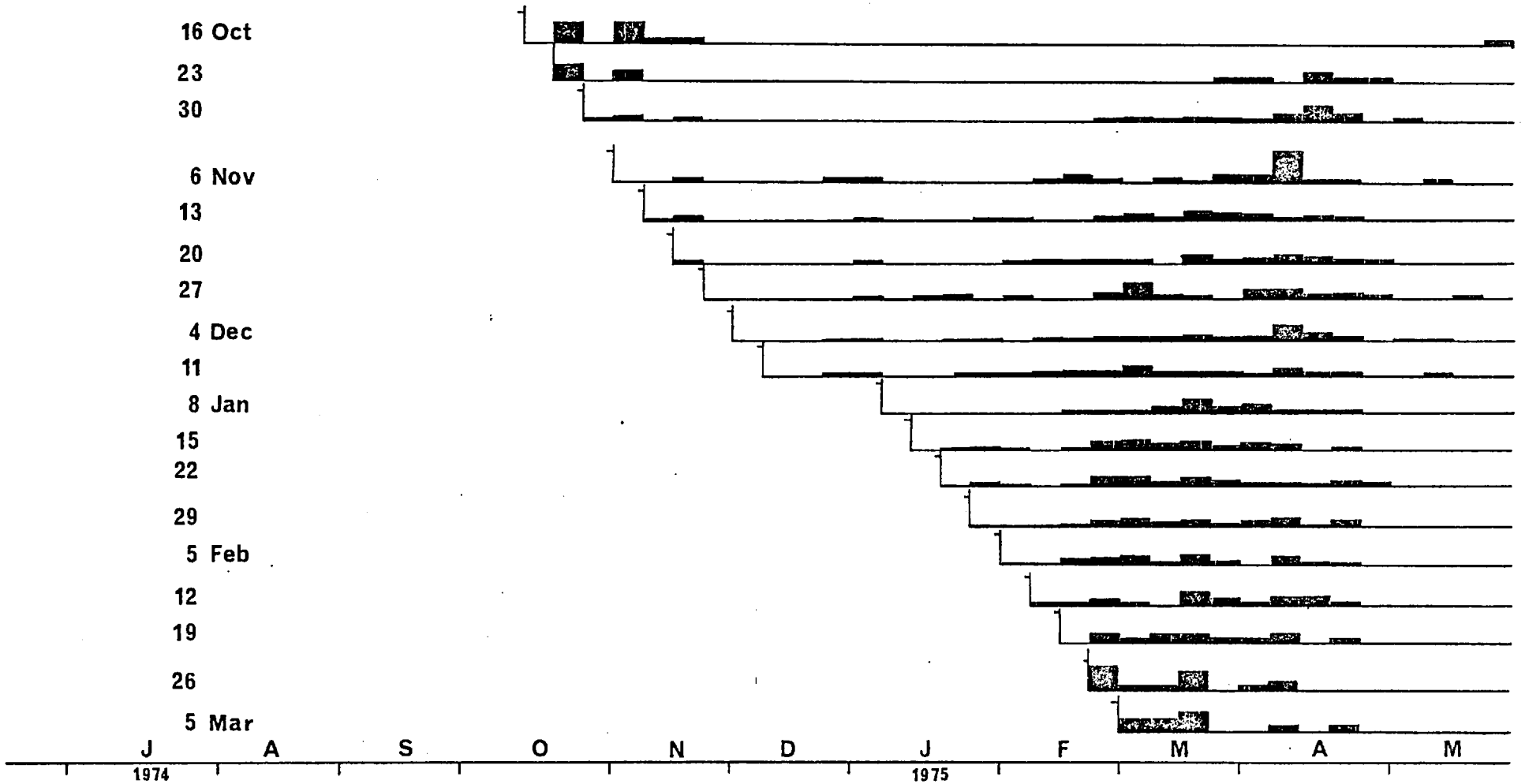
18

25

2 Oct

9

Fig. 16. The weekly emergences (expressed as percentage) of Diaretiella rapae from B. brassicae mummies collected from Silwood Bottom, 1974. Each set of histograms represents emergences from mummies collected on a different date.



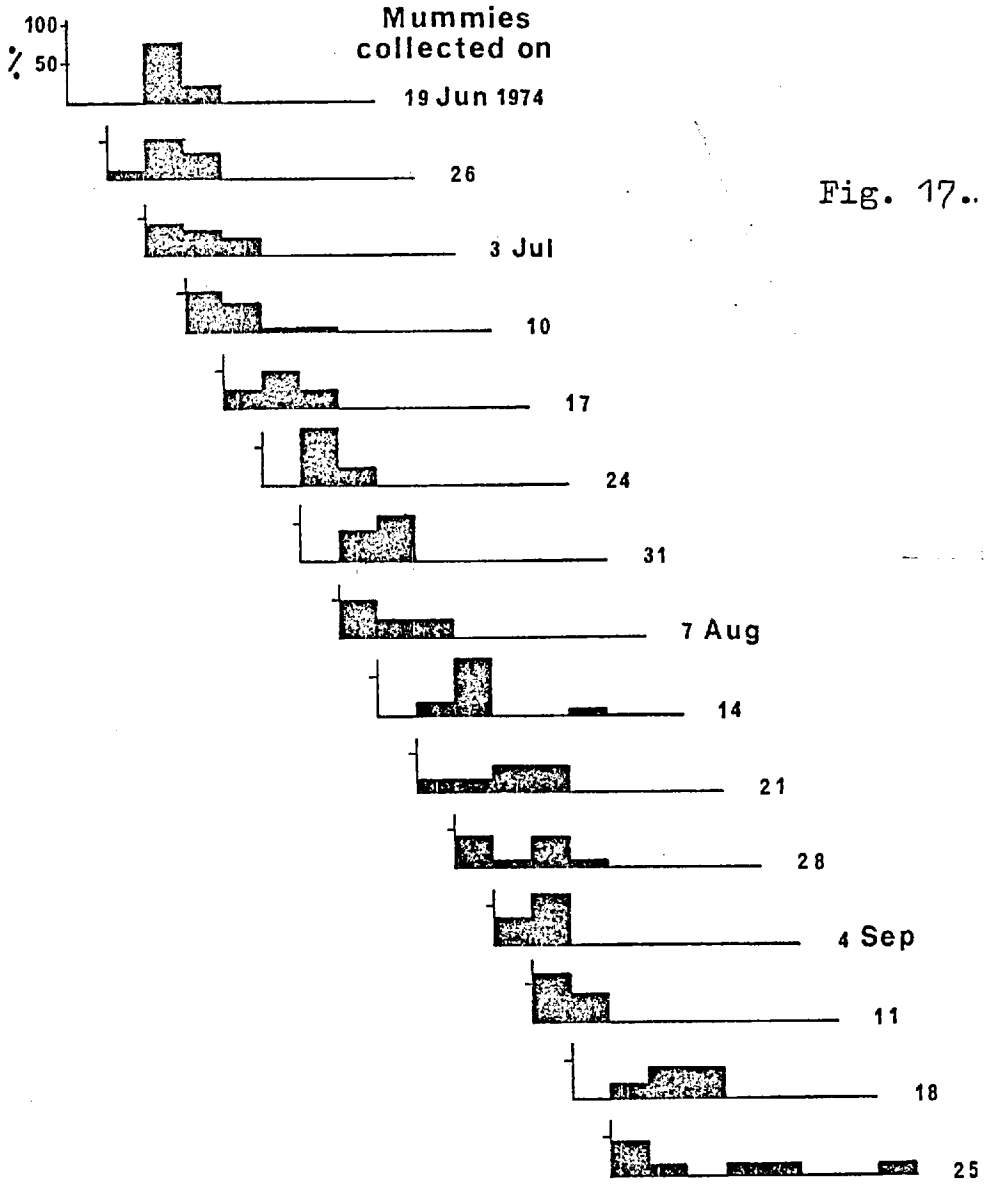


Fig. 17.. The weekly emergences (expressed as percentage)of Alloxysta brassicae from B. brassicae mummies collected from Silwood Bottom, 1974. Each set of histograms represents emergences from mummies collected on a different date.

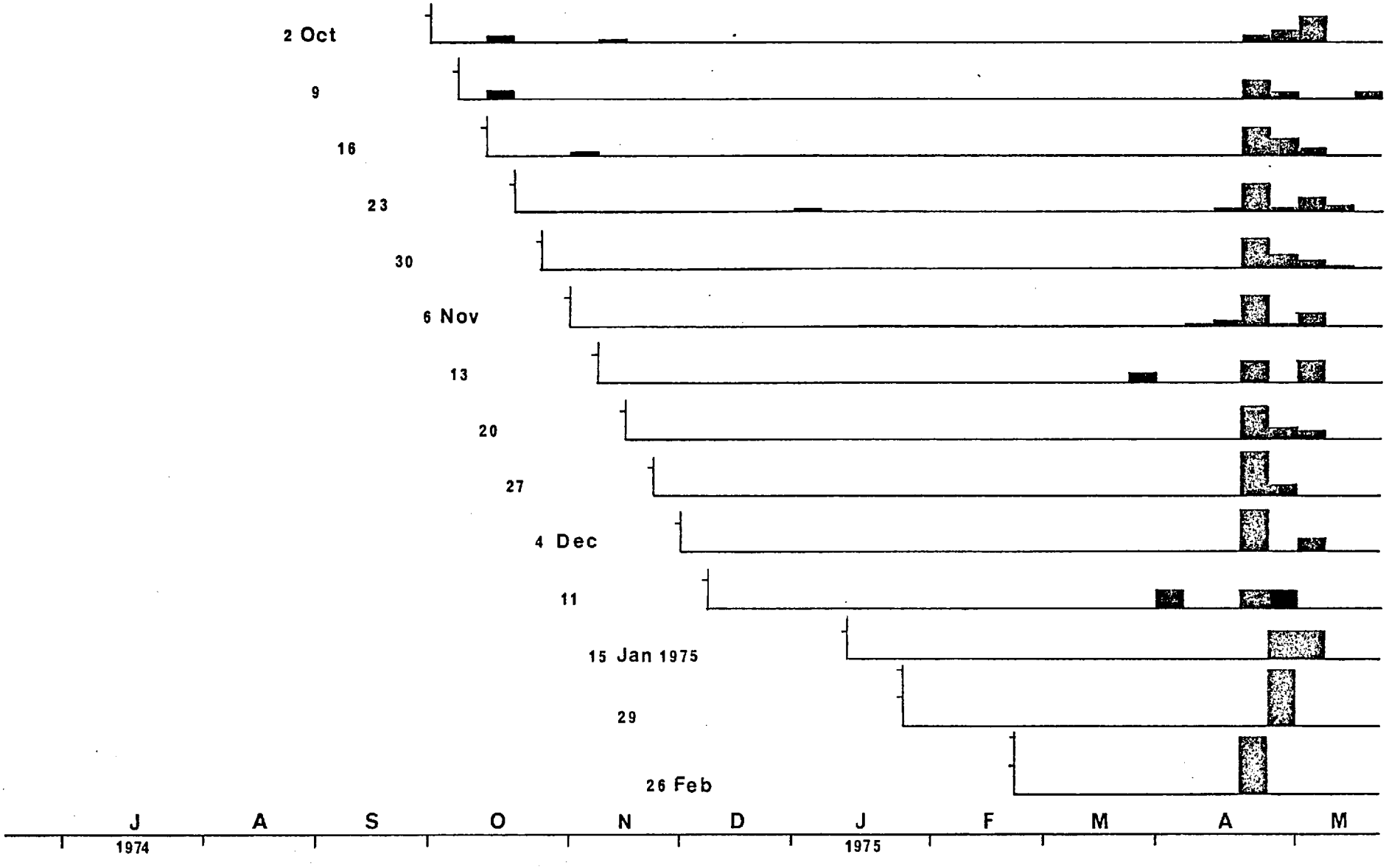

2 Oct
9
16
23
30
6 Nov
13
20
27
4 Dec
11
15 Jan 1975
29
26 Feb
J
A
S
O
N
D
J
F
M
A
M
1974
1975

Fig. 18. The weekly emergences (expressed as percentage) of *Asaphes* sp. from *B. brassicae* mummies collected from Silwood Bottom, 1974. Each set of histograms represents emergences from mummies collected on a different date.

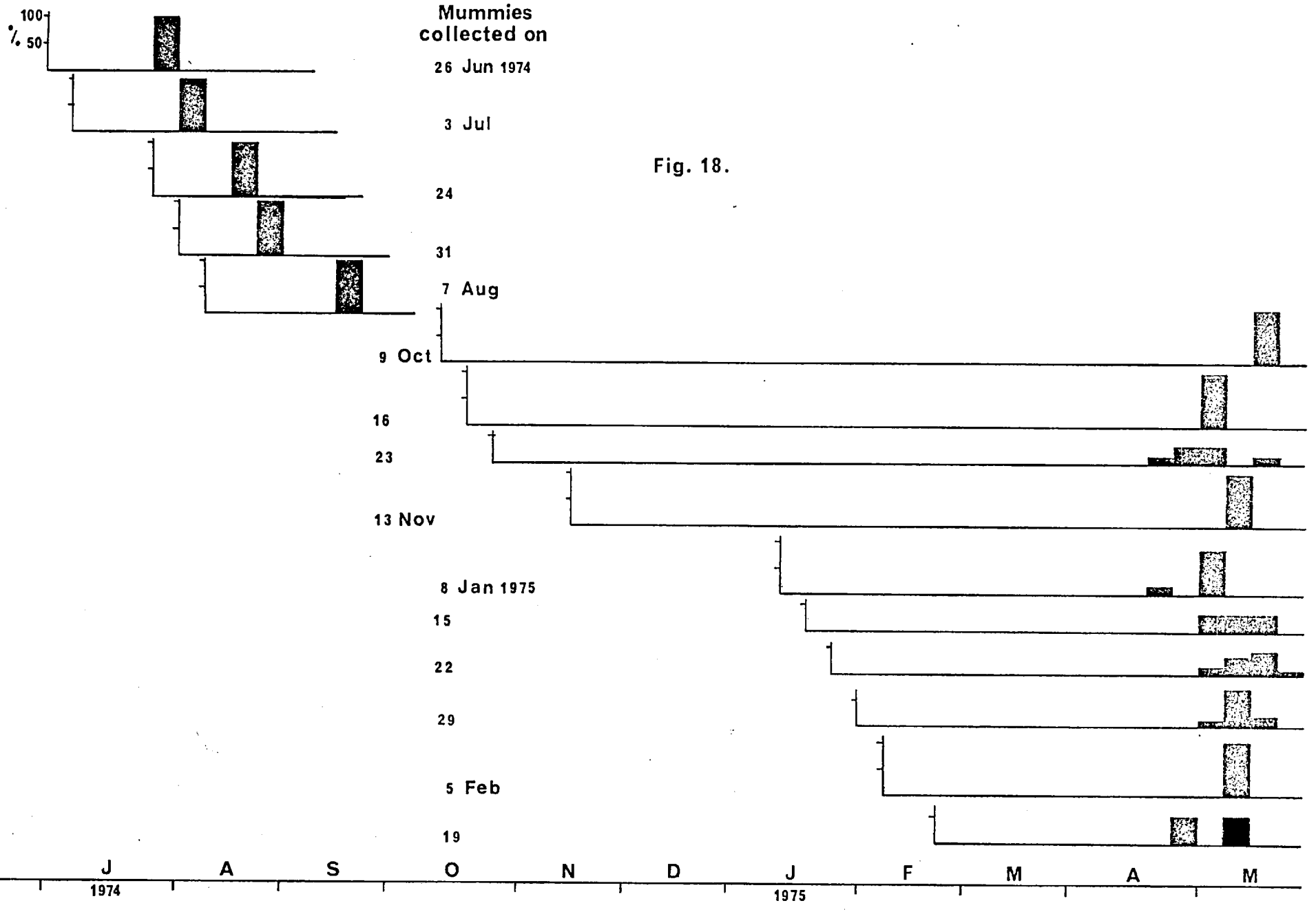

100
%. 50
Mummies collected on
26 Jun 1974
3 Jul
24
31
7 Aug
9 Oct
16
23
13 Nov
8 Jan 1975
15
22
29
5 Feb
19
J
A
S
O
N
D
J
F
M
A
M
1974
1975

Fig. 18.

of the emergence took place within a nine-week period from 20 March to 21 May 1974 and 26 February to 29 April 1975, with the respective peak in the 9th week (15 to 21 May) and the 7th week (9 to 15 April).

ii) Alloxysta brassicae (Fig. 14, 17).

A.brassicae has a very similar emergence pattern although the bulk of the summer emergence occupied a space of 2 to 3 weeks (instead of 1 to 2 weeks in D. rapae). From late September to early October collections, stragglers began to emerge in the following spring. In 1973, about half of the mummies collected during mid-October emerged in the following May, and the percentage increased to about 90% among the last 3 collections. In 1974 however, only 20% or less of the mummies collected in October emerged the same year, and from late October onwards, all parasites emerged in the following spring. The spring emergence took place within 4 to 5 weeks only, from 1 May to 4 June in 1974 and 16 April to 13 May in 1975, with the peaks in the third week (15 - 21 May) and the second week (23 - 29 April) respectively.

iii) Asaphes sp. (Fig. 15, 18).

Although the actual number of mummies involved was comparatively small, a similar pattern of emergence was still discernible. The greater part of the summer emergence took place 3 to 5 weeks after the collection. In 1973, from October onwards an increasing proportion of mummies (reaching 100% in the last 2 collections) emerged in the following spring. However in 1974, such gradually increasing proportions were not noticed and the parasites emerged from all the mummies (collected from October onwards) only in the following spring. In both years, the bulk of the spring emergence took place within 3 weeks (1 to 21 May 1974, and 7 to 27 May 1975), with the peak in the last.

C. Discussion.

In general, the main summer emergence of D. rapae, A. brassicae and Asaphes sp. took place within 1 to 2 weeks, 2 to 3 weeks and 3 to 5 weeks

respectively. This again clearly indicates the parasitic relationship between these 3 species: A. brassicae is parasitic on D. rapae while Asaphes sp. parasitises on both A. brassicae and D. rapae. In the following spring, such an emergence sequence of the parasites was also seen and has been reported by Hafez (1961), Sedlag (1964) and others. A. brassicae and Asaphes sp. had distinct spring emergence periods of 3 weeks and 3 to 5 weeks respectively. This is in contrast to D. rapae which lacked a distinctive emergence period, although more adults emerged during a nine-week period. The first D. rapae usually emerged long before the first A. brassicae or Asaphes sp., although the later stragglers of these 3 species emerged approximately at the same time.

The decrease in the parasite emergence in late autumn was no doubt caused by the unfavourable weather especially the drop in temperature (Appendix 3). This was observed as early as 1931 by Barnes.

In the 2 years under study, each species of parasite began to show quiescence about the same time. For example the first adults to emerge in the following spring were from mummies collected on 17 October 1973 and 16 October 1974 for D. rapae, on 26 September 1973 and 2 October 1974 for A. brassicae, and on 10 October 1973 and 9 October 1974 for Asaphes sp.

However, the bulk of the spring emergence (which may be of the same duration in 1974 and 1975) nevertheless began and ended at different times. For example, D. rapae's periods were 20 March to 21 May 1974 and 26 February to 29 April 1975. Similarly those for A. brassicae were 1 May to 4 June 1974 and 23 April to 27 May 1975, and for Asaphes sp. 1 to 21 May 1974 and 7 to 27 May 1975. It is clear then that the spring emergence in 1975 started one week earlier, which could be the result of the higher temperatures (Appendix 3). The high temperature of April 1975 (8.4°C) was especially important in speeding up the parasite emergence as the temperature threshold for development for D. rapae is only 6.5°C (Hafez, 1961). The temperature thresholds for the other species are not available for comparisons, but it is

doubtful if they depart very much from 6.5°C.

Similar work on parasite emergence has also been done by Barnes (1931), Hafez (1961), Paetzold & Vater (1966, 1967), and Oatman & Platner (1973). The results of George (1957), and Paetzold & Vater (1966, 1967) showed that mummies began to go into quiescence around late September which agrees with the results presented here. These authors also recorded similar spring emergence periods. Their observations however apply to both the primary and the secondary parasites. Barnes (1931) recorded that parasites emerged during April to May, with the peak in May; George (1957) reported a longer emergence period in April to July with the peak in June to July; Paetzold & Vater (1967) observed the same emergence period of April to July, but with the peak in May; and finally Hafez (1961) noted an earlier emergence period from March to June with the peak in April to May. Comparing these and the overall bulk emergence periods for all parasites recorded here viz. March to June 1974 and February to May 1975 with the respective peaks in April to May 1974 and March to May 1975, it is noticeable that the present results show an early emergence time but not an earlier peak.

The duration of the emergence periods for individuals species of parasite might vary. The shortest period recorded for D. rapae was 8 days (Paetzold & Vater, 1967) and the longest 14 weeks (Hafez, 1961). The shorter period might be attributable to the relatively low percentage of D. rapae (4-5%). The hyperparasites, on the other hand show less variations. The emergence period for A. brassicae varies from 18 days (Paetzold & Vater, 1967) to 8 weeks (Barnes, 1931) and that for Asaphes sp. varies from 3 week (present study) to 7 weeks (Barnes, 1931; Hafez, 1961). Temperature differences might contribute to the variations in the emergence periods.

Little has been mentioned about the parasites (which include all the species in 1973-74, but only D. rapae in 1974-75) emerging during the winter months and early spring. Only Hafez (1961) and Paetzold & Vater (1967) reported similar occurrences. These parasites seemed to have emerged at a time when their respective hosts were scarcely available and the environmental

conditions (especially temperature) adverse. They were not synchronised with their hosts as they were too late for the hosts in the standing crop and too early for those in the next. Probably they were wasted and did not contribute to the build up nor the continuance of the population.

The staggered emergence of D. rapae in spring might ensure that at least some of them find aphid hosts. The emergence periods of A. brassicae and Asaphes sp. which were distinct and short followed about 5 weeks after D. rapae. Hafez (1961) and Barnes (1931) reported a difference of only 1 to 2 weeks, while Paetzold & Vater (1967) only 10 days. The later emergence of the hyperparasites seems to ensure abundant hosts (D. rapae) are available for attack. This perhaps indicates that the hyperparasites are more synchronised with D. rapae and D. rapae with B. brassicae.

3. Sex ratio of parasites in spring emergence.

The sex ratios of the parasites which emerged in the springs of 1974 and 1975 were recorded weekly (Table 10 - 11).

A) Results.

i) Diaretiella rapae.

In both years, there was a predominance of females among the parasites that emerged. There was no clear-cut emergence trends, although when considering short periods, for example, 20 March to 16 April 1974 and 5 March to 22 April 1975 there appeared to be a trend of increasing female proportion. The highest female proportions (where number of parasites was 3 or more) were 0.91 (1974) and 0.81 (1975).

ii) Alloxysta brassicae.

There was a well-defined predominance of males in the early emergence, which decreased towards the end of the period. The highest female proportions

Table 10. The weekly female proportion of parasites that emerged in Spring, 1974 from *Brevicoryne brassicae* mummies collected in Silwood Bottom during the period from 3 October to 21 November, 1973.

Species: / Weeks	*Diaretiella rapae*		*Alloxysta brassicae*		*Asaphes* sp.	
	number	female proportion	number	female proportion	number	female proportion
2-8 Jan'74	11	.45	6	.40	1	0
9-15 Jan	3	.33	7	.43	1	0
16-22 Jan	-	-	10	.60	1	0
23-29 Jan	-	-	4	.50	-	-
30Jan-5Feb	-	-	3	.67	1	0
6-12 Feb	-	-	2	1.00	-	-
13-19 Feb	-	-	2	.00	3	0
20-26 Feb	2	1.00	-	-	-	-
27Feb-5Mar	1	1.00	1	1.00	-	-
6-12 Mar	-	-	1	1.00	1	0
13-19 Mar	-	-	-	-	-	-
20-26 Mar	7	.71	-	-	1	0
27Mar-2Apr	6	.83	-	-	1	0
3-9 Apr	11	.91	1	0	-	-
10-16 Apr	3	1.00	-	-	-	-
17-23 Apr	6	.50	3	.33	1	0
24-30 Apr	1	1.00	7	.29	-	-
1-7 May	2	1.00	39	.31	7	0
8-14 May	4	.75	126	.37	29	.14
15-21 May	13	.62	379	.64	29	.28
22-28 May	2	1.00	149	.84	3	1.00
29May-4Jun	3	.66	44	.87	-	-
5-11 June	-	-	1	1.00	-	-
Total	75	.71	785	.62	79	.19
Total (summer emergence)	252	.61	1103	.66	52	.54

Table 11. The weekly female proportion of parasites that emerged in Spring 1975 from Brevicoryne brassicae mummies collected in Silwood Bottom during the period from 2 October to 11 December 1974.

Species: / Weeks	Diaretiella rapae		Alloxysta brassicae		Asaphes sp.	
	number	female proportion	number	female proportion	number	female proportion
1-7 Jan'75	7	.14	1	0	-	-
8-14 Jan	-	-	-	-	-	-
15-21 Jan	1	1.00	-	-	-	-
22-28 Jan	4	.50	-	-	-	-
29 Jan-4 Feb	3	.33	-	-	-	-
5-11 Feb	4	.75	-	-	-	-
12-18 Feb	16	.31	-	-	-	-
19-25 Feb	16	.44	-	-	-	-
26 Feb-4 Mar	28	.68	-	-	-	-
5-11 Mar	42	.43	-	-	-	-
12-18 Mar	18	.67	-	-	-	-
19-25 Mar	35	.66	-	-	-	-
26 Mar-1 Apr	27	.67	1	1.00	-	-
2-8 Apr	37	.70	4	0	-	-
9-15 Apr	65	.80	1	0	-	-
16-22 Apr	43	.81	4	.50	-	-
23-29 Apr	27	.56	71	.37	1	0
30 Apr-6 May	3	.33	26	.69	2	.50
7-13 May	2	1.00	30	.70	4	.50
14-20 May	3	0	3	1.00	-	-
21-27 May	1	1.00	1	1.00	2	1.0
28 May-3 Jun	1	1.00	-	-	-	-
Total	383	.64	142	.51	9	.56
Total (summer emergence)	38	.63	7	.57	-	-

were 0.87 (1974) and 0.70 (1975), always following 2 weeks after the peak emergence.

iii) Asaphes sp.

Asaphes sp. showed very clear protandry in 1974, but it should be noted that relatively few emergences of this species were recorded. In 1975, such clear trend was not observed, though again, as in other species, the female proportions increased with the emergence period. The highest female proportions recorded were 0.28 (1974) and 0.73 (1975).

B. Discussion.

The only protandry was observed for Asaphes sp. in 1974. In all other cases, the weekly sex ratios varied tremendously although in general, the proportions of females tended to increase towards the end of the emergence period.

Hafez (1961) reported protandry in Charips ancylocera (=A. brassicae) the males of which emerged about 3 weeks before the first females. It seems then that protandry has only been observed so far among the hyperparasites. As for D. rapae, both Hafez (1961) and George (1957) recorded a greater proportion of females throughout the season.

Generally, the average proportion of females for the whole emergence periods in spring and summer did not very much and the females usually predominated. For example, the female proportions of D. rapae in summer and winter emergences respectively were for mummies collected in 1973, 0.61 and 0.71, and for mummies collected in 1974, 0.63 and 0.64. The only exception was Asaphes sp., of which males predominated in the spring emergence of 1974.

4. Factors affecting parasite emergence.

A. Introduction.

Though many authors have reported that a great proportion of the parasites of Brevicoryne brassicae overwinter as mummies, very few mentioned their physiological state. Hafez (1961), Sedlag (1964), and Way et al., (1969) described them as in a state of diapause while Paetzold & Vater (1966) stated they are in hibernation. That the parasites are in a state of developmental arrest is however beyond doubt.

Hodek (1966) distinguished two types of developmental arrest in insects viz. diapause and quiescence. He defined quiescence as a state of direct inhibition of development, e.g. due to low temperature, which is terminated immediately conditions become favourable.

That the parasites' arrest is of the quiescent type and caused by low temperature was demonstrated in three ways.

B. Effect of temperature.

i) Field-collected mummies.

About half the mummies were kept at 20°C while the other half at field temperatures. The emergence patterns shown in Fig. 19-21 represent all species of parasites.

Since the results of study on mummies collected during October to November, 1973 showed clearly that temperature was the chief factor in determining parasite emergence, it was decided in 1974 to experiment on mummies collected earlier in the season (namely June to July) to see if other factors might be involved.

There were two emergence peaks for mummies collected in 1973 and kept at field temperature (Fig. 19), one recorded in the same year while the other in the following spring. The earlier peak occurred 2 weeks after the

Fig. 19. The effect of temperature on weekly emergences (expressed as percentage) of parasites from Brevicoryne brassicae mummies collected from Brussels sprouts at Silwood Bottom, 1973. The whole emergence period lasted from 10 October 1973 to 11 June 1974.

Date	Number of mummies collected
A) 10 October	395
B) 17 October	356
C) 24 October	450
D) 31 October	538
E) 7 November	502
F) 14 November	707
G) 21 November	418

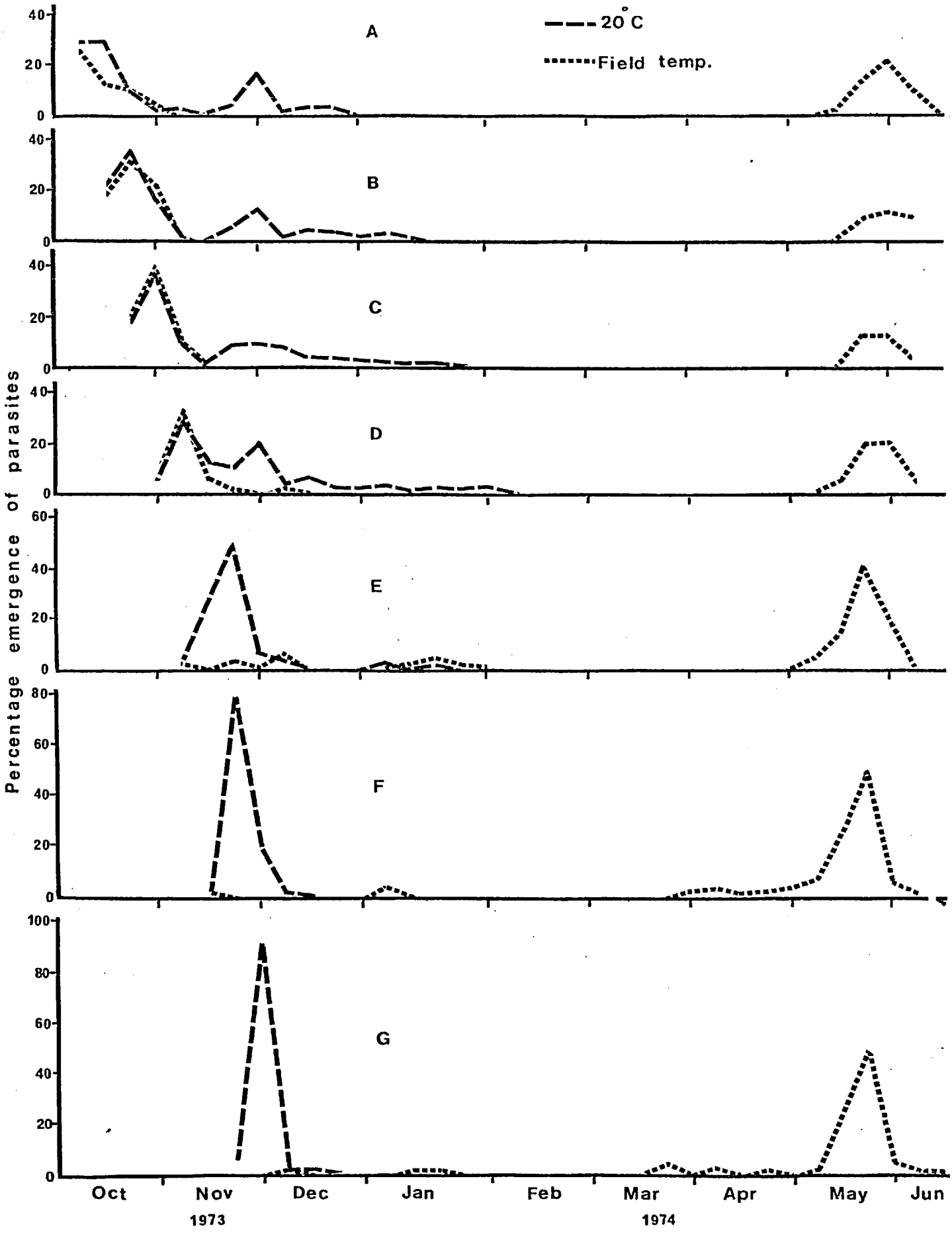

20°C
Field temp.
A
B
C
D
E
F
G
Percentage emergence of parasites
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
1973
1974

Fig. 19.

Fig. 20. The effect of day length on weekly emergences (expressed as percentage) of Alloxysta brassicae from Brevicoryne brassicae mummies collected from winter rape at Silwood Bottom, 1974. The other species of parasites have been excluded from analysis as the numbers were small.

Date of mummy collection.

A) 12 June

B) 21 June

C) 28 June

D) 5 July

Fig. 21. The effect of temperature on weekly emergences (expressed as percentage) of parasites from Brevicoryne brassicae mummies collected from Brussels sprouts at Silwood Bottom, 1974. The whole emergence period lasted from 19 June to 13 August 1974.

Date	Number of mummies collected
A) 19 June	105
B) 26 June	121
C) 3 July	104
D) 10 July	45
E) 17 July	18

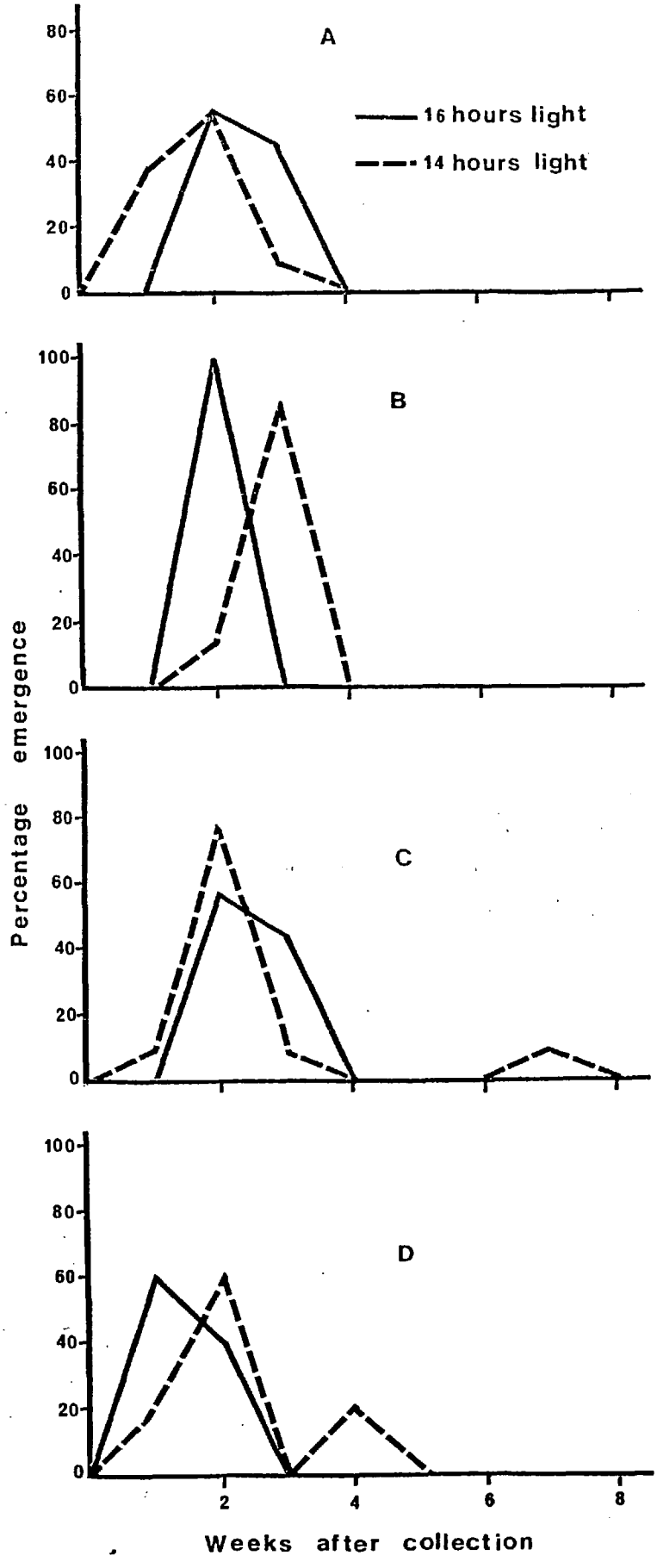

A
16 hours light
14 hours light
B
C
D
Percentage emergence
Weeks after collection
2
4
6
8

Fig. 20.

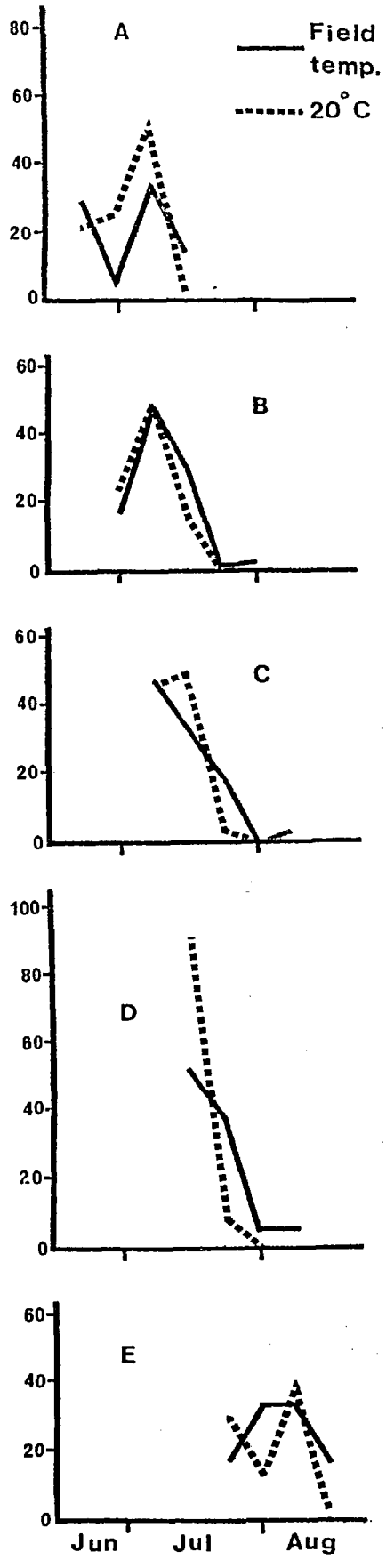

A
Field temp.
20°C
B
C
D
E
Jun
Jul
Aug

Fig. 21.

time of collection but became smaller with the lateness of collection and disappeared completely for those mummies collected in November. Conversely the second peak in the following spring increased with time and consistently occurred between 15 to 28 May.

For the mummies kept at 20°C there were also 2 peaks for the first 4 collections although both the peaks occurred within the same year. For the November collections, only one peak was seen with emergences occurring over a much shorter period.

In 1974, none of the mummies which were collected in June and July overwintered (Fig. 21). The mean temperatures for these 2 months were 14.2° and 16.2°C respectively which are well above the parasite developmental threshold (e.g. for D. rapae = 6.5°C; Hafez, 1961). This suggests that temperature is the prime factor, amongst others, in causing quiescence in the parasites. As expected the parasite emerged a little earlier from mummies kept at 20°C.

The emergence of parasites from mummies collected from rape (Table 12) exhibited the same pattern generally.

ii) Laboratory-reared mummies.

About 10 females of D. rapae were allowed to oviposit on aphids under laboratory conditions (20°C and 16 hours of light). The mummies resulted after rearing were collected at the same time and hence it seems reasonable to assume that the parasites within the mummies had reached a comparable developmental stage. The mummies were then divided into groups of 19 and each group kept at one of the following temperatures: 10°, 15°, 20°, 25°C (all 16 hours of light) and field temperature. Although the number of mummies used was small, the results are consistent.

It is clear that adult D. rapae emergence depended largely on the temperature at which the mummies were kept (Fig. 22). This is illustrated well by the emergence peak at each temperature.

Table 12. The effect of temperature and day length on weekly emergence (expressed as percentage) of A. brassicae from B. brassicae mummies collected from winter rape in Silwood Bottom, 1974. The other species of parasites which also emerged from the same samples have been excluded from analysis.

Date of collection	Total mummy	Temperature (°C)	Week of emergence							Total parasites
			1	2	3	4	5	6	7	
12 June '74	30	Field	20.0	73.3	6.7	-	-	-	-	15
	20	10°LD*	-	15.4	15.4	38.5	30.7	-	-	13
	20	20°SD**	38.5	53.8	7.7	-	-	-	-	13
	30	20°LD	-	54.5	45.5	-	-	-	-	11
21 June	50	Field	-	21.4	71.4	7.1	-	-	-	28
	25	20°SD	-	13.3	86.7	-	-	-	-	15
	25	20°LD	-	100.0	-	-	-	-	-	18
28 June	38	Field	4.3	26.1	60.9	4.3	4.3	-	-	23
	25	10°LD	-	-	15.4	30.7	46.2	7.7	-	13
	25	20°SD	7.7	76.9	7.7	-	-	-	7.7	13
	25	20°LD	-	56.2	43.8	-	-	-	-	16
5 July	30	Field	22.2	44.4	22.2	11.1	-	-	-	9
	30	10°LD	8.3	25.0	16.7	25.0	25.0	-	-	12
	30	20°SD	20.0	60.0	-	20.0	-	-	-	10
	30	20°LD	60.0	40.0	-	-	-	-	-	10

* LD = long day, 16 hours light

**SD = short day, 14 hours light

Fig. 22. The effect of temperature on daily emergence (expressed as percentage) of *Diaretiella rapae* from *Brevicoryne brassicae* mummies reared at 20° C. The number of mummies used at each temperature was 19.

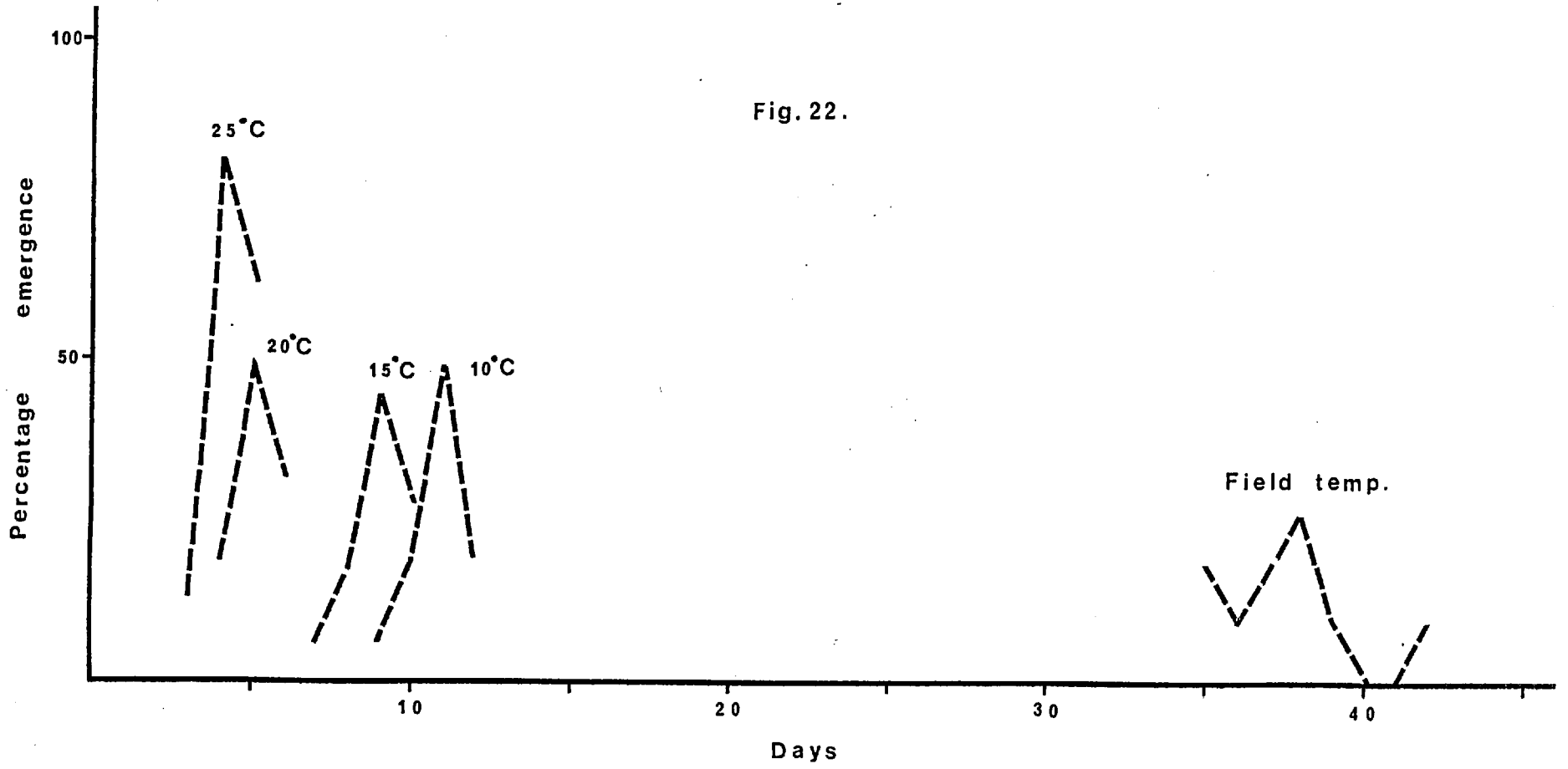

100
50
Percentage emergence
25°C
20°C
15°C
10°C
Field temp.
10
20
30
40
Days

Fig. 22.

For those kept under field conditions (from 14 March to 24 April 1975), the first D. rapae adults emerged only after 35 days. This was expected as the daily field temperatures up to the 29th day were all less than the developmental threshold of 6.5°C except on the 10th and 11th days.

C. Effect of day length.

Beside temperature, daylength was also tested on field collected mummies to see if it affected the emergence rate. As A. brassicae was the major species emerging from the mummies, the percentage emergence at each different day length was calculated for this species only. Fourteen hours of light had been used as short photoperiod since workers on thephysiology of insect diapause (e.g. Less, 1955; Jackson, 1963) had found that the critical photoperiod causing diapause is between 6 and 15 hours of light.

For 2 collections (Fig. 20 B,D), the peak parasite emergence from mummies kept at short day length was one week behind that for those kept at long day length. In the remaining 2 cases (Fig. 20 A,C) the 2 peaks coincided. These results seem to suggest that day length has little or no effect on the emergence rate of parasites from mummies.

D. Discussion.

It is clear that the parasites go into a quiescent state when the field temperature falls below the developmental threshold. Such overwintering mummies begin to appear in late September or early October, the proportion of which increases inversely with temperature, reaching 100% by December. In the following spring, the parasites begin to emerge, in small numbers at first and reaching peak during April - June when the temperature is much higher.

Since day length has been shown not to influence the parasite emergence, it must be inferred that temperature is the sole factor involved.

SECTION IV. TEST OF SYNCHRONISATION BETWEEN A) DIARETIELLA RAPAE AND BREVICORYNE BRASSICAE, AND B) ALLOXYSTA BRASSICAE AND D. RAPAE.

1. Introduction.

The statement that a parasite species is synchronised with its host appears often in entomological papers, though the definition of synchrony is rarely given. It is generally implied then that synchrony is the coincidence of the parasite and host over a certain period of time.

Thalenhorst (1950) defined coincidence as "the occurrence of susceptible host stage and parasite adult female in space and time". Griffiths (1969) considered that the amount of temporal overlap between the host and the adult parasite indicates the degree of temporal synchrony between them, the "coincidence period" of Thalenhorst (1950). He further regarded spatial synchrony as three-dimensional, both host and parasite occupying a volume of space whose boundaries are defined by their reactions to the critical aspects of their surroundings (e.g. temperature). The degree of spatial synchrony then is represented by the volume shared by the two species.

Many authors have worked on the synchrony of various parasite - host systems (Varley & Gradwell, 1958; Klomp, 1958; Franz, 1964; Embrace & Sisojevic, 1965; Cheng, 1969; Griffiths, 1969; Hassell, 1969; Macdonald & Cheng, 1970). Several others (Lees, 1955; Buck & Keister, 1956; Klomp, 1958; Schoonhoven, 1962) have also studied the physiological aspects of the synchronising mechanisms. Schoonhoven (1962), on the basis of the physiological process underlying the mechanism, sub-divided synchronisation into 2 types: a) endogenous synchronisation which results from actual stimulation or inhibition of the parasite development by the host, and b) exogenous synchronisation, which results from external stimulus, to which both host and parasite react similarly, but independently. In order to be synchronised with their hosts, the parasites usually overwinter in a state of quiescence or diapause (Barnes, 1941; Klomp, 1958; Schoonhoven, 1962; Embree & Sisojevic, 1965;

Hassell, 1969; Griffiths, 1969; Führer, 1971; Varley et al., 1973). An extreme example was cited by Barnes (1941), who reported that larvae of the wheat blossom midges, Contarinia tritici (Kirby) and Sitodiplosis mosselana (Gehin) could spend up to 3 and 4 winters respectively in the soil before pupation and the adults emerged when the wheat ears were available. Similarly, the parasites of these midges synchronised with the hosts by spending an equally long time in the soil.

Predictive studies using mathematical models on the effects of asynchrony have been carried out by Hassell & May (1973) and Griffiths (1969).

Macdonald & Cheng (1970) provided a test of synchronisation. By their definition, a parasite is synchronised with its host if the density of parasites searching for hosts remains constant from the beginning to the end of the period of host population susceptibility. Since the density of the parasite is difficult to assess accurately in the field, an indirect method reflecting parasite activity is used. This is based on the axiom that the proportion of hosts parasitised in a field sample depends on the parasite density alone, as shown by Nicholson & Bailey (1935). They showed that if synchrony exists, the plots of the proportion of parasitised hosts and the proportion of unparasitised hosts in the field samples in relation to time should coincide. However, the cumulative fractions of parasitised host (P_d), and unparasitised host (H_d) are used instead because they provide smoother curves without any loss of information.

$$P_d = \frac{1}{N_p} \sum_{i=1}^{d} p_i, \quad \text{and}$$

$$H_d = \frac{1}{N_h} \sum_{i=1}^{d} h_i,$$

where p_i, h_i = parasitised and unparasitised hosts in a field sample, and N_p, N_h = the total parasitised and unparasitised hosts over the whole sampling period.

This test, however only shows whether synchrony exists or not, and does not indicate the degree of synchronisation involved. Griffiths (1969)

introduced 2 simple indices of synchrony. He defined the index of temporal synchrony as the proportion of the life span of the female adult parasite during which the parasite and the host are in contact. A decrease in the total contact time (resulting from the parasites finding the hosts too early or too late) would then lead to a smaller value of the index. Similarly the index of spatial synchrony is the proportion of host population susceptible to attack. A decrease of susceptible hosts available for attack (arising from the hosts being in an unsuitable stage or located in a refuge) would decrease the value of the index.

Synchrony is so important in the host-parasite system that the success of biological control of pests depends largely on the synchronisation of release of parasites in space and time with the pest incidence.

Asynchrony would lead to a) a wastage of parasite eggs, as reported by Embree & Sisojevic (1965), Hassell (1969) and Cheng (1969), and a decrease in the efficiency of the parasite, and b) protection of hosts from parasitism (Varley & Gradwell, 1958; Hassell, 1969) and then to stabilising the host - parasite system (Hassell, 1969; Griffiths, 1969; Hassell & May, 1973).

2. Method of analysis.

The synchronisation test of Macdonald & Cheng (1970) was designed chiefly for Lypha dubia Fall. and its host Operophtera brumata (L.), both univoltine species. Therefore the test would be suitable for univoltine species such as those investigated in connection directly or indirectly with synchronisation studies by Klomp (1958), Embree & Sisojevic (1965), Schoonhoven (1962), Hassell (1969), Griffiths (1969) and Cheng (1970), or to multivoltine species with discrete generations (e.g. Pleoplophus basizonus (Grav.) in Griffiths, 1969). For these species, usually a lepidopteran or a dipteran, it is easy to define the susceptible stage (the second or third instar larvae) and the period of host availability (the time when the second instar is first recorded to the time when the last third instar larva pupates).

However, in the B. brassicae - D. rapae system, the test is less suitable

for the following reasons:

i) the aphid and parasite are multivoltine,

ii) the aphid generations overlap at a very early stage in the build-up of the population,

iii) all aphid stages are susceptible to attack, although with varying degree of preference and success (Hafez, 1961), and

iv) the aphids are available for attack in the crop almost during the whole year except in severe winters when only eggs will survive.

The first two objections are also applicable to D. rapae - A. brassicae system.

Although these difficulties were recognised, the test was applied to the results of the work done in 1973-74 to determine whether this, the only test available, had any applications to data of this type. Two sets of data, divided into the two simple host-parasite systems (namely B. brassicae - D. rapae and D. rapae - A. brassicae), were analysed namely i) records of the aphid populations in the field and ii) results of the "aphid-exposure" experiments. It was necessary to treat the data in different ways as explained below.

A. B. brassicae - D. rapae system.

The mummies whether yielding primary or secondary parasites were considered as hosts parasitised by the primary. This was necessary since all mummies contained primary parasites before they were attacked by the secondary parasites.

The second condition was that the first date when the percentage emergence of the primary parasite from the mummies within 3 weeks after collection was less than 90 was taken as the last date of these data to be analysed. In other words, the data recorded later than this date were ignored as most of the parasites within the mummies did not emerge until the following spring. This step was important as the test indirectly checked

the constancy of the parasite density during the period of host susceptibility. If overwintering mummies were considered in the analysis, a decrease in the parasite density would of course be included and the test then defeated.

The last collection dates before overwintering mummies exceeded 10% of the collected mummies were 31 October 1973 and 16 October 1974.

For the analysis of the aphid population and mummy number recorded in the field, the total number counted on 50 sprout plants had been used instead of the geometric mean. For the field results of 1974, the actual number of parasitised aphids had also been used in addition to the mummy number.

B. D. rapae - A. brassicae system.

The mummies which yielded D. rapae were considered as unparasitised hosts, while those yielding A. brassicae as parasitised hosts. The last dates of mummy collection before A. brassicae emergence fell below 10% were 4 October 1973 and 25 October 1974, and results later than these dates were excluded.

3. Results.

The results of the analysis are shown in Fig. 23 - 24 in which the cumulative fractions of parasitised and unparasitised hosts have been plotted. If synchrony exists, the two plots should coincide. If there is no synchrony, changes in the slope of the plot of parasitised hosts would indicate the changes in the parasite density. A higher gradient would imply an increase in the parasite density while a lower gradient a decrease.

A. B. brassicae - D. rapae system.

i) Data: field population of aphid.

In 1973 (Fig. 23A) there was no synchrony between D. rapae and the aphid, the parasite density appeared to increase continuously.

In 1974, 2 tests were carried out, one using the number of mummies recorded (Fig. 23C) and the other using percentage of parasitism (Fig. 23D).

Fig. 23. Plots of cumulative fractions of parasitised hosts, P_d(•) and unparasitised hosts, H_d(o). Data from field studies carried out at Silwood Bottom, 1973 - 74.

A) 1973, between D. rapae (•) and B. brassicae (o)

B) 1973, between A. brassicae (•) and D. rapae (o)

C) 1974, between D. rapae (•) and B. brassicae (o), data based on numbers of mummies and aphids.

D) 1974, between D. rapae (•) and B. brassicae (o), data based on numbers of parasitised and unparasitised aphids.

E) 1974, between A. brassicae (•) and D. rapae (o).

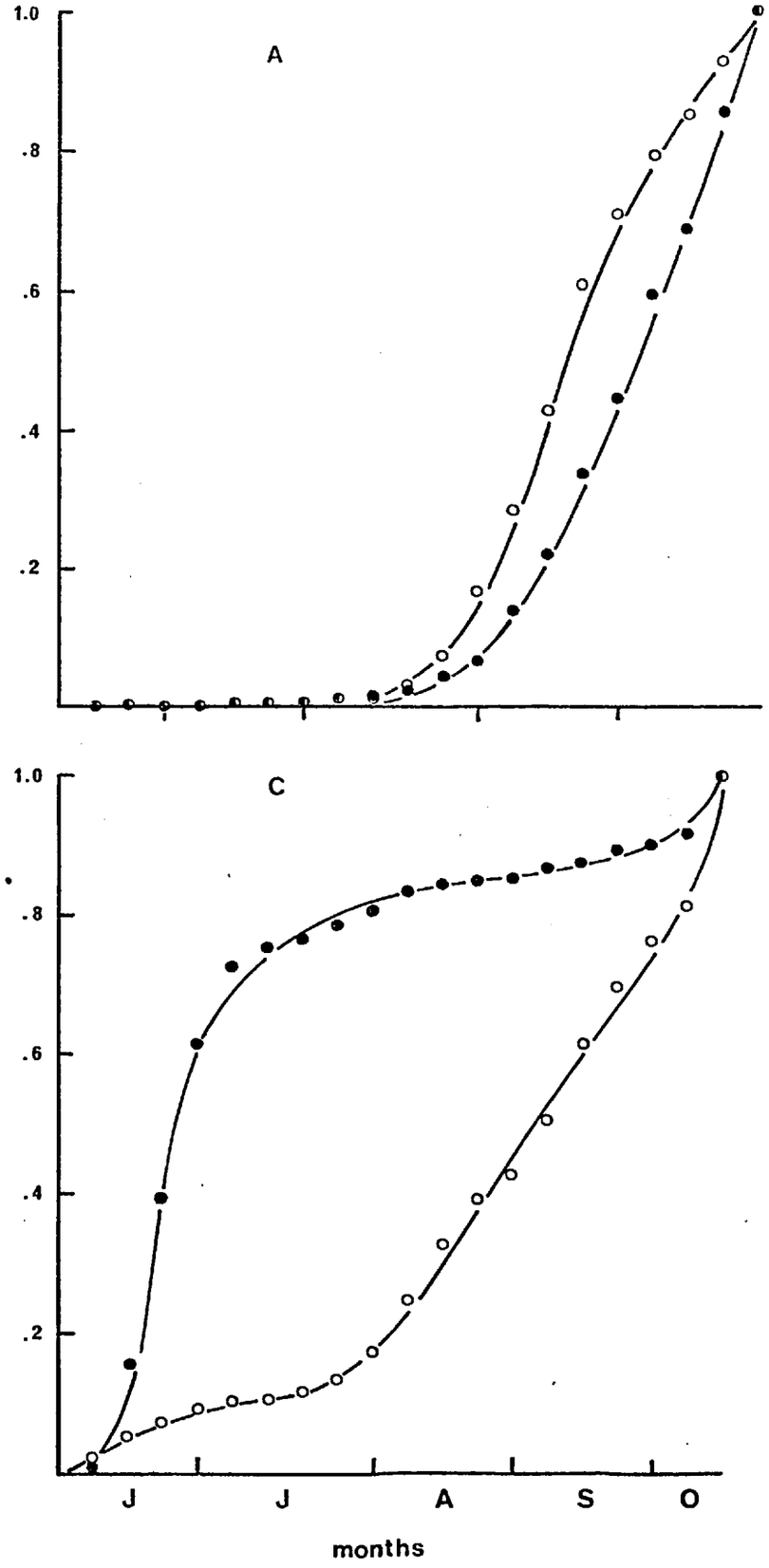


Fig. 23.

Both tests showed a lack of synchrony; the parasite density increased rather quickly in the first 5 weeks, after which it started to decline before the whole period of host susceptibility was over.

ii) Data: 'aphid-exposure' experiments.

a) aphids exposed for one week.

In both years, 1973 and 1974 (Fig. 24A, E) there was no synchrony. The parasite density was high in the early weeks, but it started to decline steadily later.

b) aphids exposed for 2 weeks.

In 1973 (Fig. 24C) there was seemingly synchrony, with a time lag of one week. The parasite density also appeared to increase continuously during the period of host susceptibility. However, the χ^2 test based on actual numbers (time lag and pooling of values of less than 5 considered) gave a value of 1452 (D.f. = 7, $P < 0.001$).

In 1974 (Fig. 24F) synchrony was also absent and the parasite density was high at the beginning and end of the season.

B. D. rapae - A. brassicae system.

i) Data: mummy collections.

In 1973 (Fig. 23B), the two curves almost coincided except at the beginning during which the density of A. brassicae increased rather slowly. No time lag of the type described by Macdonald & Cheng (1970), and Cheng (1970) was present. A probable reason is that the parasitism of D. rapae mummies by A. brassicae was not noticeable until the adult secondary parasites had emerged. The χ^2 test on the actual number of D. rapae and A. brassicae mummies yielded a non-significant value of 14.9 ($P > 0.10$, d.f. = 9).

In 1974 (Fig. 23E) there was only a slight coincidence of the curves at

Fig. 24. Plots of cumulative fractions of parasitised hosts, P_d (•) and unparasitised hosts, H_d (o). Data from aphid-exposure experiments carried out at Silwood Bottom. A-D, 1973; E-H, 1974.

A) between *D. rapae* (•) and *B. brassicae* (o), exposure period : 1 week.

B) between *A. brassicae* (•) and *D. rapae* (o), exposure period : 1 week.

C) between *D. rapae* (•) and *B. brassicae* (o), exposure period : 2 weeks.

D) between *A. brassicae* (•) and *D. rapae* (o), exposure period : 2 weeks.

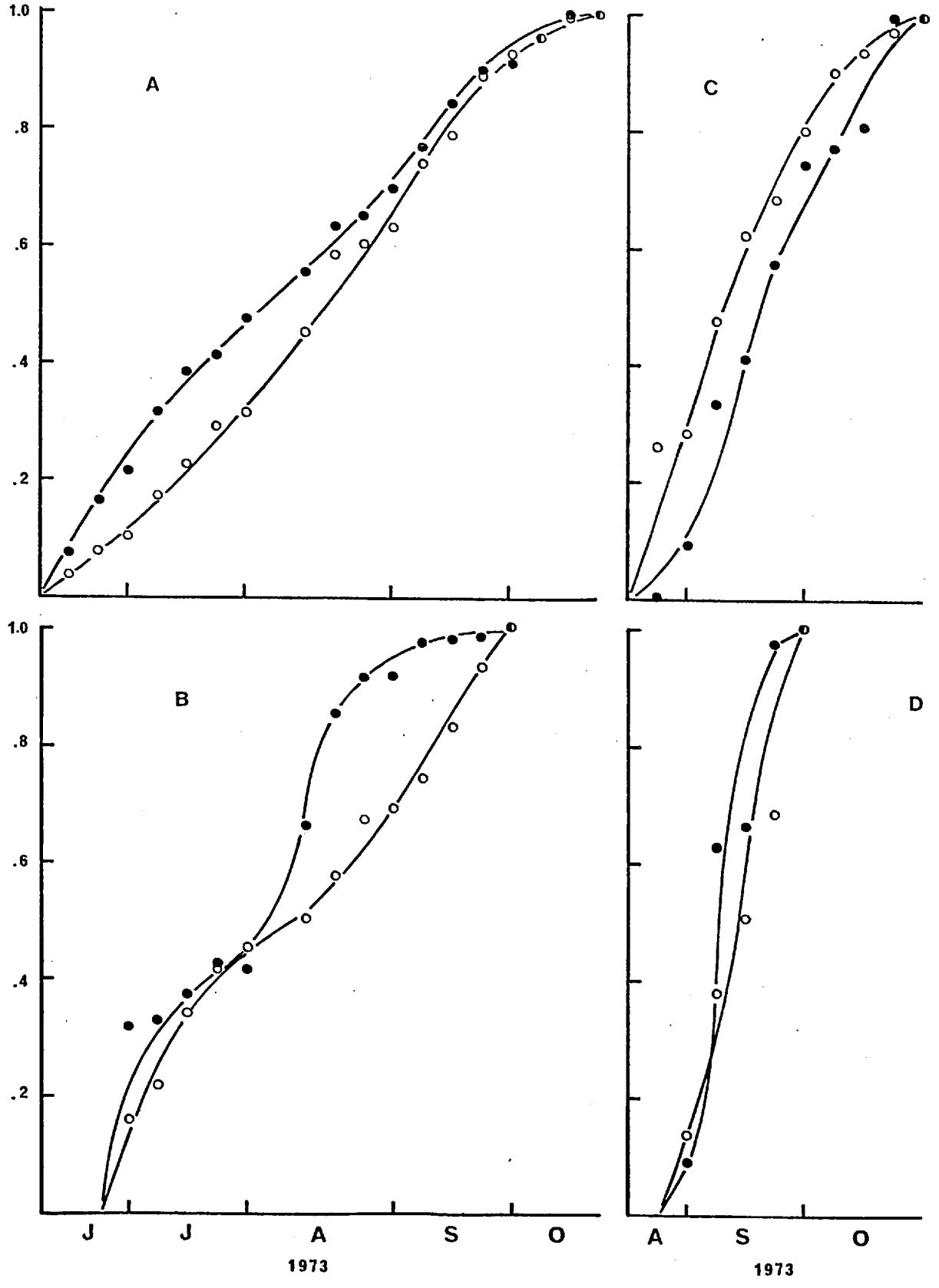


Fig. 24.

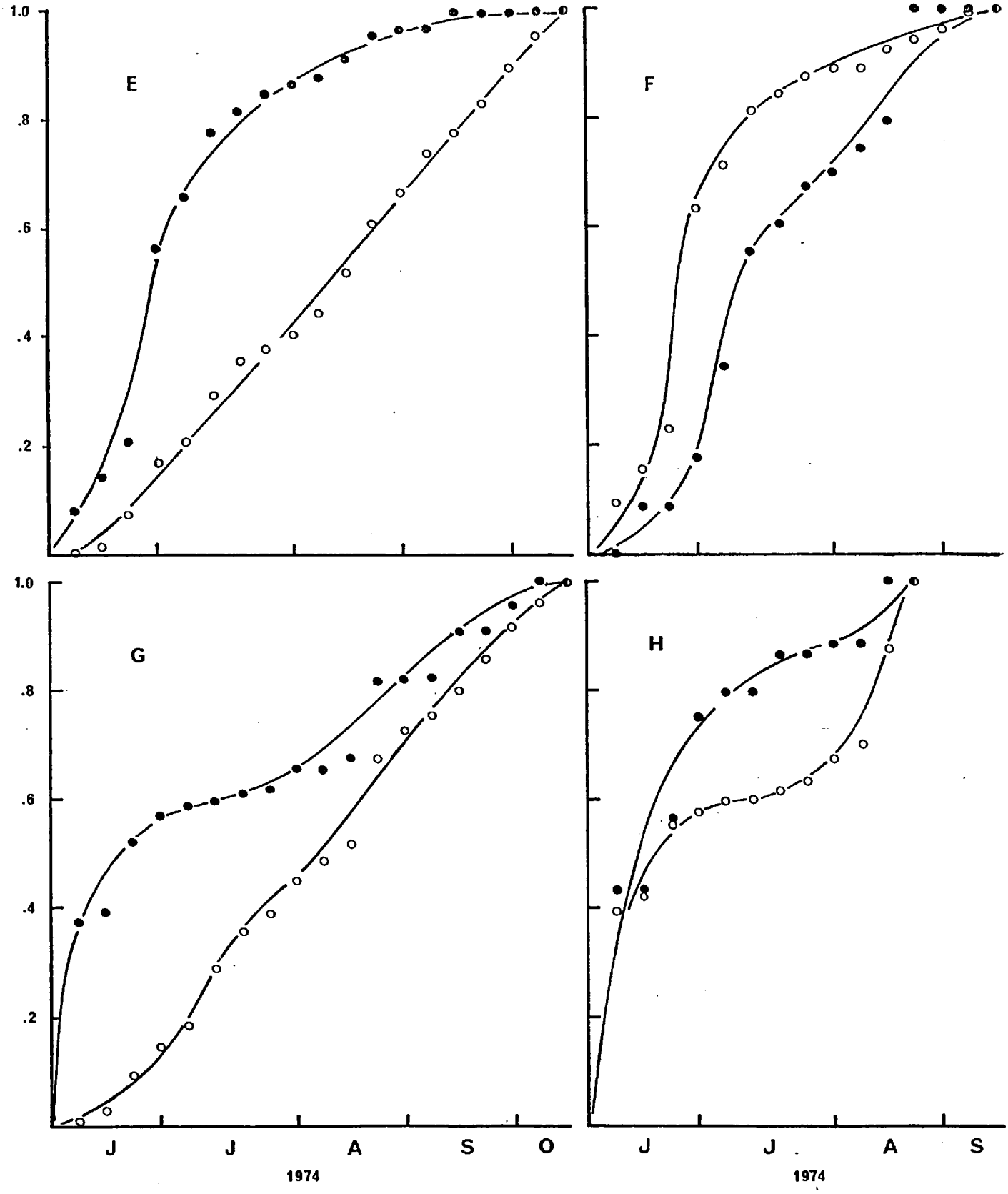
Fig. 24 continued.

E) between *D. rapae* (•) and *B. brassicae* (o), exposure period : 1 week.

F) between *D. rapae* (•) and *B. brassicae* (o), exposure period : 2 weeks.

G) between *A. brassicae* (•) and *D. rapae* (o), exposure period : 1 week.

H) between *A. brassicae* (•) and *D. rapae* (o), exposure period : 2 weeks.


E
F
G
H
1.0
.8
.6
.4
.2
J
J
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S
O
1974

the beginning and end of the period. This implies that the density of A. brassicae decreased suddenly during the intervening time.

ii) Data: 'aphid-exposure' experiment.

a) aphids exposed for one week.

In 1973 (Fig. 24B), synchrony was absent. The density of A. brassicae decreased from the 4th week onwards, then increased again during the 8th and 9th weeks, and decreased once more at the end of the season.

In 1974 (Fig. 24G), synchrony was absent too. The density of A. brassicae was high at the beginning, but it decreased before the host-susceptibility period was over.

b) aphids exposed for 2 weeks.

There was no synchrony in both years.

In 1973 (Fig. 24D) A. brassicae density was low at the beginning and end of the period of host susceptibility.

In 1974 (Fig. 24H), A. brassicae density was high at the beginning but low at the end of the host susceptible period.

4. Discussion.

The test of synchronisation of Macdonald and Cheng (1970) is based on the definition that a parasite population is synchronised with its host population if the density of the parasites searching for hosts remains constant throughout the period of host population susceptibility.

The test when applied to the B. brassicae - D. rapae system did not indicate any synchrony between the parasite and host. Generally, the density of D. rapae was high during the first 5 weeks or so of the host susceptibility period, but it dropped later and did not recover for the rest of the period. Undoubtedly the drop was caused by the secondary parasite, A. brassicae. The

decrease in D. rapae density is reflected in the gentler gradients of the graphs (Fig. 23 - 24).

In the D. rapae - A. brassicae system., synchrony was shown to be present only in one case (using the data on mummy collections in 1973). This conclusion however, was not supported by the data obtained from the "aphid-exposure" experiments. Perhaps the relatively much smaller number of hosts (D. rapae mummies) available on the experimental plants had affected the outcome of the experiments. In the other cases, synchrony appeared to be present only at the beginning of the period of host susceptibility. Then the density of A. brassicae began to drop either from the middle onwards (around the 5th week) or towards the end of the period. This drop could be due to the decrease in the availability of primary parasites after its population had been reduced during the initial attack by A. brassicae.

In the one case where synchrony was shown to exist between A. brassicae and D. rapae, the implication is, following Macdonald & Cheng's definition (p.84) that the density of the secondary parasite remained constant in the field during the period of host susceptibility. This however, does not seem to be true since the density of A. brassicae recorded on 50 sprout plants during the period tested (i.e. from 25 July to 4 October, 1973) varied from 4 on 19 September to 50 on 4 October (Fig. 9A).

To check the validity of the test, it was then decided to apply it to the earlier part of the host susceptibility period (June - July) when the density of D. rapae (and A. brassicae in 1973) was recorded (Fig. 9, 10) as being relatively steady (within sampling errors). The results (Fig. 25A-E) did not indicate that synchrony existed between D. rapae and B. brassicae within these periods (13 June - 1 August, 1973 and 5 June to 31 July, 1974), implying that the density of D. rapae was not constant (all χ^2 values significant at $P < 0.001$). Further tests were carried out on slightly longer periods namely from 13 June to 8 August, to 15 August and to 22 August, 1973 and from 5 June to 7 August and to 14 August, 1974. The results were similar to those shown in Fig. 25 A-E, also with highly significant χ^2 values. The tests

Fig. 25. Plots of cumulative fractions of parasitised hosts, P_d (•) and unparasitised hosts, H_d (o). Only data for June-July had been analysed.

A - F : between *D. rapae* (•) and *B. brassicae* (o),

G - J : between *A. brassicae* (•) and *D. rapae* (o).

A) Field studies, 1973; data based on numbers of mummies and aphids; $\chi^2 = 235^{***}$ (d.f. = 6)

B) Field studies, 1974; data based on number of mummies and aphids; $\chi^2 = 664^{***}$ (d.f. = 7)

C) Field studies, 1974; data based on numbers of parasitised and unparasitised aphids; $\chi^2 = 681^{***}$ (d.f. = 8)

D) aphid-exposure experiments, 1973; exposure period : 1 week; $\chi^2 = 279^{***}$ (d.f. =6)

E) aphid-exposure experiment, 1974; exposure period : 1 week; $\chi^2 = 352^{***}$ (d.f. = 7)

F) aphid-exposure experiments, 1974; exposure period : 2 weeks; $\chi^2 = 521^{***}$ (d.f. = 3)

G) Field studies, 1974; $\chi^2 = 19^{***}$ (d.f. = 3)

H) aphid-exposure experiments, 1974; exposure period = 1 week; $\chi^2 = 35^{***}$ (d.f. = 4)

I) aphid-exposure experiments, 1974; exposure period = 2 weeks; $\chi^2 = 10^{**}$ (d.f. = 2)

J) aphid-exposure experiments, 1973; exposure period : 1 week; $\chi^2 = 149^{***}$ (d.f. = 5)

*** value significant at $P < 0.001$

** value significant at $P < 0.01$.

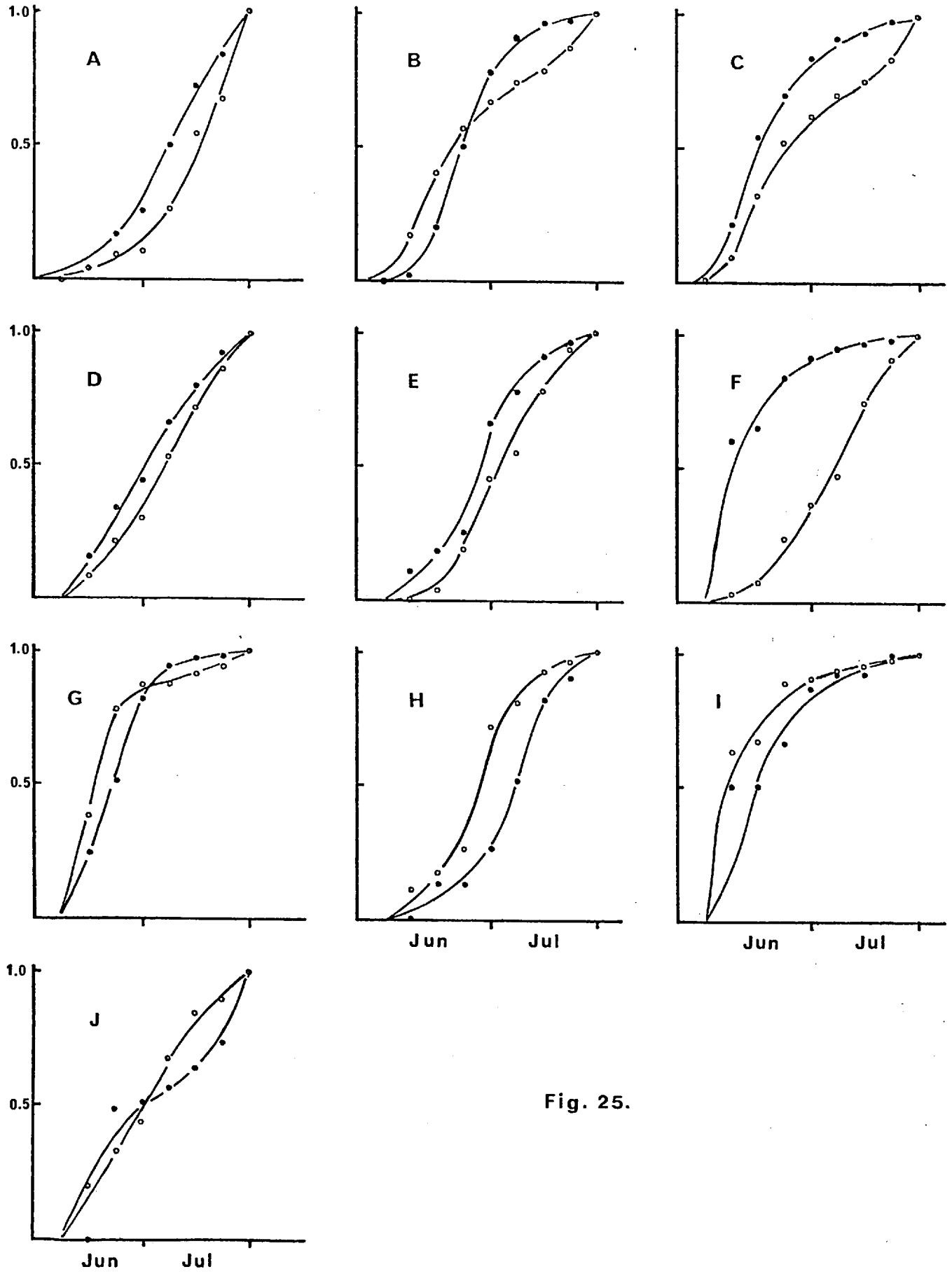


Fig. 25.

carried out on A. brassicae - D. rapae system for the same period (June-July) also did not indicate synchrony except for the data on aphid-exposure experiments (Fig. 25H, I). In both these cases the number of parasitised hosts were small and some pooling of data was necessary before applying the χ^2 test, but there appeared to be some degree of synchrony; the χ^2 values however were significant and did not support the hypothesis of synchrony.

It would then appear that the same test applied to the 2 parasite species produced information contradicting to that obtained by a different and independent method (viz. counting in the field). For A. brassicae, the test revealed synchrony (Fig. 23B) when the parasite density recorded in the field was not constant. For D. rapae, despite the relatively constant density recorded during June - July, the test did not show synchrony for this short period (Fig. 25 A-E). These results tend to put the value and validity of the test in question, especially when applied to the aphid-parasite systems.

It seems more reasonable to follow Griffiths' (1969) and treat synchrony as the coincidence of the female parasite and the susceptible host stage in space and time. This would imply that D. rapae was synchronised with B. brassicae since both were recorded in the field during the same period. Similarly, A. brassicae would be considered as synchronised with D. rapae.

If anything, the synchrony test at least illustrated well the decline in the primary parasite density from the middle of the season onwards. This supports the earlier view (p. 46) and the findings of other workers (e.g. Hafez, 1961; Sedlag, 1964; Paetzold & Vater, 1966 etc.) that the failure of D. rapae to control the aphid population is mainly due to its decrease in density caused by secondary parasites. Thus there is a high percentage of mummies of percentage parasitism of the aphids only up to about late July (Fig. 4C).

Van Emden (1966) reported that the predators (especially syrphids) are not well synchronised with B. brassicae, and he concluded that good control of the aphids was achieved until mid-August (van Emden, 1963). These results of low parasitism and predation concur with the view put forward by Varley & & Gradwell (1958) that a lack of synchrony is equivalent to a protection of

some hosts from parasitism (or predation), and as Hassell (1969) pointed out this results in a loss of potential parasite (or predator) progeny. However, it is uncertain whether the asynchrony observed here had the ultimate effect of quenching the competitive curve between the hosts and the parasites as postulated by Varley & Gradwell (1969), or stabilising the host and parasite population as speculated by Hassell (1969), Griffiths (1969) and Hassell & May (1973).

SECTION V. LABORATORY STUDIES ON PARASITES OF B. BRASSICAE.

1. Study on synchronisation : The effect of time of arrival of Diaretiella rapae on population of B. brassicae.

A. Methods and materials.

Three sets of experiments were carried out with two systems: Set I with System A which had only one sprout leaf in a box, and Sets 2 and 3 with System B which involved a sprout plant within a Doncaster cage.

The experiments were conducted in triplicate in 20°C and 16 hours of light.

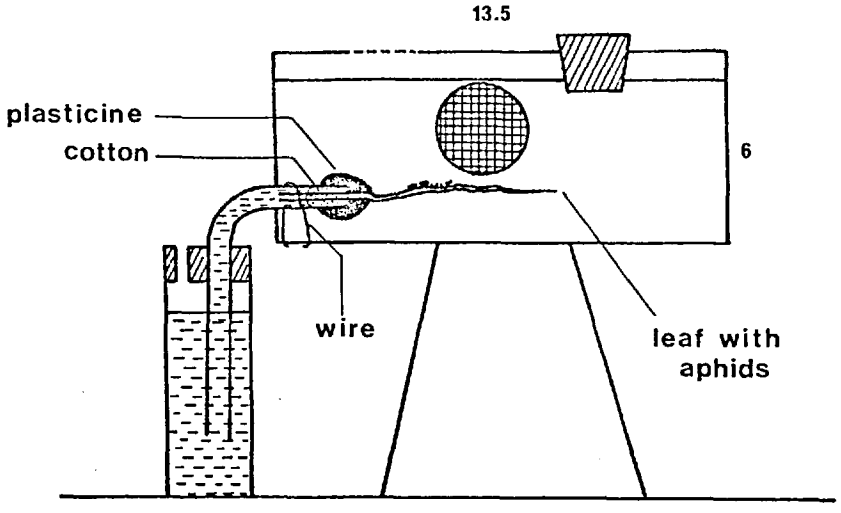
i) System A (Fig. 26A).

The plastic box was 13.5 x 7.5 x 6 cm^3. The leaf was connected to a vial of nutrient solution by a flexible plastic tubing which was anchored securely in place by a piece of wire. Nutrient solution was added when necessary to the vial through a small hole in the cork. To prevent the leaf drying up and to maintain the capillary flow of solution, the petiole was wedged in position by cotton wool and covered with plasticine.

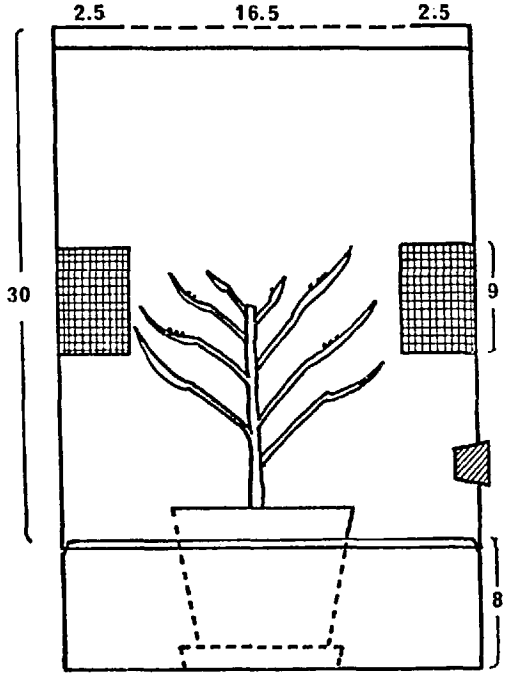
The box had 3 windows (2 on the sides and one on the lid) which were covered by nylon mesh. The lid had also a hole through which the parasites were introduced or removed (when counting). For stability, the box was fixed to an inverted plastic cup.

When the leaf became yellow and senescent it was replaced by a young fresh cut leaf. The old leaf was placed on top of the new one until all aphids had transferred across.

Two alates were introduced at the start of the experiment (Experiment Set 1), and the aphid population allowed to increase. A pair of parasites (the female possible already mated) were then introduced on one of the



A



B

Fig. 26. The closed ecosystems used in the experimental studies on the synchronisation between D. rapae and B. brassicae. Dimensions are given in centimetres.

A) System A.

B) System B (a Doncaster cage).

following days: 4, 8, 11 and 21. Counts of aphids and parasites were made at intervals of 3 to 5 days until the experiment was terminated.

ii) System B (Fig. 26B).

The Doncaster cage was cylindrical, of diameter 21.5 cm and height 38.0 cm. The lid and base were made of metal and the side of cellulose acetate. There were 3 windows, one on the lid and 2 on the sides, which were covered by fine nylon mesh. The parasites were introduced or removed (during counting) through a hole which was stoppered at all other times. The plant was replaced by a fresh one when senescence of leaves or signs of ill-health (e.g. heart rot caused by stem borers) were observed. The leaves were cut from the old plant and placed on the new so that the aphid colonies could transfer onto the fresh plant.

In the first set of experiments carried out with this cage (Experiment Set 2), the number of leaves on the plant was variable, but with a minimum of 8 leaves, and 10 first instar aphids were introduced. The parasites were introduced on one of the following days: days 0, 1, 3, 4, 5, 6, 9, 14 and 22. Since the aphids do not begin reproduction before the tenth day, the populations only increased substantially in the 14th and 22nd day introductions.

The aphid and parasite counts were made every third or 4th day at the beginning of the experiment but weekly later.

In the second set (Experiment Set 3), the number of leaves on the plant was limited to 8 and the terminal shoot was nipped off. Different initial aphid numbers of 10, 20, 40 and 80 (all of first instar) were used. On the 4th day after commencement of experiment, when the aphids were about late second or early third instar, the parasites were introduced into the cages. The aphids and parasites were counted weekly.

ii) Population assessment of aphids and parasites.

In assessing the populations, all live aphids and parasites were counted,

and the dead ones removed and preserved in alcohol to be counted later. Intact mummies were marked red and unmarked mummies with emergence holes were considered to have been missed or too soft to be marked at the count immediately previous and were recorded as belonging to that count.

Live aphids that strayed away from the plant to the side or bottom of the cage were replaced on the leaf or plants.

Each parasite was counted only once, either as live or as dead. Since the parasites live on the average 5 days under ideal conditions, it was assumed during counting that live parasites in one count would be dead by the next. Therefore the dead parasites were not recorded unless their number exceeded the total live parasites in the previous count, in which case the additional dead parasites must have emerged during the intervening period between the two counts.

The system was kept going until the aphid population was exterminated by the parasites.

For control experiments, parasites were not introduced.

B. Results.

i) Experimental Set 1 (Fig. 27).

It can be seen that delaying the introduction of parasites allows the aphid population to reach a higher peak before the parasites are able to bring about its collapse. The time the parasites took to reduce aphid population to zero varied from 59 to 98 days. The two extreme times resulted from introductions on the 8th and 4th days when the aphid densities did not differ much from each other at 18 and 15 respectively.

The proportion of female parasites that emerged from mummies varied considerably and this undoubtedly affected the time when the aphids were exterminated completely.

Fig. 27. The results of experiments on synchronisation between *D. rapae* and *B. brassicae*: Experiment Set 1 using System A (for explanation see text). Starting aphid density = 2 alates.

A) Control: *D. rapae* was not introduced.

D. rapae was introduced on:

B) Day 4,

C) Day 8,

D) Day 11,

E) Day 21.

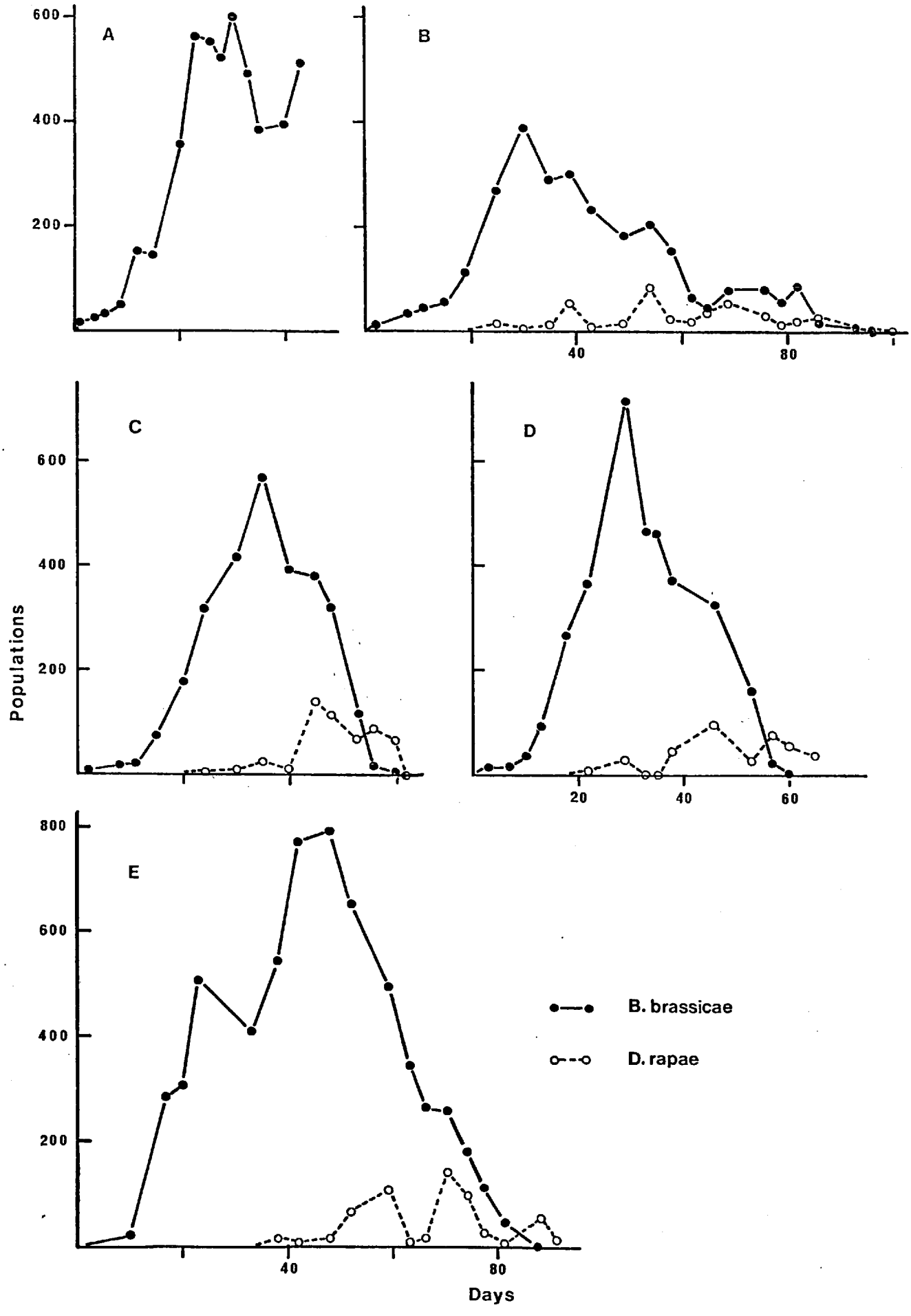

A
B
C
D
E
600
400
200
800
40
80
20
60
Populations
Days
B. brassicae
D. rapae

Fig. 27.

ii) Experimental Set 2 (Fig. 28).

With the exception of parasite introduction on the 14th and 22nd days the aphid population was only 10. This essentially meant the parasites were introduced to the same number of aphids, but of a different age.

The parasites introduced on days 0 to 3 and day 9 did not become established. The failure for the introductions on days 0 to 3 was probably due to the unsuitable age of the aphids for parasitism as they were still in the first or second instar. Since the aphid density was low, casualty from excessive ovipositional jabbings was also high. However, for the day 9 introductions, it is not known why the parasites failed to parasitise the aphids as the aphids were still in a stage quite suitable for parasitism.

For introductions on days 4 to 6, all aphid populations were reduced to zero between 100 to 130 days. It can also be seen that the earlier the parasite introduction, the greater the aphid population became before declining. The maximum aphid populations for parasite introductions on days 4, 5 and 6 were respectively 1127, 718 and 372.

On the other hand, the parasites introduced on the 14th and 22nd days took 113 and 139 days respectively to eliminate the aphids, and the respective maximum aphid populations recorded were 2434 and 1450.

Using the time the parasites took to eliminate the aphid populations as a basis, it would appear that the 'right' time for parasite introduction is on the 14th day. On days 4 to 6, the aphid density was only 10 which was too few for the parasites to establish themselves immediately and with certainty. On the other hand, the aphid population (= 76) on the 22nd day was too high and the number of hosts parasitised was governed by the fecundity of the female parasite, that is egg limitation was the important factor.

iii) Experimental Set 3 (Fig. 36 , 38).

In these experiments the parasites were introduced into aphid populations

Fig. 28. The results of experiments of synchronisation between *D. rapae* and *B. brassicae*: Experiment Set 2 using System B (for explanation see text). Starting aphid density = 10 first-instar nymphs. *D. rapae* was introduced on the following days:

A) Day 0,
B) Day 1,
C) Day 3,
D) Day 9,
E) Day 4,
F) Day 5,
G) Day 6,
H) Day 22,
I) Day 14.

For control experiments (i.e. parasites were not introduced) see Fig. 36.

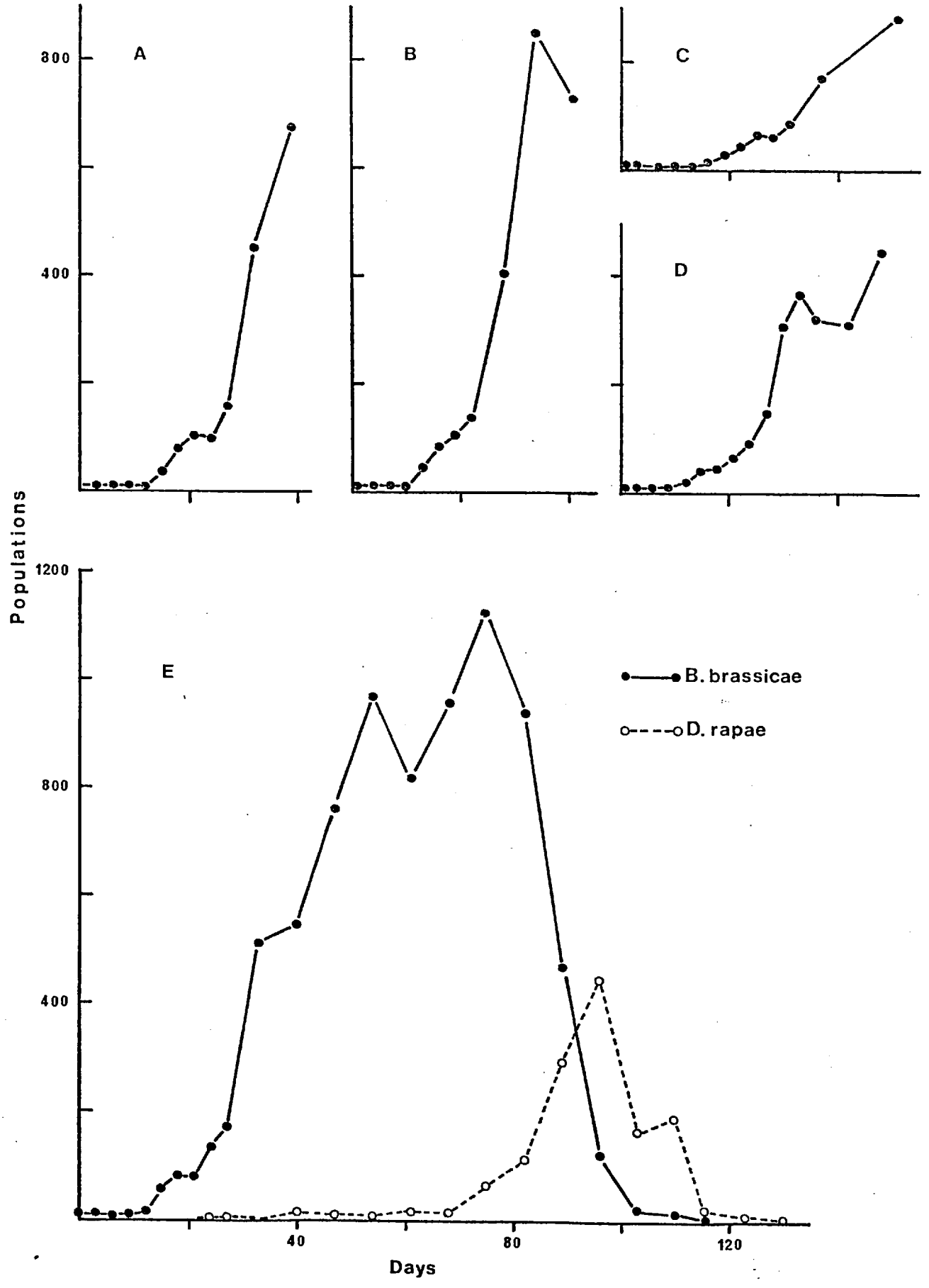
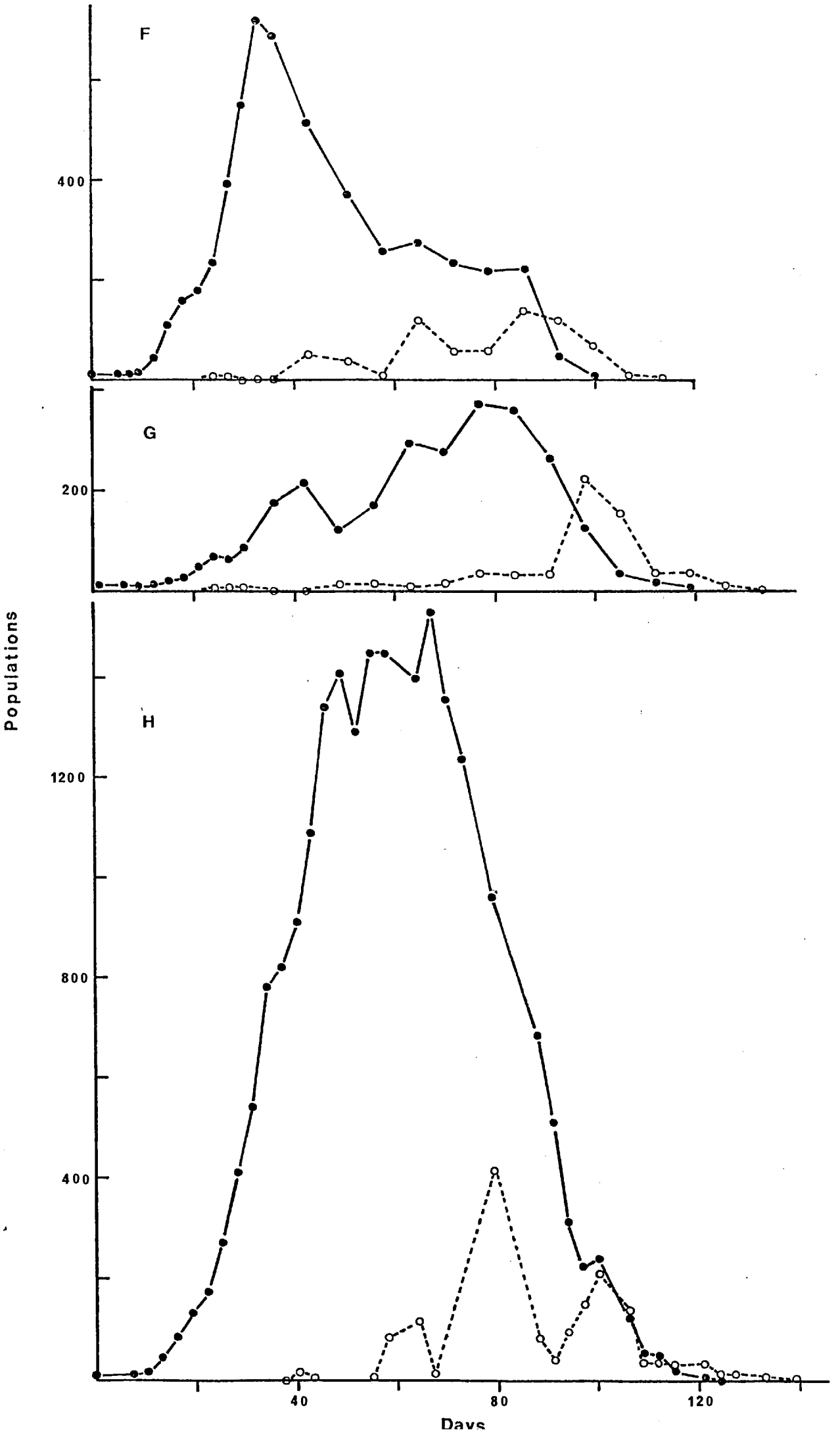
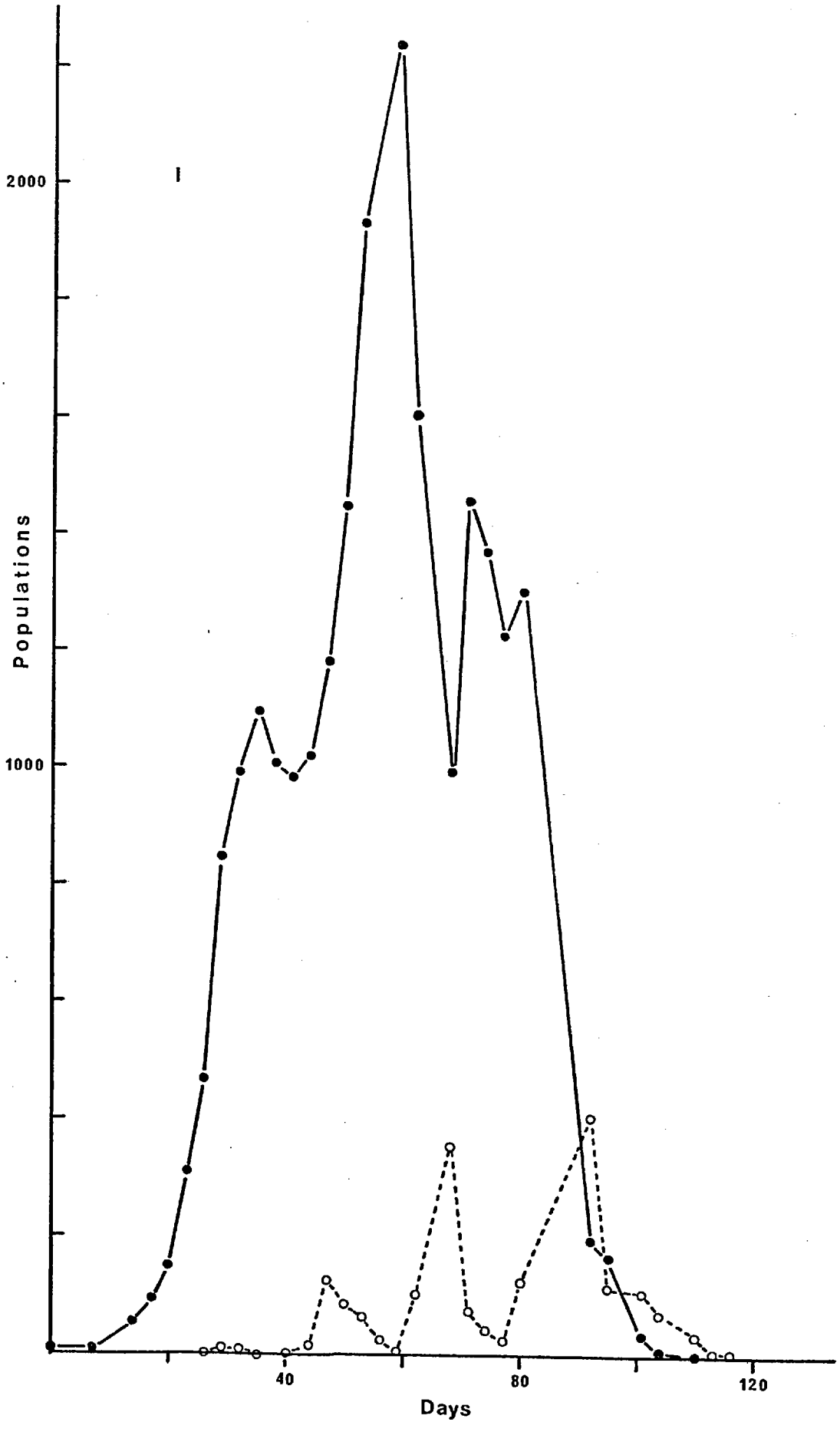

A
B
C
D
E
800
400
1200
800
400
Populations
B. brassicae
D. rapae
40
80
120
Days

Fig. 28.


F
400
G
200
H
1200
800
400
Populations
40
80
120
Days


2000
1000
Populations
40
80
120
Days

of different sizes but all the aphids were in the late second or early third instar.

In general, the aphid peak population increased as the starting aphid density was decreased. The respective maximum populations for starting densities of 10, 20, 40 and 80 were 1384, 830, 781 and 443. The shortest time to aphid extinction namely 9 weeks, occurred for the starting density of 80. For the other lower densities, the extermination time was about 12 weeks.

The number of mummies which first result after the parasite introduction depends on the available host density at the time of introduction. For the densities of 10, 20, 40 and 80 aphids the mummy numbers were 2, 6, 14 and 29 respectively; and the parasite efficiency as a proportion of aphid density becoming mummified were then 0.2, 0.3, 0.35 and 0.36 respectively.

C. Discussion.

The experimental systems used in the study were all essentially of a closed type. After the initial introduction of aphids and parasites, no immigration nor emigration of both alate aphids and adult parasites was allowed. Under such conditions it is logical to assume that the searching efficiency of the parasite was very important. Other equally important factors (e.g. superparasitism) had been disregarded or not given appropriate considerations. Undoubtedly, when the parasite - host ratios were high, superparasitism was prevalent and this led to a wastage of parasite eggs and and increased mortality rate of aphids from excessive ovipositional stabbings by the parasites. Hyperparasitism which would reduce the efficiency of the primary parasite had also been omitted.

The two criteria which have been used here to assess the ideal timing of parasite introduction are a) the maximum aphid population reached before the parasites finally bring it down, and b) the time the parasites take to

eliminate the aphid population.

The 3 sets of experiments illustrate the effect of time of arrival of D. rapae on B. brassicae population under 3 conditions, namely:

a) the alates (equivalent to the immigrants in the field) were left to build up the population before the parasites arrived, hence the populations were of different densities and the aphids of different ages,

b) the aphid populations were of the same density but the aphids differed in age, and

c) the aphid populations were of different densities but the aphids were of the same age.

It is clear that for the parasites to have maximum effects on the aphids, they must arrive when the aphid population is not too low nor too high.

In the system under study, the facotrs which affected the success of the parasite establishing itself were the host density, and the maximum fecundity of the female parasite. When the parasites are released into a low aphid population, the parasites have few hosts to attack. This leads to few second generation parasites and thus there is long delay before a high rate of parasitism is achieved. On the other hand if the aphid population is too high, only a limited number of aphids (equivalent to maximum fecundity of the parasite) would be parasitised. By the time the second generation of parasites becomes adult, the unparasitised aphids increase to such large numbers that a) economic damage to the plant is caused (which, however, has not been assessed in this study), and b) a much longer time elapses before the aphids are eliminated.

Finally, if the parasites are introduced to the 'right' aphid population level, the situation is ideal for the immediate increase of parasites. The 'right' aphid population is considered here as a population not much more than the parasite maximum fecundity so that the full complement of eggs can be laid by the parasite and not too many aphids left unparasitised

to reproduce. This would result in the maximum parasite progeny and the least available host number in the second generation.

The best results to illustrate these points come from Experiment Set 3. Initial aphid densities of 10, 20 and 40 were too low for the introduced parasites to act with full efficiency. The indices of efficiency, expressed as the proportion of the aphid population which became mummies, were 0.2, 0.3 and 0.35 respectively which were all slightly lower than 0.36 when the initial population was 80. However, the absolute numbers of mummies formed were 2, 6, 14 and 29 which led to widely different ratios of female parasite - available host in the second generation, namely 1/349, 2/392, 5/545 and 19/448. This no doubt shows the advantage of the parasite finding an aphid population which is not too small.

Experiments with initial aphid population of over 80 have not been attempted, but it is expected that there would be a decrease in the efficiency of the parasite. This is proposed as the basis of the results of Experiment Sets 1 and 2.

In Set 1, conditions similar to those in the field were simulated with respect to the arrival of immigrant alates. It is clear that the introduction of the parasites on different days is equivalent to introduction to aphid populations of different sizes. Parasite introduction on the 8th day led to extermination of aphid population within the shortest time while earlier or later introductions led to longer extinction times. Under the prevailing experimental conditions, it appears that the population density of 18 was the 'right' density for System A.

In Set 2, the parasite introduction on the 14th day when the aphid population was 35 led to shorter extermination time than an introduction on the 22nd day when the population was 176 (Table 13). Set 2 also illustrated the effects of aphid age on parasite establishment. Not only must the parasites be released at a time when the aphid population is not too low nor too high, but also the aphids must be of a suitable age to be parasitised.

Table 13. Summary of synchronisation experiments.

Experiment	Parasite introduction			Maximum aphid density before collapse was observed	Day when aphid population was exterminated
	day	aphid density	aphid age (instars)		
	4	15**	I - III	389	98
Set 1	8	18	I - V	568	59
System A	11	35	I - V	714	65
	21	304**	I - V	792	88
	0	10	I	-*	-*
	1	10	I	-*	-*
	3	10	II	-*	-*
Set 2	4	10	late II	1127	116
System B	5	10	III	718	114
	6	10	III	372	126
	9	10	late IV	-*	-*
	14	55	I - V	2434	113
	22	176**	I - V	1450	139
	4	10	II - III	1384	12 week
Set 3	4	20	II - III	830	12 week
System B	4	40	II - III	781	12 week
	4	80	II - III	443	9 week

* the parasites did not establish themselves.

** aphid number on actual day of parasite introduction not recorded, so figures given are only estimations.

The results clearly indicate that aphids of instar I to early instar II and late instar IV are not suitable, while late instar II to instar III are. Hafez (1961) also recorded that D. rapae prefers half-grown nymphs (presumably instar III) to any other stage.

In conclusion, the synchronisation experiments showed that the rate of growth, the size of the parasite population and the level of parasitism that results are determined critically by the initial aphid host density and the age of the aphids. Under the experimental conditions, these critical factors would ultimately determine the maximum aphid density and the time taken to eliminate the aphids completely.

Extrapolating these results to field conditions, it is clear that there is a particular aphid population which is ideal for the arrival of the primary parasites as far as the build up of the parasite population and the parasite efficiency are concerned.

Early arrival of the parasites when the aphid population is low could result in a reduction of their average efficiency, leading to a slow build up of the parasite population. Late arrival when the host density is too high would lead to the aphid population increasing to above the economic threshold and causing damage before the parasites manage to curb it.

However, in the field, conditions are quite different. Firstly, it is very unlikely that all the aphids would belong to one particular age group, except perhaps at the very beginning of the sprout season, when there are only immigrant alates. In this case, the effects of the aphid age on the parasite establishment are minimal. Secondly the immigrant parasites do not arrive only at one time. This is clear from the study on parasite emergence from the mummies in spring which shows that primary parasites emerge over a period of 9 weeks and presumably they would immigrate over the same period.

Knipling and Gilmore (1971) did a theoretical study on the population density relationships between hymenopterous parasite and their aphid hosts similar to the present experimental work. The difference was that they

modelled the release of 100 or 1,000 parasites (instead of 2) at a particular aphid generation. Nevertheless, they arrived at identical conclusions. They found that if parasites were released into the first or second aphid generation (population = 1,000 and 16,000 respectively) then a high rate of parasitism takes a long time to achieve, while doing the same at the fourth generation (population = 2,240,000) does not prevent the aphid population from shooting up above the economic threshold. They concluded that parasite release at the third generation (population = 224,000) achieves the desired effects of curbing the aphid population and obtaining the maximum parasitism.

2. Studies on the responses of *Diaretiella rapae* and *Alloxysta brassicae* to variations in host and parasite densities.

A. Introduction.

Although much of the biology of *D. rapae* has already been studied and comprehensively summarised by Stary (1970), computer simulations of the interactions of *D. rapae* and its host, *B. brassicae* would still require information on the responses of *D. rapae* to variations in host and parasite densities. The same can be said of the secondary parasite, *A. brassicae* which is relatively less studied. Such information is vital for a better understanding of the population interactions as it has been shown and accepted that the searching efficiency of a parasite is affected by both the host and parasite densities, (Hassell & Varley, 1969; Hassell, 1971; Hassell & May, 1973; Diamond, 1974; Rogers & Hassell, 1974; Beddington, 1975).

B. Materials and Methods.

A young potted sprout plant (13 to 20 cm. tall) bearing 260 hosts was used in each of the experiments. The number of leaves per plant was limited to 9 and the excess was removed. Each leaf was then trimmed along the edge using a circular disc (5.5 cm. diameter) as a guide, so that all the leaves were of approximately the same area.

The distribution of the 260 hosts on the leaves were: 2 leaves with 2 hosts each, another 2 with 4 hosts each and the remaining 5 leaves with one of the following number of hosts: 8, 16, 32, 64, and 128. This pattern of uneven host distribution mimics field conditions and offers the parasites a choice of a range of host densities at the same time. The density on each leaf was randomly decided and no 2 plants had identical host distribution with respect to the leaves. The experiments were carried out in Doncaster cages with parasite densities per cage of 2, 4, 8, 16, 32, 64 and 128.

The experiments were conducted at 20°C and 16 hours of light.

i) Diaretiella rapae.

To obtain enough aphids, all of approximately the same age, about 100 apterous adults were introduced on the the leaves. As the aphids produce about 3 nymphs each within 24 hours, their distribution was done in such a way that the required density of young aphids was obtained on each leaf. After 24 hours, the nymphs were counted and if the total was less than 260, the adults were left for another day before removal.

On the fifth day, when the aphids were either late second or early third instars, they were counted once more to check that the required density was present on each leaf; excess aphids were removed.

Female parasites, both mated and virgins of half to one day old were allowed to feed on honey solution for half an hour or so. Then they were introduced into the Doncaster cage and left for an hour to allow the parasites

to settle. Observations on the parasite activity were then made within the next 2 hours.

Two females were randomly chosen for this purpose and were observed for one half hour period each. In the case where only one parasite was present, it was observed for the full hour. The following parasite activities were recorded: a) number of ovipositions, b) number of encounters with other females, and c) amount of time spent with the hosts. The time spent on any particular host density was however not recorded. The parasite was considered to be with the hosts only if it stayed on the leaf blades where the hosts were.

After 24 hours, the parasites were removed. The aphids were counted and then left undisturbed to grow until those parasitised became mummified.

The experiments were done in duplicates.

To determine the effects of interference from male parasites, a series of experiments was done using equal numbers of females and males. The parasite densities used were 4, 8, 16, 32, and 64.

ii) Alloxysta brassicae.

Aphids parasitised by D. rapae and which were about to become mummified within a period of 3 days or so were used as hosts for A. brassicae. These aphids, usually in the late fourth and fifth instars were easy to handle, easily recognisable and hence only a few errors were made.

Each individual parasitised aphid was removed from the stock culture by disturbing it gently with a pair of fine forceps until when it usually fell off the leaf. They were then collected and placed on the leaves of the experimental plant, and the experiments were conducted as for D. rapae.

Since it is impossible to distinguish the mummies parasitised by A. brassicae, it was found necessary to record all the mummies after the experiment and keep them until the parasites emerged.

These experiments were not repeated.

C. Results.

i) Diaretiella rapae.

The relation between log area of discovery and log parasite density (Fig. 29A) is best described as linear. The mutual interference constant, m, is 0.60. This relationship is not due solely to intense overcrowding of the parasites (Hassell, 1971), as can be seen from the same relative drop in searching efficien cy when parasite density was doubled from one to 2 per cage as when doubled from 64 to 128.

It is clear that at a parasite density of 8 or less, the number of encounters is practically nil (Fig. 30A & C) and the parasites spent all their time with hosts (during the observation period), although not necessarily ovipositing. This seems to indicate mutual interference was absent or almost negligible at these low densities. However, during the observation period ovipositions were observed only from parasite density of 4 onwards (Fig. 30B).

The relationship between the number of encounters and parasite density is curvilinear, similar to what was recorded for Nemeritis by Hassell (1971). However, Hassell used a much smaller cage (0.006 m^3) compared to the Doncaster cage which is 13.795 m^3). With the greater volume of space, a parasite can spend relatively longer times without encountering others. This explains why Hassell was able to record encounter even at the parasite density of 2.

At all parasite densities, a curvilinear relationship is seen between the number of parasitised hosts (indicated by the number of mummies) and the host density (Fig. 31). The highest number of parasitised hosts was recorded for the intermediate parasite densities of 8 to 64, while the lowest was recorded at the extreme densities of 1, 2 and 128. A lower parasite density would of course result in a lower number of parasitised hosts. At the highest parasite density (128) however, the lower number of mummies formed was a result of greater aphid mortality due to excessive ovipositional probings by the parasites.

At the female parasite density of one, the number of mummies recorded was 37 (Fig. 31A) which gives a percentage parasitism of 14.2%. However, from

Fig. 29. The relationship between searching efficiency (expressed as log area of discovery) and log density of searching parasites.

A) *D. rapae* (only females present),

$y = -0.10 - 0.60 X$

B) *D. rapae* (males and females present),

$y = 0.14 - 0.70 X$

C) *D. rapae* (males and females present),

$y = -0.016 - 0.59 X$

} see text for explanation.

D) *A. brassicae* (only females present),

$y = -1.13 - 0.55 X$

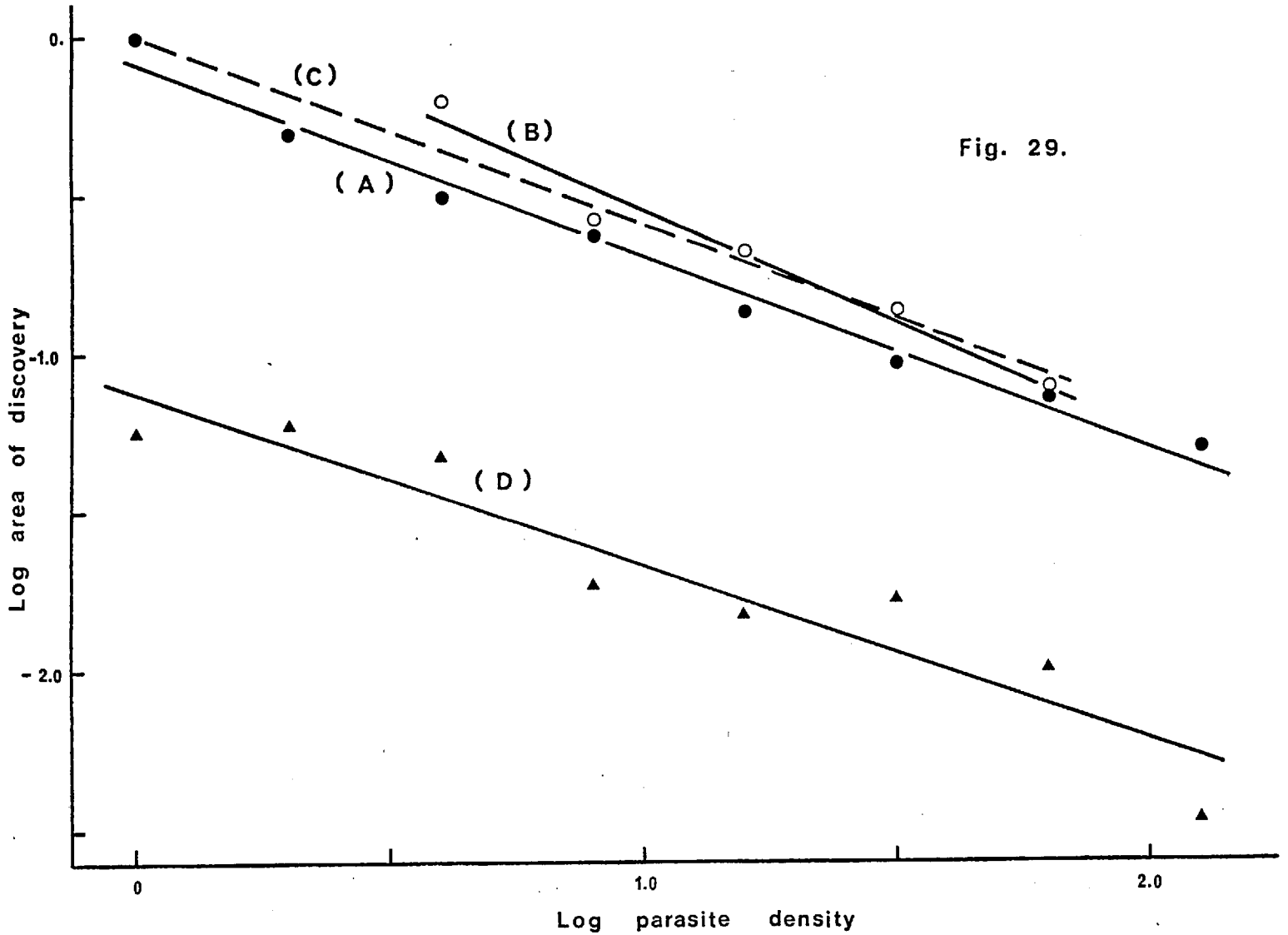

0.
-1.0
- 2.0
(C)
(B)
(A)
(D)
Log area of discovery
0
1.0
2.0
Log parasite density

Fig. 29.

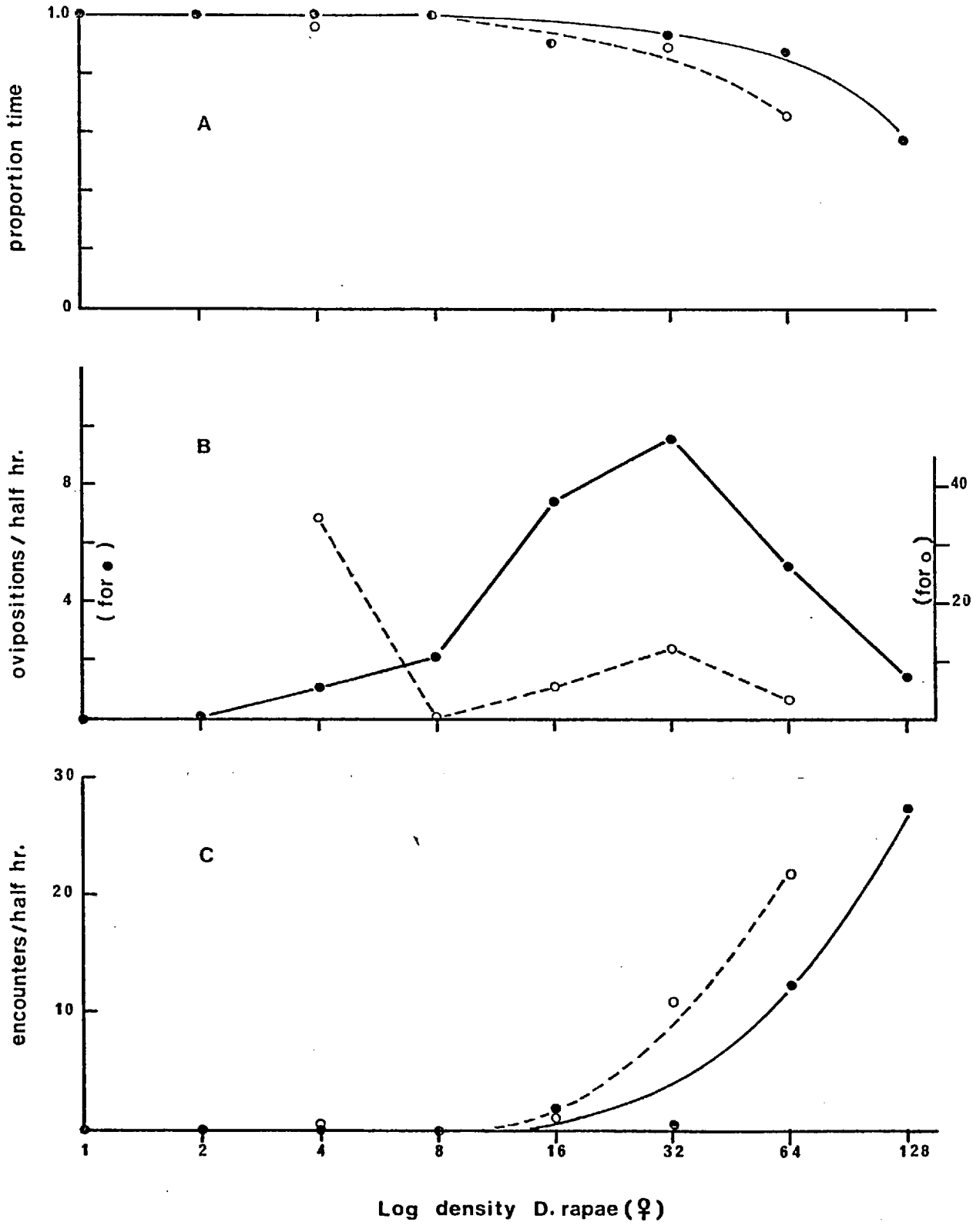


Fig. 30. The behavioural responses of D. rapae at different densities.
(• only female parasites present; o male and female parasites present)

A) The relationship between the proportion of time ($\frac{1}{2}$ hour) the parasites spent with hosts and the parasite density.

B) The relationship between the number of ovipositions during a half-hour period and the parasite density.

C) The relationship between the number of encounters between adult parasites per half-hour period and the parasite density.

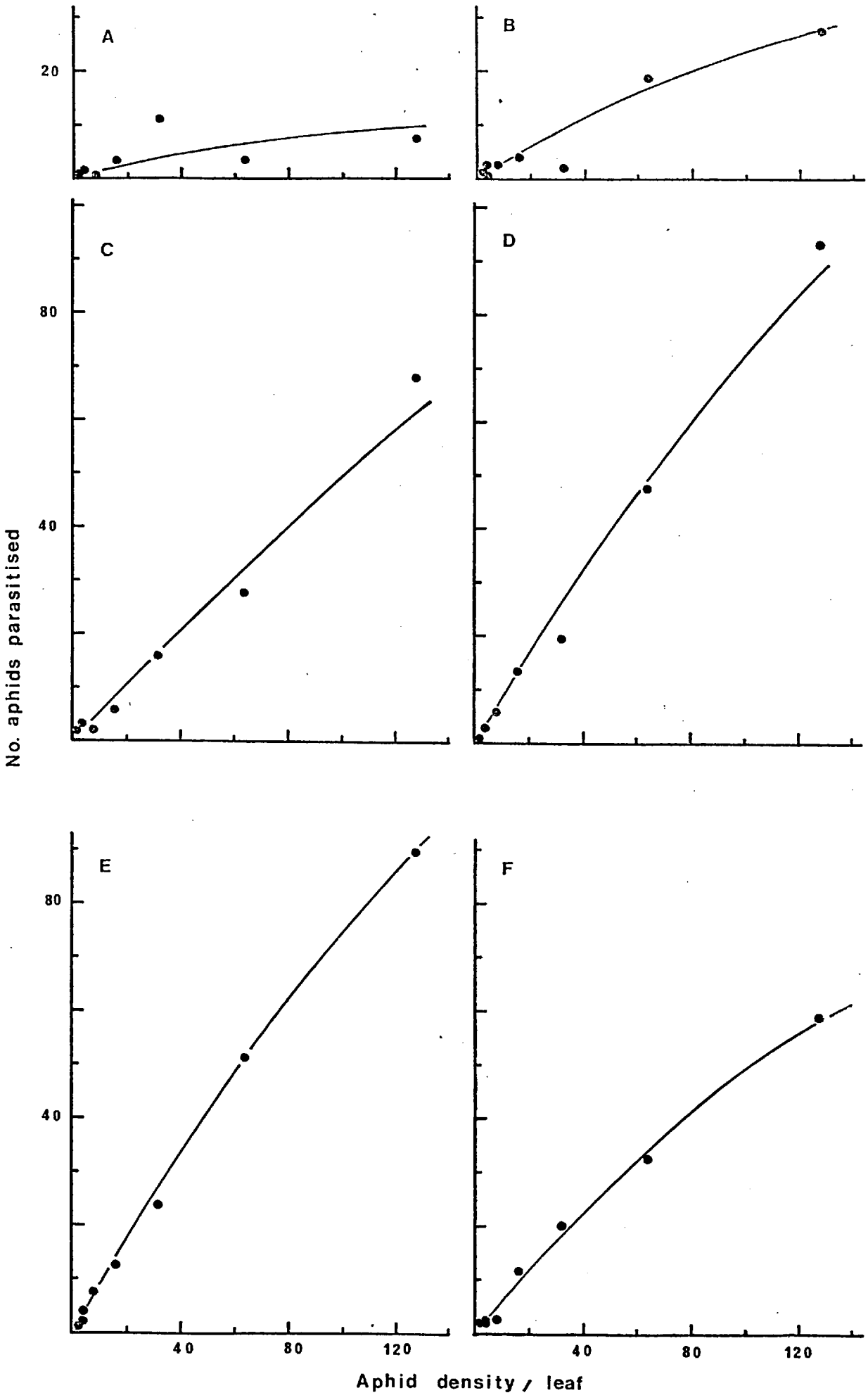

A
B
C
D
E
F
20
80
40
80
40
40
80
120
40
80
120
No. aphids parasitised
Aphid density / leaf

Fig. 31

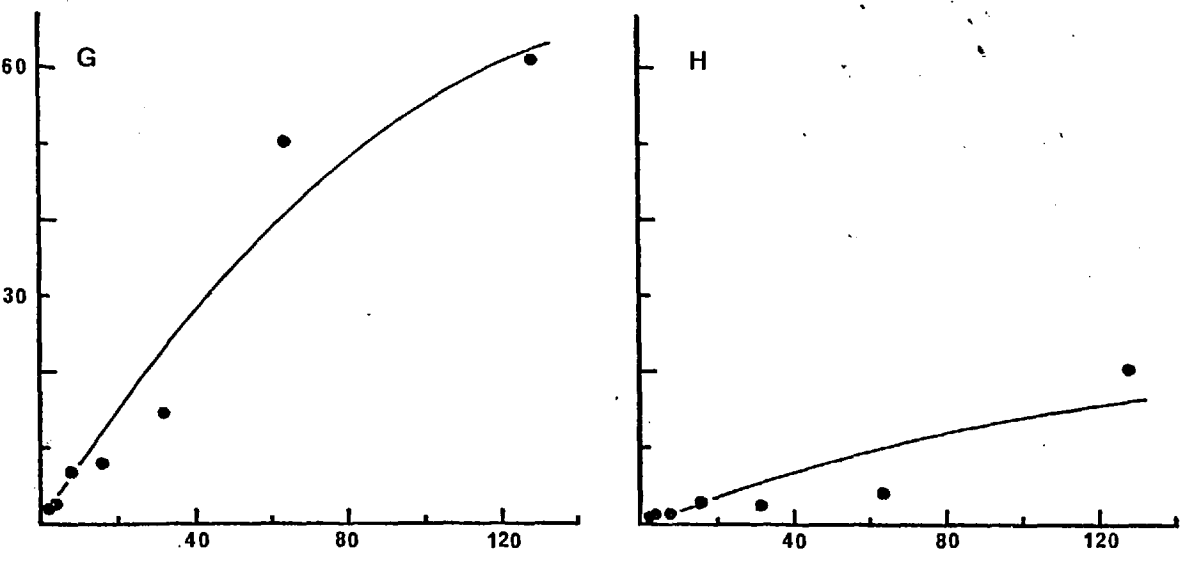


Fig. 31. Behavioural responses of D. rapae to an uneven host distribution. The number of hosts parasitised is plotted against the host density per leaf of the experimental plant. Each graph shows the results obtained using a different parasite density per cage.

A) 1 parasite,

B) 2 parasites,

C) 4 parasites,

D) 8 parasites,

E) 16 parasites,

F) 32 parasites,

G) 64 parasites,

H) 128 parasites.

the equations: $a = QP^{-m}$ and $a = \frac{1}{P} \log_e \left(\frac{U_i}{U_s} \right)$, where

a = area of discovery,

Q, m = quest and interference constants,

P = parasite density, and

U_i, U_s = initial and surviving (after parasitism) host densities,

it can be shown that when $P = 1$, $U_s = 118$. This indicates 142 hosts were parasitised, giving a percentage parasitism of 54.6%. The difference in the percentage parasitism can be explained by the fact that in the calculation of a, U_s represents the number of live aphids counted when mummification of the parasitised aphids was completed. Hence the value of 54.6% includes aphids killed by natural mortality (including multiple probes), as well as successful parasitism, while the value of 14.2% represents the number of mummified aphids.

The relationship between log area of discovery and log female parasite density (where both females and males were present together) is represented by 2 straight lines (Fig. 29B, C). It would appear from Fig. 29B ($y = 0.14 - 0.70 x$) that the females were "super-efficient" since the quest constant, Q is 1.38! However, the equation was calculated from values of a obtained at parasite densities of 4 or more. Recalculating the line using the value of a (= 0.9860) obtained at the density of one female parasite seems reasonable since it is unlikely that interference from the male (at a parasite density of one female and one male) would be great and produce a much different value of a. The second recalculated line (Fig. 29C) gives a Q value of 0.96. Both these lines have greater Q's than where only females were present (Fig. 29A) which seems to indicate that females search more efficiently in the presence of males. The slopes of the lines, and hence the values of m, differ only slightly so that mutual interference appeared constant.

ii) Alloxysta brassicae.

It is important to note here that the number of hosts used in these experiments was actually less than the planned density of 260 because some of the aphids were not parasitised by D. rapae. This was however rectified after the fourth experiment in which a density of 8 parasites was used.

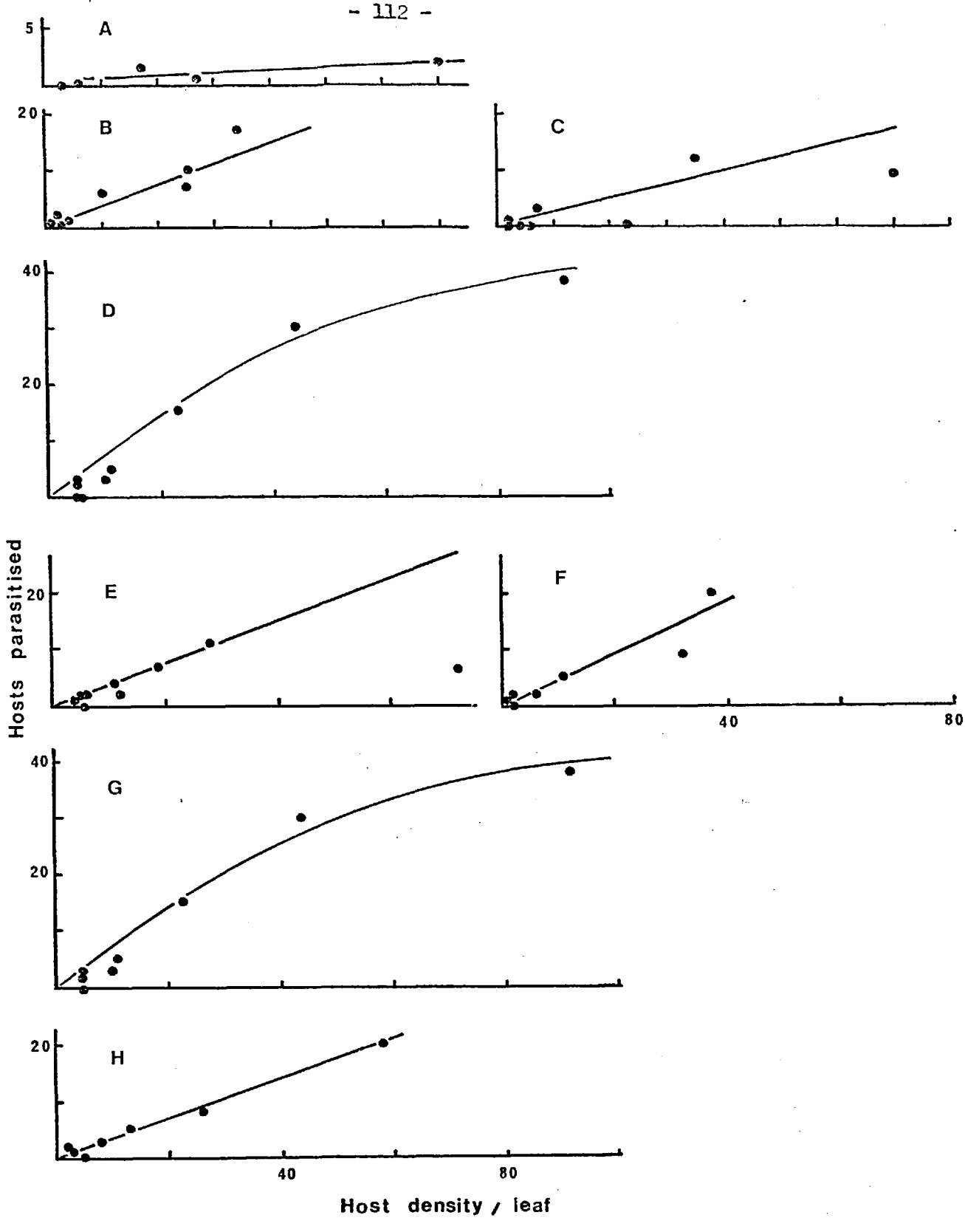


Fig. 32. Behavioural responses of A. brassicae to an uneven host distribution. The number of hosts parasitised is plotted against the host density per leaf of the experimental plant. Each graph shows the results obtained using a different parasite density per cage: (A) 1, (B) 2, (C) 4, (D) 8, (E) 16, (F) 32, (G) 64, (H) 128.

Since the highest number of hosts parasitised by A. brassicae was only 96 (actual host density = 201, parasite density = 64), it seems reasonable to assume that the number of hosts parasitised at each parasite density would not have changed very much had 260 hosts been available. This is especially true at the lower parasite densities. Nevertheless, the area of discovery calculated from the D. rapae - parasitised hosts available for attack (varying from 100 to 230) given an acceptable relationship (Fig. 29D).

This relationship is also linear, although the fit is not as good as for D. rapae. This might be expected as the data were based only on one replicate. The mutual interference and quest constants, (0.55 and 0.07 respectively) are both lower than for D. rapae., indicating that A. brassicae has a lower searching efficiency.

The relationship between the number of hosts parasitised and the host densities varied from linear to curvilinear (Fig. 32).

D. Discussion.

In both D. rapae and A. brassicae, a linear relationship between log area of discovery and log parasite is observed. Such a linear relationship has also been recorded for other parasites (Hassell & Varley, 1969; Hassell, 1971; Hassell & Rogers, 1972; Cheke, 1974). However more recently there is a tendency towards claiming the relationship to be of a curvilinear nature (Rogers & Hassell, 1974; Beddington, 1975) except when the mutual interference constant, m, is 0.5. Royama (1971) also showed theoretically that the relationship is curvilinear at low parasite densities. A possible curvilinear relationship might be conceivable for A. brassicae, although more experimental evidence is clearly required.

The lower quest constant, Q, of A. brassicae seems to indicate that it is less efficient than D. rapae in host searching. For all parasite densities, the k-value for parasitism of A. brassicae is lower than for D. rapae (Fig. 33). However, judging from the high field parasitism of D. rapae mummies by A. brassicae, one would assume that the latter is not an inefficient species. These two conflicting statements can nevertheless be reconciled if we consider the results of the synchronisation tests of

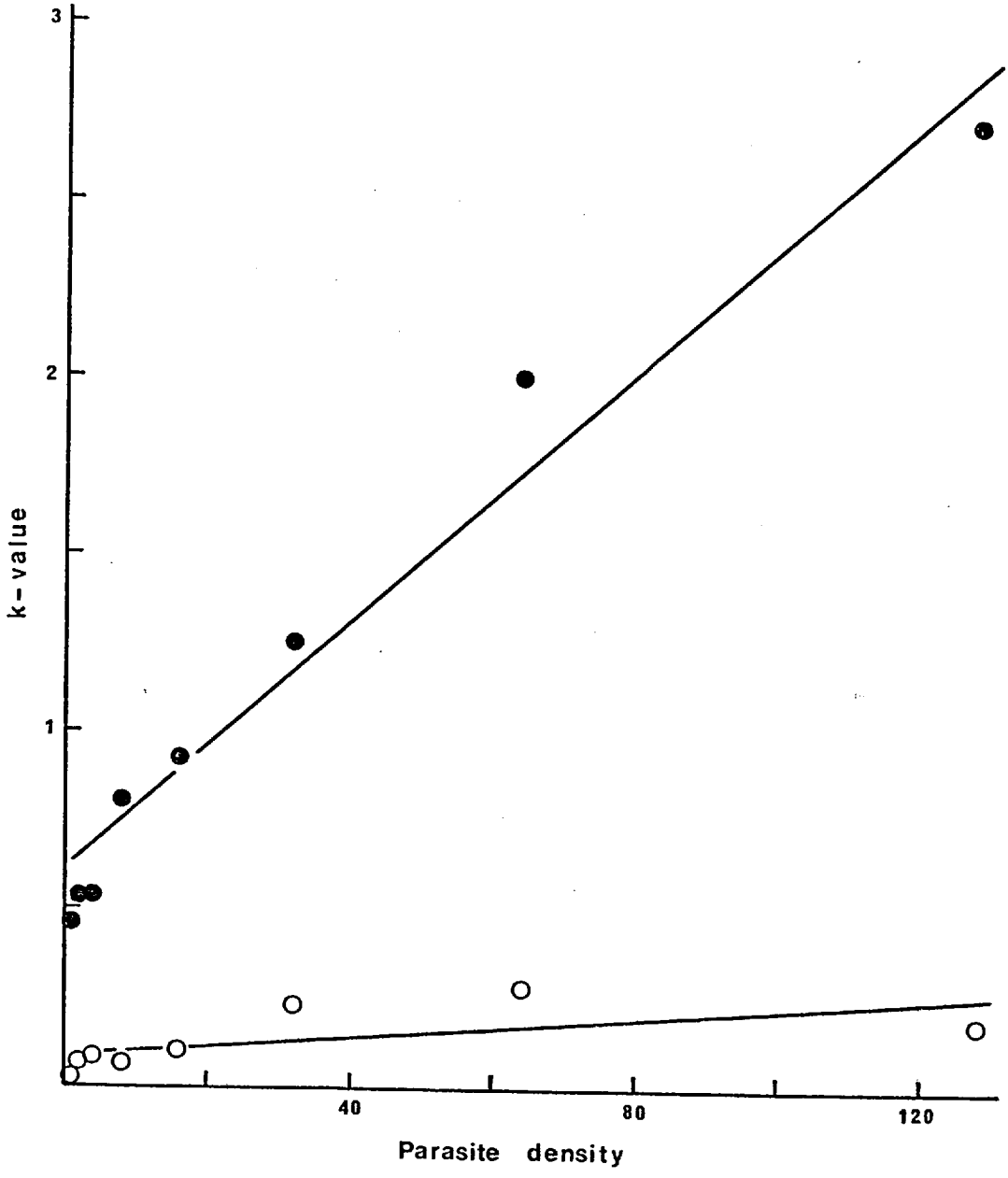


Fig. 33. The relationship between the proportion of hosts parasitised (expressed as k-values) and the parasite density for D. rapae (●) and A. brassicae(O). Equations of the fitted lines are:
for D. rapae: y = .58 + .18x ,
for A. brassicae: y = .09 + .001x .

Macdonald & Cheng (1970). The tests show synchrony exists between A. brassicae and D. rapae, but not between D. rapae and B. brassicae. It is very plausible that this synchrony was the cause of the high percentage parasitism of D. rapae by A. brassicae recorded in the field. This hypothesis concurs well with the view that a hyperparasite cannot afford to be more efficient than its host, the primary parasite, since Nicholson (1933) clearly pointed out that a too efficient hyperparasite could ultimately lead to its own extinction.

High searching capacity (indicated by Q) is no doubt associated with a higher mutual interference constant, m. This is confirmed by the higher values of Q and m for D. rapae. Rogers & Hassell (1974) claimed this direct relationship arises because both parameters are dependent on the level of the parasite's searching activity. When m and Q of both D. rapae and A. brassicae (the respective corrected values of Qm^2 per parasite per day being 0.0336 and 0.0032) are plotted on the graph of Rogers & Hassell, the points fall reasonably close to their fitted line.

The total number of aphid hosts parasitised by D. rapae rises with an increase in parasite number up to the density of 16 (Fig. 31). Further increases then only resulted in a decrease of parasitised hosts per parasite. The increment in the number of hosts parasitised is quite proportionate up to a parasite density of 4 which seems to indicate that this is the density below which interference was negligible in the present set of experimental conditions. This observation is strengthened by the fact that encounters between parasites were recorded (during the observation period) only at parasite density of 8 or more. Such a limit to parasite density below which parasite interference is negligible has also been noted by Royama (1971) and Hassell & May (1975).

SECTION VI. COMPUTER SIMULATION STUDIES ON SYNCHRONISATION.

1. A simulation model of the population growth of Brevicoryne brassicae in the absence of parasites.

A. Introduction.

Computer models simulating the population growth of various aphid species have been constructed by several workers. The species studied include B. brassicae (Hughes & Gilbert, 1968; Gilbert & Hughes, 1971), Aphis fabae Scop. (Crawley, 1973), Masonaphis maxima (Mason) (Gilbert & Gutierrez, 1973), Microlophium evansi Theob. (Perrin, 1974), Aphis craccivora Koch (Gutierrez, et al., 1974), Rhopalosiphum maidis and R. prunifolia (Shiyomi, 1974).

Almost all these models are deterministic, that is the predicted values may be computed exactly. The exceptions are those by Gilbert & Hughes (1971), and Shiyomi (1974), which are stochastic and the predicted values depend on probability distributions. A stochastic model might be better but it provides little more information than a deterministic one, as Gilbert & Hughes (1971) have shown.

These models can serve as a sueful tool to delve more deeply into the interactions of various factors affecting the insects' population. They certainly can verify whether or not one's understanding of these interactions is complete, and indicate at the same time whether substantial relationships have been overlooked. Models have also been used to determine the optimal biological attributes of an aphid predator which maintains the aphid population below an economic threshold (Crawley, 1973).

The chief aims of the present simulation work were a) to build a model which would reproduce reasonably well B. brassicae population growth under experimental conditions, b) to simulate the effects of temporal synchrony by varying the aphid population density at the time of introduction of

of the primary parasite, and c) to study the effects of secondary parasite, Alloxysta brassicae on the populations of both the aphids and the primary parasites. The latter was of particular importance since no experimental work was done.

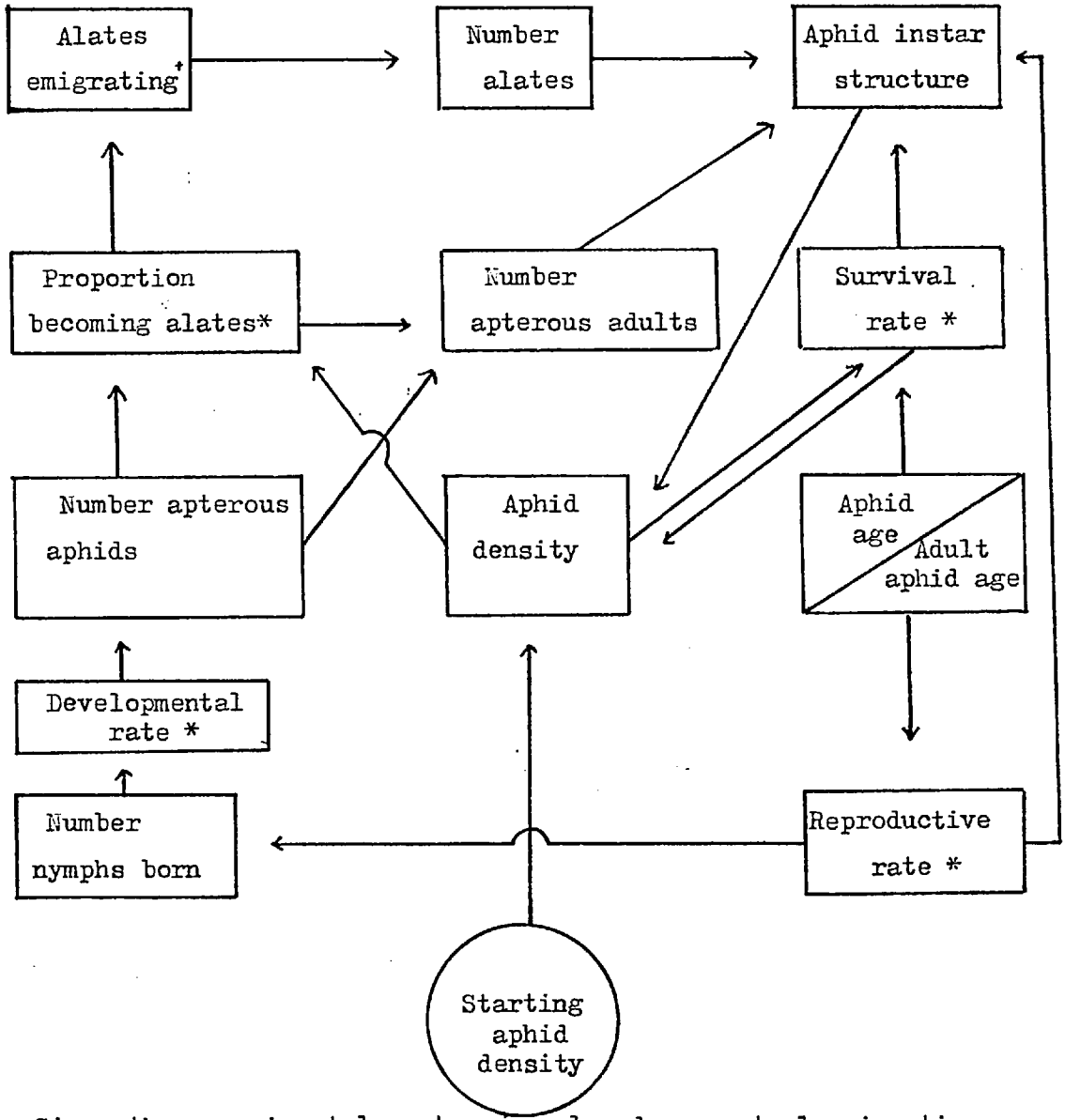
The present deterministic model is similar to Crawley's (1973). The flow chart indicating the different processes incorporated in the model is depicted in Fig. 34, and Table 14 gives the sources of the data used to quantify the variables in the simulations.

The basic model, BREVBRA (Appendix 4), did not include the effects of predation or parasitism or even plant growth but only simulated the aphids' population growth in the control experiments (i.e. no introductions of parasites were involved, see p. 92). Although the effects of plant growth were important in the models of Hughes & Gilbert (1968), Crawley (1973), Gilbert & Gutierrez (1973), Perrin (1974) etc., it was nevertheless considered reasonable to ignore them in the present work as the host plants in the experiments were replaced when necessary. Abiotic factors such as variations in the temperature and daylength have also been omitted as the experiments were conducted in constant and almost ideal conditions (20°C and 16 hours of light).

The experimental data used in the simulations include the density effects on survival rate, the proportion of population becoming alates and emigrating, all of which were based on the results of the control experiments (Fig. 35).

Although this model was built specifically for experimental conditions, it could still be used to simulate population changes in the field provided predation, parasitism, temperature effects on reproduction, survival and alate formation, and emigration are included, perhaps together with plant growth information.

Fig. 34. Flow chart of program BREVBRA.



+ Since the experimental system was closed, no actual emigration of alates took place.

* Temperature effects on proportion becoming alates, rates of survival, reproduction and development have been excluded since the model simulates B. brassicae population at 20°C.

Table 14. Sources of data used in programs BREVBRA, SYSTEM.

	Data	Fortran symbols	Sources
1.	Development; day degrees	DEGTHR	Akinlosotu (1973)
2.	Survival rate	ALASURV,APTSURV	Instars I-IV:Akinlosotu, 1973 Adults: Hafez, 1961
3.	Fecundity	FECALA,FECAPT	Hafez, 1961
4.	Density effect on fecundity	DFEC,X3,Y3	'control' experiments (i.e. parasites were not introduced) (Fig. 35C)
5.	Density effect on survival	DSURV,X4,Y4	'control' experiments (Fig. 35D)
6.	Proportion becoming alates	PROP2,X1,Y1	'control' experiments (Fig. 35A)
7.	Proportion alates emigrating	PROPEM,X2,Y2	'control' experiments (Fig. 35B)

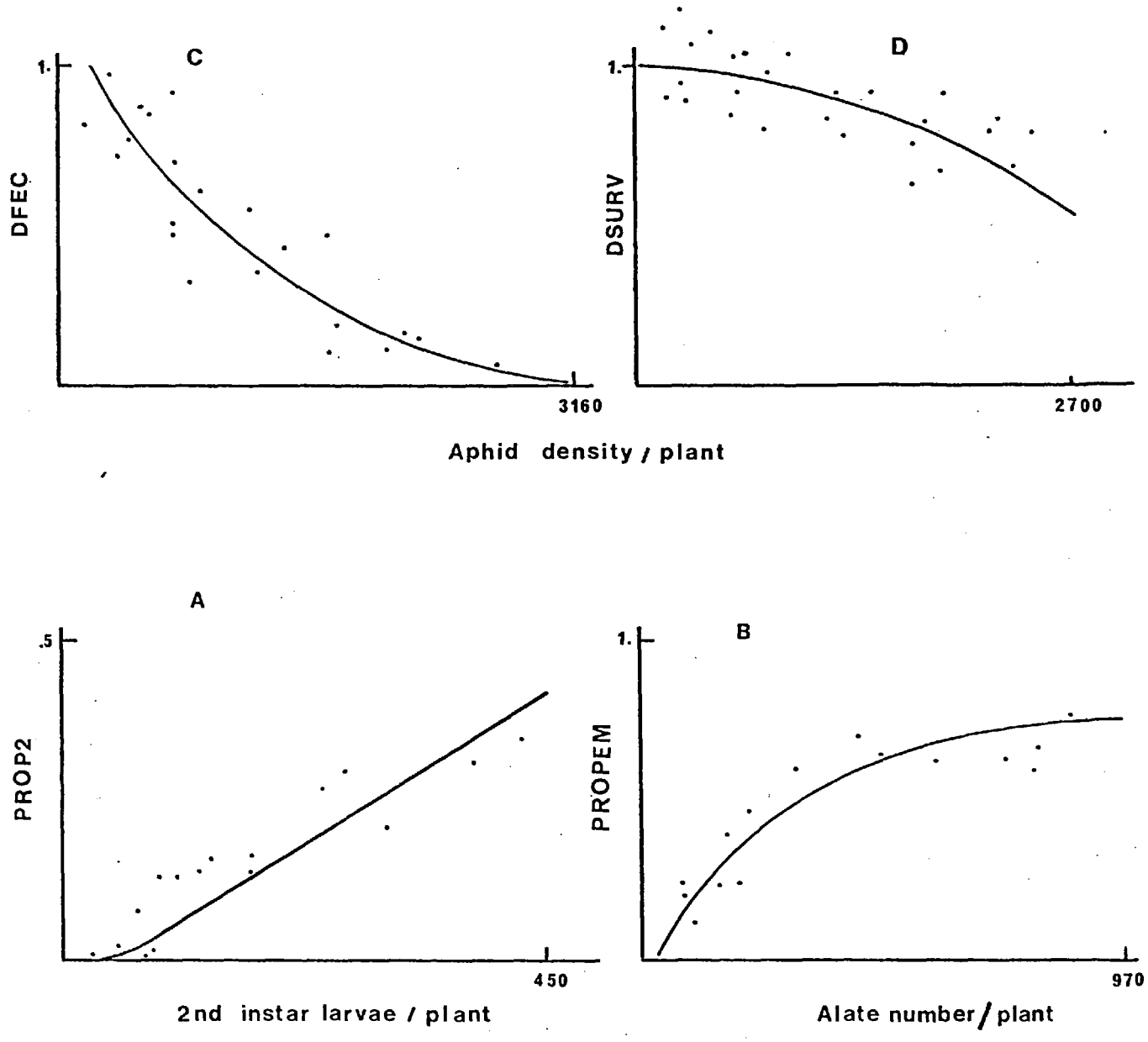


Fig. 35. The relationships between aphid density per plant and:

A) proportion of aphids becoming alates (PROP2),

B) proportion of alates emigrating (PROPEM),

C) relative fecundity (DFEC),

D) relative survival (DSURV), used in the computer simulations.

B. Rationale.

The assumptions and formulations of processes affecting aphid populations are discussed below.

i) Rate of development.

The models of Hughes & Gilbert (1968), Gilbert & Hughes (1971), Gilbert & Gutierrez (1973) and Gutierrez et al., (1974) were based on a physiological time scale called instar periods. This they divided into similar quarter instar periods termed "quips". The present model was run with real time units (days).

The aphids were assumed to need to experience a constant number of day degrees (D^{o} = day x mean temperature) for development. Akinlosotu (1973) showed that the developmental requirements for the first 4 instars are almost equal (50D°). In other words the aphids need to experience 200D^{o} to grow from a new-born nymph to a reproducing adult. At 20°C, this is equivalent to 10 days.

ii) Rate of reproduction.

Since the model did not simulate population fluctuations under field conditions, the infestation was started by the introduction of young apterous aphids instead of the arrival of immigrant alates as in the model of Hughes & Gilbert (1968), Gilbert & Hughes (1971), Crawley (1974), Gilbert & Gutierrez (1973) etc. In the experiments, the aphids introduced were already a half-day old, that is they had experienced a development of 10D^{o}.

The number of nymphs born to each adult female (both alate and apterous) was considered as a function only of her age and the density of the population. This was simulated by the following equations:

BORN = APTERAE (I) * FECAPT (K) * DFEC

BORN = ALATAE (I) * FECALA (K) * DFEC, where

APTERAE (I) and ALATAE (I) are the number of aphids of age I days, FECAPT (K)

and FECALA (K) are the larviposition rates. On the average, the aphids reproduce only for the first 14 days of the adult life, hence $K \leq 14$. DFEC is the effect of aphid density on the reproductive rate (Fig. 35C).

iii) Rate of survival.

In the model by Gilbert & Hughes (1968), there is a mortality factor called 'background mortality' which is actually mortality caused by abiotic and biotic processes, excluding parasitism. Since the main aim of the present model was to simulate the effects of the time of arrival of the primary parasite on the aphid population, the only mortality factors incorporated in the model at this juncture were a) natural death due to old age and b) decrease of survival rate as a result of higher density, simulated by the following equations:

ALATAE (I) = ALATAE (I) * ALASURV (I)* DSURV

APTERAE (I) = APTERAE (I) * APTSURV (I) * DSURV,

where ALASURV, APTSURV are the survival rates of alate and apterous aphids, DSURV the effect of density on the survival rate, and I = 1, 33, the age of the aphids in days.

iv) Proportion of dates and emigration.

The number of alates produced is dependent mainly on the density of B. brassicae (Kawada, 1964). Other cumulative and density - related factors which could influence alate production include the condition of the host plant (Lees, 1966; 1967), the increase of honey dew, and rates of encounter between aphids etc. All these factors have been pooled together as one termed "filth" in Crawley's (1973) model. This approach, though realistic enough, has not been adopted here as much of the cumulative plant effects were eliminated when the plant was replaced periodically. Thus, the proportion of alates produced was assumed to be purely a function of the total aphid density on the plant i.e.

PROP2 = F (TOTAPH).

Similarly the proportion of emigrating alates was considered as a function of the total alate number i.e.

PROPEM = F (ALA(5)).

v) Updating.

As the model was run on the unit time of days, all the above mentioned processes were simulated once every day. Before the beginning of the next days' simulation, all the aphids and their parameters were updated by one day. This was done by looping vectors through their subscripts from the maximum to the minimum, removing aphids of maximum age from the population in the process e.g.

```
DO 303 J = 1, 32
I = 34 - J
APTERAE (I) = APTERAE (I-1)
DAYDEG (I) = DAYDEG (I-1)
303 CONTINUE
```

Any outputs (e.g. total number of aphids etc.) required at the end of the day were printed at this point.

C. Results and Discussion.

Generally, the predicted density showed more or less the same fluctuation trend, although the values were usually lower than the observed density which was the geometric mean of 3 replicates (Fig. 36). For example, the predicted maximum density was only 1,277 compared to 1,567 from the experiments. Comparisons of the predicted and observed age structure indicated the difference was contributed not from any particular age group, but from every instar. The predicted population fluctuated quite widely only at the beginning when it was building up. Later when the density-related restraints came into operation, the population became relatively

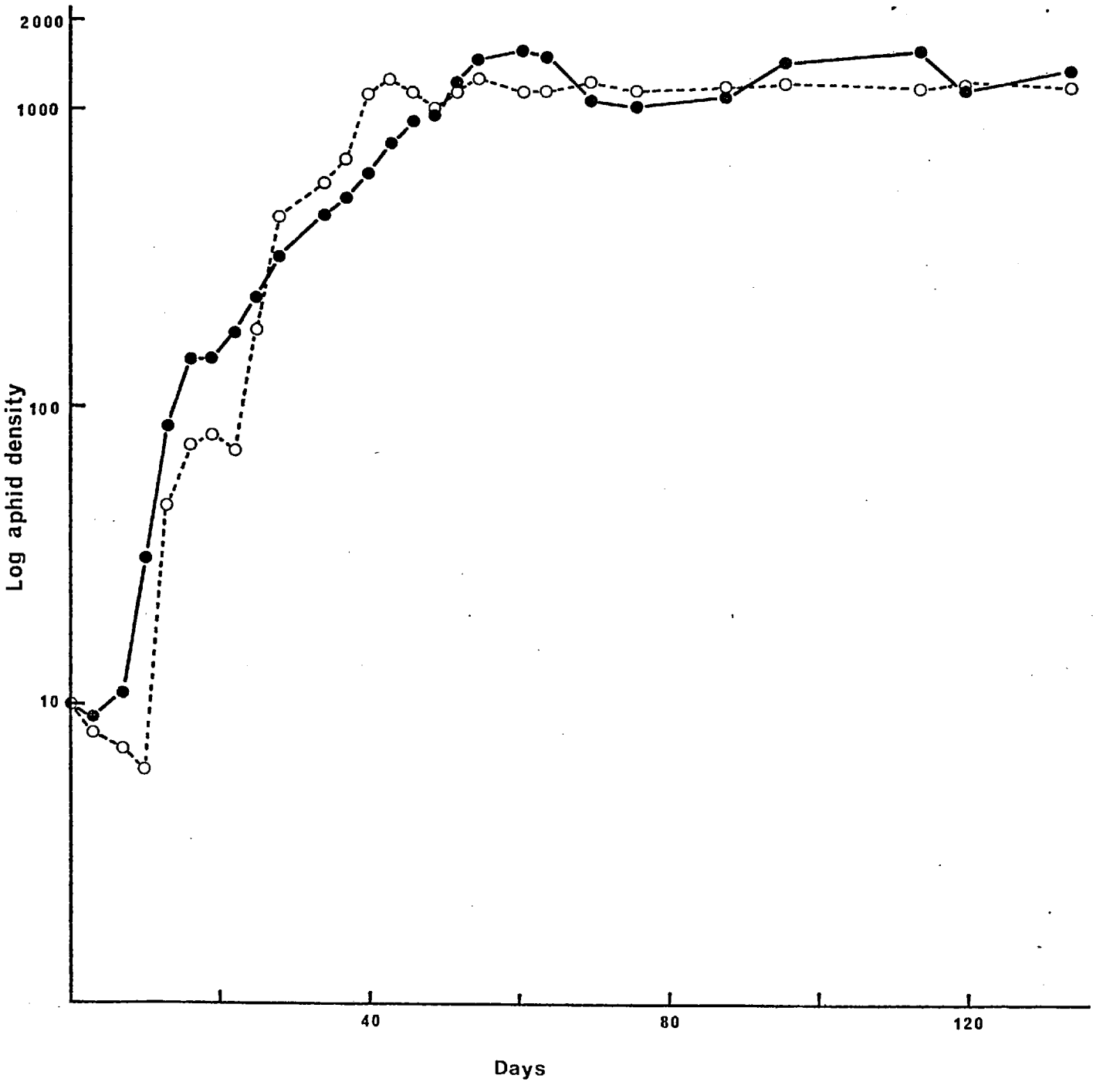


Fig. 36. The observed (•) and predicted (o) populations of E. brassicae in the absence of parasites.

stable from day 76 onwards with the density varying from 1,160 to 1,200 and with a fairly stable age distribution. The observed density however, showed wider fluctuations from 1,000 to 1,560.

The effects of absence of various density - related mechanisms have not been simulated as they have already been considered sufficiently by Hughes & Gilbert (1968), Crawley (1973) and Perrin (1974). From their work it could be reasonably speculated that without the density effects on reproduction, survival, alate production and emigration, which all tend to decrease the aphid number, the population would build up to an enormous, and unrealistic number of individuals per plant. The fact that the observed maximum density per plant was only 1,567 indicates that these density - related restraints were operating. Simulations using different initial aphid density of 20, 40 and 80 showed clearly that the starting density did not affect the final stable population. This could be expected as the density restraints would operate in the same way.

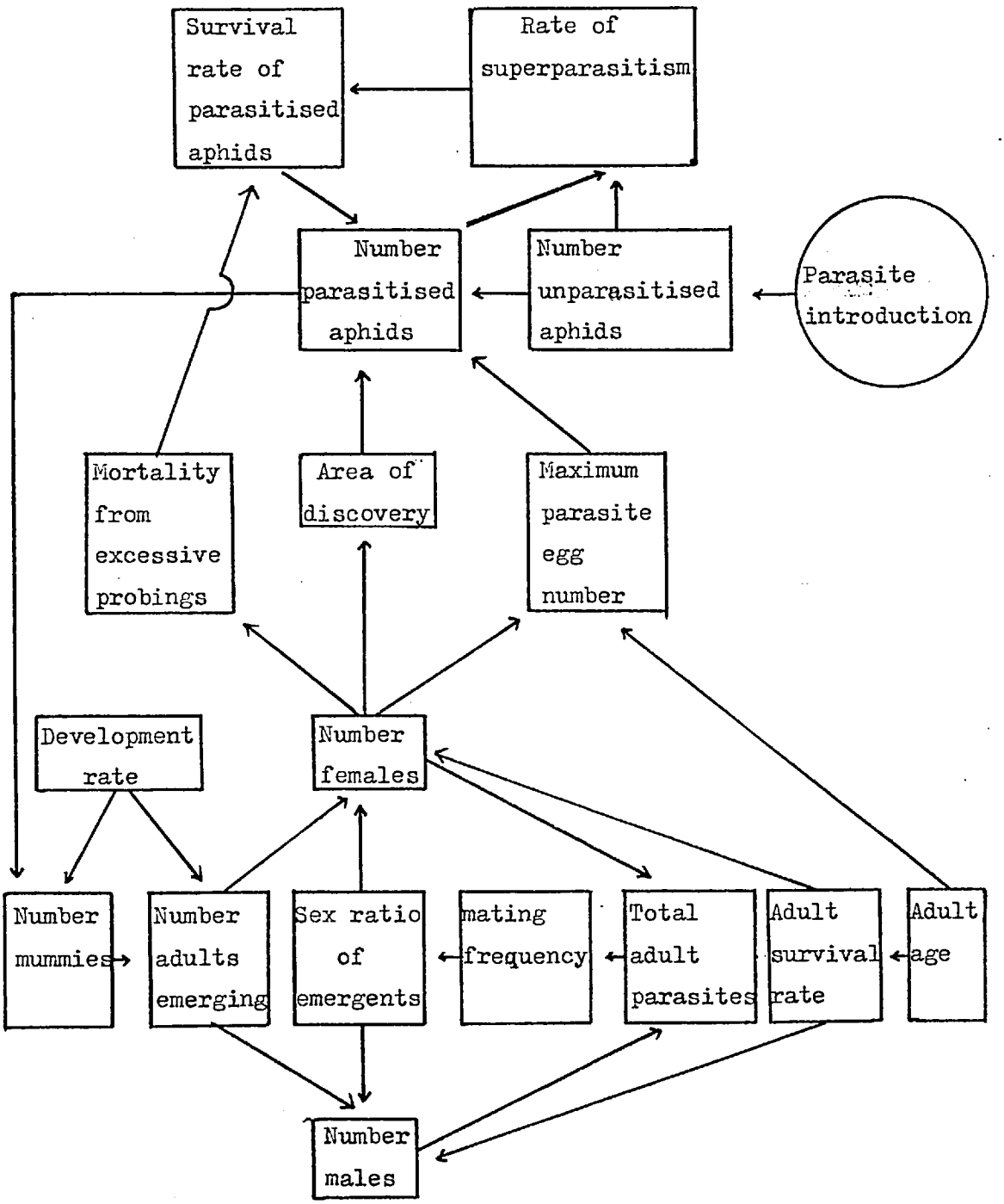
As the simulation model only denoted, in mathematical terms, the ecological relationships that determine population changes, it is not surprising that the absolute values of the predicted density did not concur precisely with the observed. Although the model was no more accurate than the biological information it contained, the agreement between the predicted and observed values could be improved by various small alterations. Such alterations however can only be pure guesswork and hence are not desirable.

2. The effect of introduction of Diaretiella rapae on aphid population of different sizes.

A. Introduction.

The program SYSTEM (Appendix 5), using BREVBRA and a subroutine PRIMARY (Fig. 37) was used to simulate the effects of primary parasites arriving at

Fig. 37. Flow chart of subroutine PRIMARY



different population densities of B. brassicae. This is equivalent to simulating the effects of varying the time of arrival of the parasite into an aphid colony because the size of the colony is determined, other conditions being identical, by the time it is allowed to develop.

The data used in PRIMARY (Table 15) were independent of the experiments on synchronisation except for the number of mummies formed at the start of a run when the parasites were first introduced.

B. Rationale.

The biological assumptions and the mathematical formulations of processes of the rates of parasitism, parasite development etc., which acted to increase or decrease parasite numbers are examined below..

i) Rate of parasitism.

Since Hafez (1961) reported aphids of all instars are susceptible to attack it was decided to treat the susceptible age of aphids as between one to 13 days. Older apterous adults usually have a waxy covering and are not very much preferred. Moreover, in a closed system (as in the experiments conducted, p. 94) the aphids were usually parasitised before they became adults. The total susceptible aphid hosts available for attack (AVAILA) included unparasitised (UNPARA) as well as parasitised but mummified aphids (PARAFID); superparasitism could then occur. However, the term PARAFID only included aphids containing larvae of one to 6 days old, as older larvae would be big enough to cause the aphids to be distended, making them less acceptable.

At the start of a run, the rate of parasitism was based on the results of synchronisation experiments (p. 94).

For the rest of the run, the model of Hassell & Varley (1969) was used, which involved interference and quest constants (CM and Q). The number of hosts attacked (PAHOST) was based on random attacks and the searching

Table 15. Source of data used in program SYSTEM and subroutine PRIMARY.

	Data	Fortran symbols	Sources
1.	Quest and interference constants.	Q,CM	Experiments
2.	Preference for different aphid stages	PREFAL,PREFAP	Hafez, 1961
3.	Fecundity of female parasites	FECPAR	Hafez, 1961
4.	Survival rate of adult parasites	FSURV,MSURV	Experiments
5.	Development rate of parasites, parasitised aphids	THRESPH THRESPA	Hafez, 1961; experiments
6.	Fecundity of parasitised aphids	FECAFID	Akinlosotu, 1973
7.	Proportion of female in the progeny	FEMALE	Intuitive (=0.5)
8.	Survival rate of immature primary stages	PARSURV	Intuitive (for larvae = 0.95, for pupae = 1.0)
9.	Mortality of aphids from excessive probing by female parasites	SURVJAB	Experiments

efficiency was dependent on the density of adult female parasites (PARASF), namely: PAHOST = AVAILA $(1-e^{Z})$ where

$$Z = -Q\ (PARASEF^{B}), \text{ and}$$

$$B = (1 - CM).$$

However, the final number of hosts parasitised is limited by the maximum parasite egg number (EGGMAX). This was simulated by the equation:

PAHOST = AMIN1 (PAHOST,EGGMAX) where

AMIN1 is a computer function which selects the smaller value between PAHOST and EGGMAX.

It was assumed that female parasites do not discriminate between parasitised and unparasitised hosts (Hafez, 1961) although a recent reanalysis of Hafez's work (Rogers, 1975) suggests that some discrimination does occur. The assumption in the model therefore implies that a parasitised aphid which is still susceptible has an equal chance of being parasitised again as an unparasitised host. Therefore the number of superparasitised hosts (SUPERPH) is given by:

SUPERPH = (PARAFID/AVAILA) * PAHOST, and the number of hosts newly parasitised (TODAYPH) by:

TODAYPH = PAHOST - SUPERPH.

ii) Preference for aphids of different ages.

The number of aphids of a particular age which was parasitised depended on the number available and the preference for them by the parasites. The "preference factor" is calculated by:

APTPREF(I) = APTERAE (I) * PREFAP (I), and

ALAPREF (I) = ALATAE (I) * PREFAL (I)

where APTERAE (I), ALATAE (I) are the apterous and alate aphid numbers, PREFAP (I) and PREFAL (I) the indices of preference (based on Hafez's 1961 results), for aphids aged I day, where I = 1, 13. The preference factors were then summed (= PREFER) and the numbers of aphids of age I parasitised are given by:

APTPAR (I,1) = TODAYPH * APTPREF (I)/PREFER, and

ALAPAR (I,1) = TODAYPH * ALAPREF (I)/PREFER.

iii) Rate of development.

Since no data are available on the developmental rate of each larval instar of the parasite, the problem was simplified by dividing the whole developmental period into only two separate parts. The first represents the time when the parasite egg is laid to the time when the larva becomes full-grown or pupates, which is indicated roughly by mummification. The second represents the time between mummification and parasite emergence. The effects of the aphid age on parasite developmental rate (see Hafez, 1961) have been ignored and all parasites were assumed to take 10 days to reach pupal stage (or mummy stage) and a further 5 days to emerge from the mummies.

It was found convenient to designate the parasitised aphids by ALAPAR (I,J) and APTPAR (I,J) where I and (J - 1) represent respectively the ages of the aphids and parasites in days. Thus for newly parasitised aphids, J = 1, and when the aphids become mummified the parasite would be in the 11th day of its development, hence J = 12. Similarly when the parasite emerges, J = 17. Adult parasites were also represented by FEMPAR (I), and MALPAR(I) where I = 1, 5, the ages in days.

iv) Rate of survival.

The survival rates of parasite larvae and pupae were given the arbitrary values of 0.95 and 1.0 respectively. In the actual experiments (p. 94),

parasites failed to emerge from a small number of mummies, but this mortality was due mainly to careless handling during marking.

v) Fecundity of parasites.

Though Hafez (1961) recorded that females oviposited up to the 12th day of their life, only the fecundity of the first 5 days have been used as the females in the present study were found to live an average of only 5 days.

vi) Proportion of females among the progeny.

In the experiments on synchronisation, the proportion of females among the progeny varied from 0.4 to 0.7. To simplify computations, a constant female proportion of 0.5 was used in the simulations, although the sex ratio among the progeny might have been influenced by the sex ratio of the adult parasites.

vii) Reproduction by parasitised aphids.

The number of nymphs born to parasitised aphids before mummification depends on the age when the aphids are parasitised (Hafez, 1961; Akinlosotu, 1973). In the experimental closed systems, however, the aphids were usually parasitised while they were still in their early instars. Hence only the fecundity of aphids parasitised in the third instar, which is 2 nymphs per aphid (Akinlosotu, 1973), was used in the simulations.

viii) Output from the computer.

As in the experiments, the computed adult parasites were counted once, either when live or dead. This was done by summing the number of adults emerging daily (FRESHAD) for the whole week.

C. Results.

Although the aphid and parasite numbers predicted by the model did not agree with those of the experiments in absolute values, the general trends were nevertheless similar (Fig. 38, 39). The predicted aphid populations usually started to increase or decrease later than the experimental populations although both the predicted and experimental populations became extinct about the same time. The predicted maximum aphid population was close to that observed only in one case viz. with starting aphid population of 40 aphids (Fig. 39B), while it was either higher or lower than the observed in the simulations with starting populations of 10, 20 and 80 (Fig. 38, 39A).

The predicted parasite populations usually had higher peaks than the observed, and appeared discrete (although this might not be obvious from the graphs for generations later than the second) which could be a direct result of assuming a uniform developmental rate for the parasites. The simulations also showed that the aphid populations were totally eliminated by the third generation of the parasites.

It was thought that the greater aphid populations predicted by the model (e.g. Fig. 38B) might be a result of assuming a lower and constant female proportion of 0.5. This is lower than the experimental values which could be as high as 0.7, and seen in the first parasite generation for the starting aphid population was 80. Substituting the higher value of 0.7 in the simulations did not however depress appreciably the aphid population (Table 16). This would seem to indicate that the use of the value of 0.5 was reasonable.

Simulations of the aphid - parasite system with higher initial populations (e.g. 160, and doubling the density each time) produced the same general population trends for both the aphids and parasites as with starting population of 80. The aphid extinction time remained at 9 weeks while the maximum densities varied with the initial population (Table 16).

Fig. 38. The observed and predicted populations of B. brassicae and D. rapae. Starting aphid density:

A) 10 ,

B) 80 nymphs of instar II - III.

D. rapae was introduced on Day 0 of the experiments (Experiment Set 3 using System B).

B. brassicae: ■ observed,

□ predicted,

D. rapae: ▲ observed,

△ predicted.

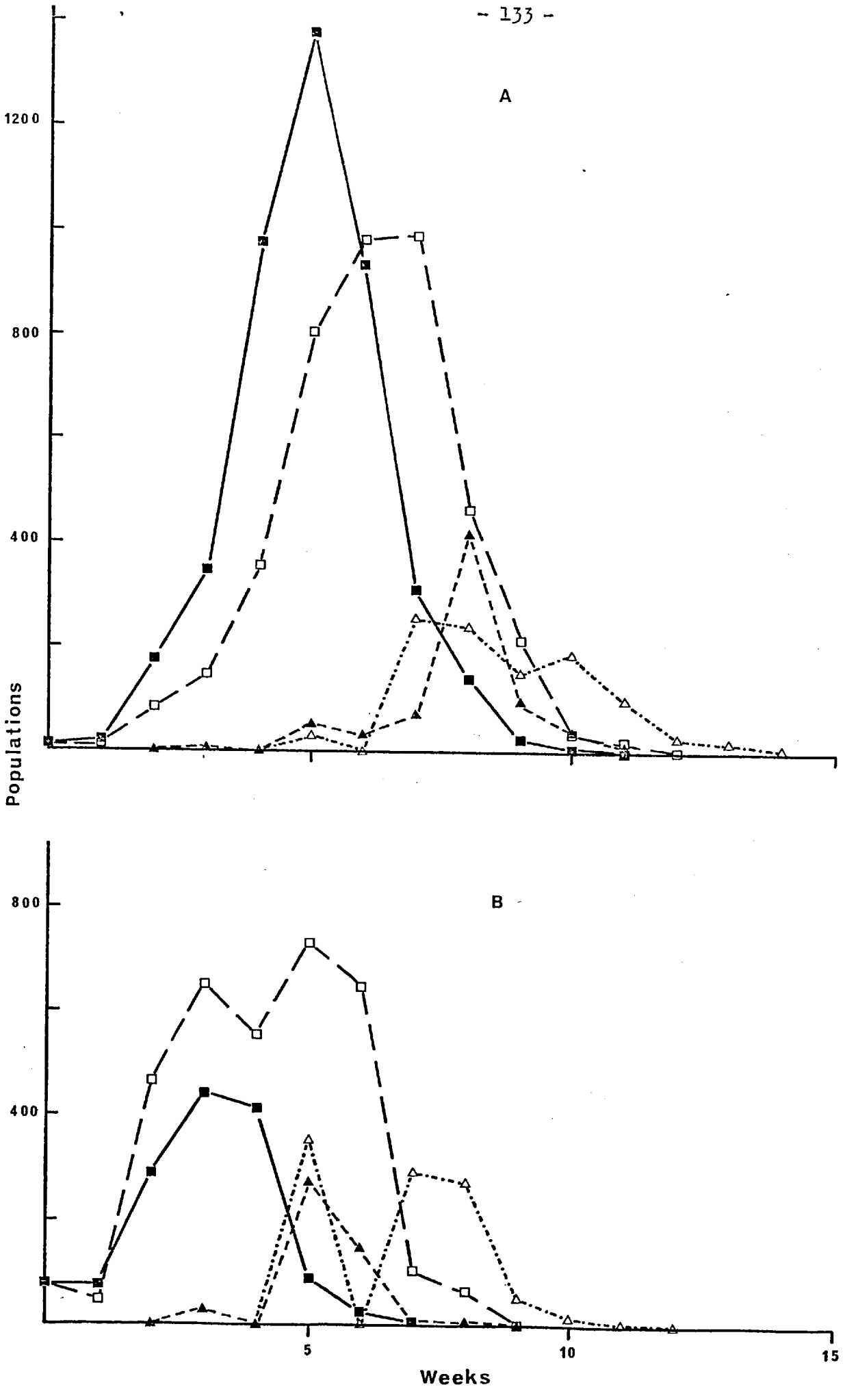


Fig. 38.

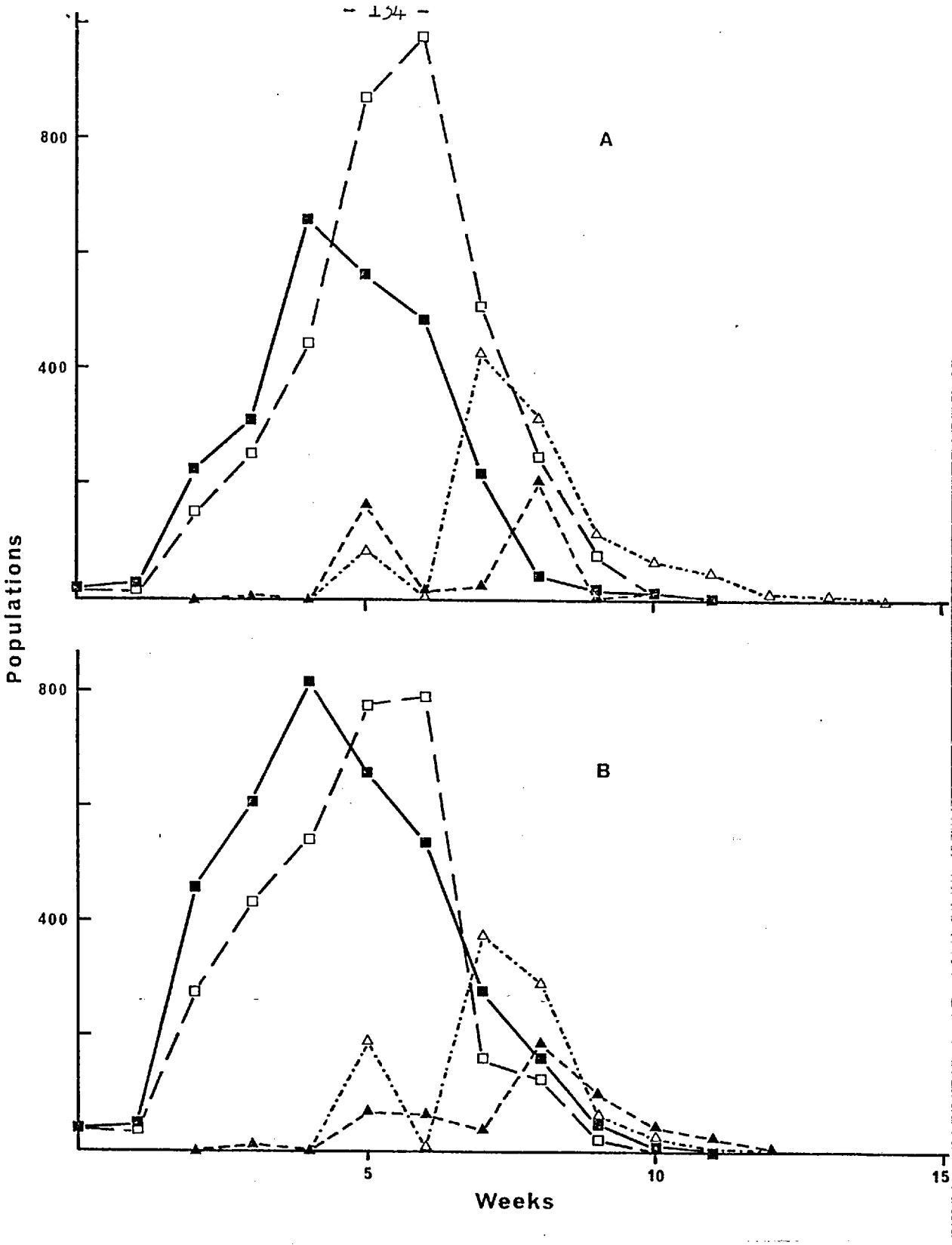


Fig. 39. The observed and predicted populations of B. brassicae and D. rapae. Starting aphid density:

A) 20 ,

B) 40 nymphs of instar II - III.

D. rapae was introduced on Day 0 of the experiments (Experiment Set 3 using System B).

B. brassicae: ■ observed,
□ predicted,

D. rapae: ▲ observed,
△ predicted.

Table 16. The inter-relationships between starting density, maximum population and extinction time of Brevicoryne brassicae, as predicted by the model.

Proportion of female among progeny	Aphid population		Extinction time (weeks)
	Initial	Maximum	
0.5	10	1130	11
	20	890	11
	40	810	10
	80	810	9
	160	900	9
	320	1026	9
	640	1133	10
	1280	1187	9
0.7	80	742	9

The lowest maximum aphid populations were achieved with the starting populations of 40 and 80, while the shortest aphid extinction times were obtained with starting populations of 80 or more. The maximum aphid population gives a rough picture of the possible economic damage to the plant, while the aphid extinction time would indicate relative efficiency of the parasite at different host densities. Using these as criteria, it can be inferred that the initial population of about 80 aphids is the "right" population for the introduction of D. rapae since this produced both the lowest maximum aphid population and the shortest extinction time. Similarly in terms of synchronisation, the parasites might be considered as synchronised with the aphids if their arrival is timed in such a way that the ratio of parasites to aphids is about 1:80.

D. Discussion.

The model simulated a very artificial aphid - parasite system in which a) the physical conditions such as temperature and photoperiod remained constant, b) emigration of aphids and thus possible escape from parasitism were not allowed, c) dispersal of parasites was non-existent, and d) predation was not considered.

Basic biological assumptions such as the uniform developmental rate of parasites, unvarying fecundity of parasitised aphids before mummification, total elimination of plant effects through regular plant replacement etc. and inaccuracies of the data used all contributed to the differences between the predicted and observed aphid and parasite populations. It is also conceivable that some other processes which might influence the populations had not been included and these would no doubt affect the accuracy of the model. A good example is the effect of parasite density on their survival. Preliminary experiments with different female densities showed that there was a drop of 0.1% in the survival rate of each female as the density increased from 2 to 32 females. This drop could reach higher values for densities of more than 32 like those encountered in the predicted populations.

Despite these limitations and the inaccuracies involved, the model predicted aphid and parasite population trends very similar to those observed and adequate for the present study.

With the model, it has been shown that the initial aphid populations affect both the maximum population and the extinction time. Furthermore, using these 2 variables as a basis for comparison, it might be concluded that the parasite is synchronised with the aphids if it arrives when the ratio of parasites to aphids per plant is about 1:80. To reach such a conclusion by experiments would no doubt involve much time and labour.

3. The effects of Alloxysta brassicae on synchronisation between Diaretiella rapae and Brevicoryne brassicae.

A. Introduction.

To explore the effects of A. brassicae on a B. brassicae - D. rapae system, a subroutine SECOND which was a simplified version of subroutine PRIMARY was used. Since the biology of A. brassicae has not been well studied, the data used were scanty and all obtained in the present study. These included fecundity, parasitism rate, developmental rate and adult survival rate.

B. Rationale.

The biological assumptions of various processes involved in the simulations are discussed below.

i) Rate of parasitism.

The model of Hassell & Varley (1969) was also used in calculating the number of D. rapae parasitised by A. brassicae. The quest and interference constants were respectively 0.07 and 0.55. Mature final instar larvae and newly formed pupae of D. rapae were considered as susceptible, i.e. the susceptible age was taken to be between 8 and 13 days. Preference for any

particular age was not considered, and the number of hosts parasitised by any female was limited by the maximum egg production.

Again, as for D. rapae in PRIMARY, it was assumed that a female A. brassicae does not discriminate between parasitised and unparasitised D. rapae mummies. This assumption seems reasonable as female A. brassicae had been observed in the laboratory to oviposit in mummies already parasitised. However superparasitism was confined to mummies containing A. brassicae of age between one and 3 days.

ii) Rate of development.

Since no information is available on the development of immature stages of A. brassicae, it was decided to use a single value for development from egg to adult of 300 day degrees since at 20°C this usually occupies 15 days. The possible effects of host age on parasite development were ignored.

iii) Others.

The interspecific effect of density on rates of parasitism and survival of both species have not been taken into account.

A sex ratio of 1:1 among the progeny was adopted.

As for D. rapae, the number of A. brassicae was recorded as the total adults emerging weekly.

C. Results and discussion.

Simulation was first carried out on the effect of introduction of A. brassicae on different days to the first generation of D. rapae. A pair of A. brassicae was introduced on the 8th, 10th or 12th day (after the start of the B. brassicae - D. rapae system) when the D. rapae stages would be respectively 8, 10 or 12 days old and susceptible to parasitism. The starting aphid density of 80 was chosen as it had been shown earlier (p. 136) that with this initial density, D. rapae could bring about

the aphid extinction within the shortest time.

The results (Fig. 40) show that the later the introduction of A. brassicae, the fewer D. rapae mummies were parasitised. This was a direct consequence of there being less hosts available for attack during the whole life span of the A. brassicae female as more mummies aged and became non-susceptible. Despite the different A. brassicae introduction days, the population trends of B. brassicae, D. rapae and A. brassicae were similar up to the 10th week. In the earlier introductions, however (namely on the 8th and 10th days), the aphid population began to increase from the 11th week onwards after D. rapae was exterminated by A. brassicae. On the other hand, when A. brassicae was introduced on the 12th day (Fig. 40B), a comparatively smaller number of D. rapae mummies were parasitised initially. This resulted in higher D. rapae populations in the later generations which were able to exterminate the aphid population.

The second set of simulations was on the effect of introducing A. brassicae to the second generation of D. rapae, i.e. between 18th and 30th days. Again, this was done only with starting aphid population of 80. The simulated population trends of B. brassicae and D. rapae (Fig. 41A) were generally similar to those which resulted from A. brassicae introductions on the 12th day (Fig. 40B). D. rapae appeared to be able to exterminate the aphid population before it itself was eliminated by A. brassicae.

Finally, simulations were done on the introduction of A. brassicae on the same day viz. the 12th day but to an aphid population generated by different starting densities viz. 10, 20 and 40 aphids. This was equivalent to varying the number of D. rapae mummies.

For the starting aphid densities of 10 and 20, the number of D. rapae mummies available for attack by A. brassicae at the time of introduction was small (viz. 2 and 6 respectively). Consequently, the number of D. rapae mummies parasitised by A. brassicae was also negligible (viz. zero and one respectively). In both cases, A. brassicae failed to establish itself and the populations of B. brassicae and D. rapae were similar to those obtained in

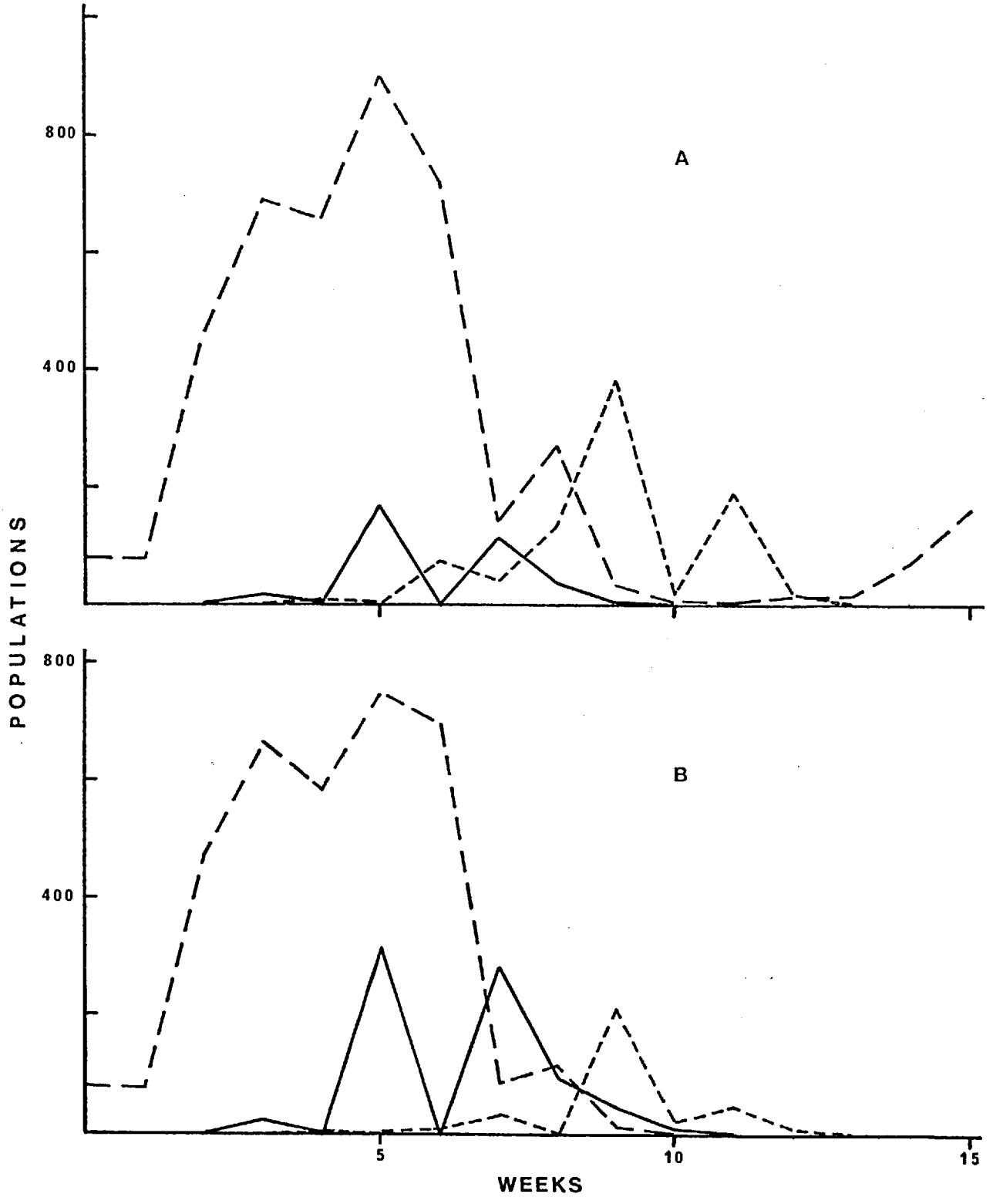


Fig. 40. The populations of B. brassicae, D. rapae and A. brassicae as predicted by model. Starting aphid density : 80 nymphs of instar II-III. A. brassicae was introduced on the following days:

A) Day 8, B) Day 12.

B. brassicae — — —

D. rapae ————

A. brassicae - - - - -

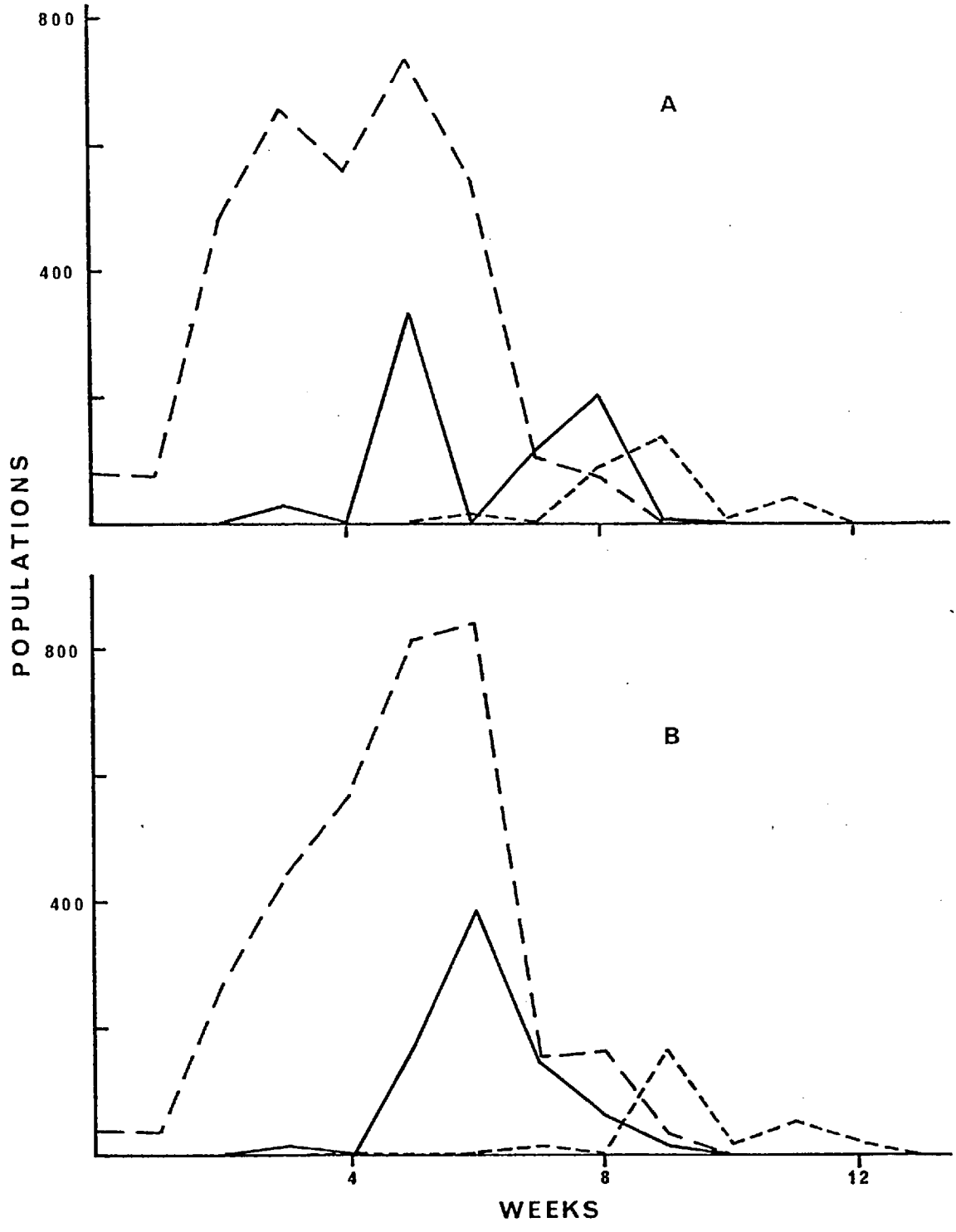


Fig. 41. The populations of B. brassicae, D. rapae and A. brassicae as predicted by model.

A) Starting aphid density: 80 nymphs of instar II-III. A. brassicae was introduced on the 20th day.

B) Starting aphid density: 40 nymphs of instar II-III. A. brassicae was introduced on the 12th day.

B. brassicae — — —

D. rapae ————

A. brassicae - - - - - -

the simulations where A. brassicae was absent. For the starting aphid density of 40 (Fig. 41B), A. brassicae managed to establish itself and later bring about the extermination of D. rapae, but not before D. rapae eliminated the aphid population. The extinction of D. rapae was followed 3 weeks later by A. brassicae.

The results of these simulation studies seem to indicate that in a closed system, A. brassicae could eliminate D. rapae. However, whether this happens before the aphid population is exterminated by D. rapae would depend on the time of introducing A. brassicae into the system. For A. brassicae introduction on the 8th and 10th days, D. rapae failed to exterminate the aphid population which began to increase from the 11th week onwards. The success of A. brassicae in establishing itself appeared to depend much on the number of D. rapae mummies available at the time of A. brassicae introduction. A. brassicae failed to establish itself when introduced to system generated by starting aphid densities of 10 and 20.

GENERAL DISCUSSION.

Knipling and Gilmore (1971) in a theoretical study concluded that it was feasible to mass produce a parasite or a parasite complex well adapted to the environment and to release enough at an optimum time to effectively manage an aphid population in a monoculture environment. The release should be synchronised such that the aphid host population is still far below the level where economic damage will result but sufficiently high to permit the parasite to increase progressively to a high and effective level. The importance of such synchronisation between an aphidophagous insect and the aphid population has also been stressed by van Emden (1966). However, the examples of Knipling and Gilmore did not cite specific species with verified parameter values and previous studies on the natural enemies of Brevicoryne brassicae have indicated that biological control of the aphid is not feasible for the following reasons.

Firstly, the most voracious predators, namely the syrphids, have little or no effect on aphid numbers (Way et al., 1969), probably because they are not well synchronised with the aphids and they reach the crops rather late (van Emden, 1966). Secondly, pathogenic fungi usually do not appear until the time of peak aphid density in early October when economic damage would already have been done (Way et al., 1969; van Emden, 1963). Lastly, and perhaps, most important of all, the primary parasite, Diaretiella rapae never becomes important as a control agent because of the high rate of hyperparasitism especially by Alloxysta brassicae. Other factors also contribute to the failure of D. rapae to check the aphid population e.g. the parasitised aphids only lose a part of their reproductive capacity and hence each aphid is able to produce a small number of nymphs before mummification is completed (Hafez, 1961; Sedlag, 1964; Paetzold & Vater, 1967; Akinlosotu, 1973).

Way et al., (1969) have also shown that biological and chemical controls could not be reliably integrated.

The present studies have shown that although D. rapae becomes quiescent in mid-October, about 2 to 3 weeks later than A. brassicae and Asaphes sp., it nevertheless emerges from the mummies in the following spring 4 to 5 weeks before the secondary parasites. However, the spring emergence of D. rapae is rather too early since catches in water traps indicate that D. rapae can be active in the field as much as 3 weeks before the sprouts have been planted. This lack of synchrony between D. rapae and B. brassicae on sprouts is also shown by tests of synchronisation on other field data.

The level of parasitism of B. brassicae in the field by D. rapae early in the season is relatively high, especially before the hyperparasites have emerged. This is explained by the high density of D. rapae early in the season, at least for the first 5 weeks or so after the sprouts have been planted, and the high rate of parasitism (up to 46%) among the immigrant alates. However, later in the season, the effect of D. rapae on aphid population is drastically reduced by A. brassicae which could account for 70 to 80% of the parasites that might emerge from the mummies, even though in the laboratory, A. brassicae has been shown to search for hosts less efficiently than D. rapae . The success of A. brassicae can be ascribed to the better synchronisation between it and D. rapae. In 1975, for example, A. brassicae was first caught by water traps 4 weeks after D. rapae, or 7 weeks after the sprouts were planted. The intervening period of 4 weeks would certainly ensure a density of D. rapae mummies high enough for the immediate establishment of A. brassicae.

In the closed ecosystem of laboratory experiments, D. rapae clearly demonstrated the capacity to eliminate completely the aphid population. These studies also showed that it is not necessarily advantageous for the parasite to be present when the aphid density is low, for example, in the field early in the season.

This situation can actually be detrimental to parasite population growth and survival, and certainly inhibits the rapid development of a high parasite population.

It is clear that there is a critical B. brassicae density which is ideal for the immediate establishment of D. rapae, a situation in which the primary parasites can lay their full complement of eggs, and yet not leaving too many aphids to allow the population to increase to a level which would be uncontrollable by future generations of parasite. This would result in the maximum efficiency of control by the parasite, and an aphid population below the economic level.

The computer simulations show that in a closed ecosystem, the hyperparasite, A. brassicae is as capable of eliminating a D. rapae population as D. rapae is capable of exterminating the aphid population in the absence of A. brassicae. What is more important is that the simulation model predicted that if the introduction of A. brassicae is delayed until after the 11th day, D. rapae can achieve a high level of parasitism of the aphids sufficient to result in the extinction of the aphid population.

To sum up, it is suggested that the efficiency of the primary parasite to control aphid population is governed by the following interacting factors:

a) the time of emergence from mummies, and the time of arrival of D. rapae into a crop,

b) the number of D. rapae in relation to the number of aphid hosts at the time of arrival of the parasite,

c) the searching efficiency of the parasite, and

d) the degree of hyperparasitism of the parasitised aphid hosts.

There is evidence then that the efficiency of D. rapae as a control agent of B. brassicae could possibly be increased in the following way. Overwintering mummies should be collected and stored in cold temperature conditions (about 5°C) to delay parasite emergence until after the new crops are planted. Then the mummies would be placed near the sprout plants and the first D. rapae allowed to emerge, after which the remaining unhatched

mummies should be destroyed before many of the hyperparasites emerge. There appears to be some margin for error here since the first individuals of A. brassicae and Asaphes sp. to emerge would be mostly males and would have little effect on the D. rapae population. Essentially this should delay the build up of the hyperparasites' populations until at least half way through the season.

SUMMARY

1. The population dynamics of Brevicoryne brassicae (L.) and its parasites were studied at Silwood Park from 1973 - 75. Diaretiella rapae (McIntosh) was the only primary parasite recorded, while the hyperparasites included Alloxysta brassicae (Ash.), Asaphes vulgaris Walk., A. suspensus (Nees), Pachyneuron minutissimum (Förster) and Dendrocerus carpenterii (Curtis). The methods used in sampling and estimating the populations and rate of parasitism were described.

2. The B. brassicae populations recorded on Brussels sprouts usually had 2 peaks, a smaller one in mid-July and a larger one later in mid-September.

3. The proportion of mummies was generally less than 20% and higher values (up to 55%) were recorded only at the beginning of the season. The percentage parasitism, a rather inaccurate measure of primary parasite activity, was also usually low (less than 15%) except in the early part of the season, when the values could be over 50%. Among the immigrant alates, the percentage parasitism was high (46%).

4. Vertical sticky traps seemed to catch more alates but less parasites than those placed horizontally. The main species caught by sticky and water traps were D. rapae, A. brassicae and Asaphes sp. The D. rapae peak was always recorded a few weeks before those of the hyperparasites. The water traps first caught B. brassicae alates and D. rapae about 3 weeks before the sprouts were planted, whereas the first A. brassicae was recorded 4 weeks after D. rapae. The water traps were found to be suitable for the present work as they are not only easy to handle but also catch more alates and parasites per 1000 sq. cm. than the sticky traps.

5. 'Aphid - exposure' experiments confirmed that the density of D. rapae was high during the early part of the season, but that it gradually declined

as the season progressed. The higher percentage of mummies recorded at the end of the season was largely due to the relatively smaller and decreasing aphid population.

6. The percentage of each species of parasite among the emergents from mummies collected in the field varied, although D. rapae usually comprised less than 30% while A. brassicae could reach 70 to 80%. The other species were very low in numbers. The percentage of D. rapae was usually higher in the early part of the season.

7. Temperature was found to be the main factor causing the parasite to become quiescent from September onwards, and also affected the spring emergence. D. rapae tends to become quiescent later, and to emerge earlier than the hyperparasites. The sex ratio of D. rapae did not very much in summer and spring emergences, while the hyperparasites had more males in the spring emergence.

8. Using the test of synchronisation of Macdonald and Cheng (1970), it was found that A. brassicae was more synchronised with D. rapae than D. rapae with B. brassicae. The better synchronisation between A. brassicae and D. rapae was the probable reason for the high rate of hyperparasitism.

9. Synchronisation experiments in the laboratory indicated that to eliminate a B. brassicae population in the shortest time, D. rapae must be introduced to the aphid population of a certain density (viz. 80 per plant, or the parasite to aphid ratio of 1:80) and age (viz. second to third instar).

10. It was shown that A. brassicae is less efficient than D. rapae in searching for hosts.

11. Computer simulations indicated that A. brassicae could eliminate a D. rapae population, as D. rapae could exterminate a B. brassicae population in the absence of A. brassicae.

12. Steps which could increase the efficiency of *D. rapae* in the field were discussed.

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APPENDIX 1. List of authors who recorded the same parasite species.

Species	Authors
Diaretiella rapae	Shorey, 1963; Kaitozov, 1965; Paetzold & Vater, 1966; Al-Azawi 1966; Godfrey & Root, 1968; Way et al., 1969; Daiber, 1971; Oatman & Platner, 1973.
as Aphidius rapae (Curtis)	Hafez, 1961.
as Aphidius brassicae Marsh	Newton, 1934.
as Diaretus rapae (Curtis)	Gourlay, 1930; Petherbridge & Mellor, 1936; Todd, 1957; Lowe, 1959.
Alloxysta brassicae	Oatman & Platner, 1973.
as Charips brassicae (Ashm)	Mellander & Yothers, 1915; 1917; Gourlay, 1930; Newton, 1934; Todd, 1957; Godfrey & Root, 1968.
Asaphes vulgaris	Newton, 1934; Petherbridge & Mellor, 1936; Bilanovskii, 1938; George, 1957; Hafez, 1961; Way et al., 1969.
Asaphes suspensus	Way et al., 1969.
Pachyneuron minutissum	Hafez, 1961.
as Pachyneuron aphidis Bouche (see de Graham 1969)	Bilanovskii, 1938.
Dendrocerus carpenterii	-
as Lygocerus aphidovorus Kieff (sic!), (see Dessart, 1972)	Hafez, 1961.
as Lygocerus testaceimanus Kieff.	Petherbridge & Mellor, 1936.

APPENDIX 2. Percentage of parasite species that emerged from B. brassicae mummies recorded by other workers. (Species recorded in synonyms are all placed under the following 5 species only.)

Author Country	Mummy number	D. rapae	A. brassicae	P. minutissimum	Asaphes sp.	D. carpenterii	Others
Barnes England (1931)	4366	12.0	78.0	-	10.0	-	-
Newton* England (1934)	not given	15.0 (62.5	1.0 4.2	-	8 33.3)	-	-
Bilanovskll (1938) Crimea	125	25.6	52.8	11.2	4.8	-	2.4+
George** (1957) England	12964	45.2	12.2	-	3.6		-
	(1953)	(74.1	20.0	-	5.9		-
	1036	34.1	18.6	-	18.4		-
	(1953)	(48.0	26.1		25.9		
Sedlag Germany (1958)	4417	66.0	22.0	1.0	11.0	1.0	-
Hafez**Holland (1961)	16568	26.0	44.0		14.0	0.07	-
	(1959)	(30.9	52.3		16.7	0.08)	
	8338	16.0	38.0		24.0	0.6	-
	(1960)	(20.4	48.3		30.5	0.7)	
Sedlag Germany (1964)	not given (1959)	30.9	52.3		16.7	0.1	-
	not given (1960)	20.4	48.3		30.5	0.7	-
	not given (1954-9)	63.5	20.4		15.5	0.5	-
Paetzold & Vater Germany (1967)	13650	6.0	46.0	27.0	21.0	0.04	0.04++
	3175	17.0	57.1	18.9	7.0	-	0.09++
Daiber**South (1971) Africa	547	5.0	5.0		8.0	-	10.0+++
		(17.8	17.8		28.6		35.7)
Oatman California & Platner (1973)	3260	18.3	64.2	4.5	13.0	-	-
Akinlosotu** (1973) England (Silwood Park)	not given	23.2	48.2	-	6.2	0.3	-
		(29.8	61.9	-	7.9	0.4	

+ Tetrstichus rapae Wlk. ++ Aphidencyrtus sp. +++ Aphidensystus africans Gahan

** percentage based on mummy number (recalculation based on parasites that emerged are given in brackets)

* percentage based on aphid sample.

APPENDIX 3. Mean monthly temperatures (°C) at Silwood Park.

Year / Month	1973	1974	1975
January	4.2	6.3	7.3
February	4.0	5.6	4.7
March	5.8	5.4	6.4
April	7.1	8.0	8.4
May	11.9	11.3	10.1
June	15.4	14.2	15.1
July	15.7	16.2	17.7
August	17.2	15.0	-
September	14.3	11.8	-
October	8.7	7.0	-
November	5.8	7.3	-
December	5.1	8.3	-

Appendix 4.

```
      PROGRAM BREVBRA (INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
      COMMON/DOG/ISTART
      DIMENSION TOTAL (8)
      DIMENSION FMODEL (28)
      DIMENSION JDAYS(28),AMEXPT(28),GMEXPT(28),EXPT(2)
      DIMENSION
     +APT(5),ALA(5),
     +ALATAE(33),APTERAE(33),
     +IAGEAD(33),INSTAR(33),
     +ALASURV(33),APTSURV(33),
     +FECALA(14),FECAPT(14),
     +SALA(5,200),SAPT(5,200),STOT(200),
     +SEMIG(200),STAGE(5),SSTAGE(5,200),
     +DAYDEG(33),DEGTHR(4)
      DIMENSION
     +X1(4),Y1(4),
     +X2(21),Y2(21),
     +X3(4),Y3(4),
     +X4(8),Y4(8)
C.....DATA DAYDEG INPUT TO BE CHANGED
C.....DEPENDING ON AGE OF APHID IMMIGRANT( IF IMMATURE)
C.....FOR NEW BORN NYMPHS AND ADULTS DAYDEG=33*0.
      DATA
     +APT,ALA/10*0./,
     +ALATAE,APTERAE/66*0./,
     +DEGTHR/50.,100.,150.,200./,
     +DAYDEG/33*10./,
     +FALEM/33*0./,
     +INSTAR/33*1/
      DATA
     +FECAPT/.4,3.1,5.4,3.,3.2,3.8,3.5,2.2,1.5,.8,.6,3*.3/,
     +FECALA/.04,2.1,3.2,2.4,2.5,1.3,1.2,.8,.8,.6,.5,.2,.3,.2/,
     +APTSURV/10*.945,23*.899/,ALASURV/10*.945,23*.924/
      DATA
     +X1/25.,60.,85.,450./,
     +Y1/0.,.015,.035,.42/,
     +X2/25.,36.,66.,125.,208.,239.,264.,292.,316.,339.,363.,385.,
     +   415.,420.,447.,495.,550.,620.,755.,920.,970./,
     +Y2/0.,.05,.13,.26,.42,.45,.51,.55,.58,.61,.63,
     +   .65,.67,.68,.69,.71,.73,.75,.77,.78,.782/,
     +X3/200.,315.,1000.,3160./,
     +Y3/1.,.86,.51,.04/,
     +X4/200.,700.,1200.,1700.,1950.,2200.,2450.,2700./,
     +Y4/1.,.968, .9,.815,.765,.705,.63,.55/
      DATAJDAYS/1,2,3,7,10,13,16,19,22,25,28,34,37,40,43,46,49,52,55,
     +     61,64,70,76,88,96,113,120,134/
      DATA AMEXPT/10.,10.,9.,47.,55.,121.,160.,162.,214.,291.,397.,498.,
     +    523.,637.,927.,1028.,986.,1271.,1552.,1675.,1557.,1077.,1083.,
     +    1130.,1457.,1567.,1187.,1487./
      DATA GMEXPT/10.,10.,9.,11.,31., 87.,145.,145.,178.,234.,321.,439.,
     +    495.,616.,776.,909.,963.,1242.,1485.,1567.,1499.,1069.,1015.,
     +    1115.,1453.,1567.,1181.,1355./
      PRINT 545
  545 FORMAT(1H1,*DAY*,2X,*0*,19X,*1*,19X,*2*,4X,*LOG DENSITY*,4X,*3*,
     +19X,*4*,19X,*5*,2X,*TOTAPH*)
      PRINT 546
  546 FORMAT(*   0*,2X,1H.,10(9(1H-),1HI), *  MODEL*,
     +3X,*  OBS(AM)*,*  OBS(GM)*)
C.....INTRODUCTION OF APHIDS/IMMIGRATION OF ALATES
      APTERAE(1)=10.
```

```
      INSTAR(1)=1
      INSTAR(11)=5
      IAGEAD(11)=10
      TOTAPH=0.
      TEMP=20.
      NDAYS=135
      DO 1 IDAY=1,NDAYS
C.....CALCULATE DAY-DEGREES EXPERIENCED
      DO 301 I=1,33
301   DAYDEG(I)=DAYDEG(I)+TEMP
C.....COMPUTE NUMBER BORN TODAY
      INSTAR(1)=1
      BORN=0.
      DFEC=F(TOTAPH,X3,Y3,4)
      DO 200 I=1,33
      IF (INSTAR(I).NE.5) GO TO 200
      K=I-IAGEAD(I)
      IF(K.GE.15) GO TO 201
      BORN=BORN+AINT(APTERAE(I)*FECAPT(K)*DFEC+.5)
      BORN=BORN+AINT(ALATAE(I)*FECALA(K)*DFEC+.5)
200   CONTINUE
201   CONTINUE
C.....CALCULATE FUTURE ALATES
      IF (TOTAPH.LE.35.) GO TO 500
      DIF=0.
      IF(APT(2).LE.0.) GO TO 500
      PROP2=F(APT(2),X1,Y1,4 )
      DO 501 I=1,11
      IF (INSTAR(I).NE.2) GO TO 501
      DIF=(APTERAE(I)*PROP2)
      APTERAE(I)=APTERAE(I)-DIF
      ALATAE(I)=ALATAE(I)+DIF
501   CONTINUE
500   CONTINUE
C.....CALCULATE ALATES EMIGRATING
      EMIG=0.
      IF(IDAY.LT.10) GO TO 527
      IF(ALA(5).LT.25) GO TO 527
      PROPEM=F(ALA(5),X2,Y2,21)
      DO 5261 I=11,20
      EM=ALATAE(I)*PROPEM
      ALATAE(I)=ALATAE(I)-EM
      EMIG=EMIG+EM
5261  CONTINUE
527   CONTINUE
C.....COMPUTE DAILY SURVIVORS
      DSURV=F(TOTAPH,X4,Y4,8)
      DO 528 I=1,33
      APTERAE(I)=APTERAE(I)*APTSURV(I)*DSURV
      ALATAE(I)=ALATAE(I)*ALASURV(I)*DSURV
528   CONTINUE
C.....UPDATE INSTARS
      DO 302 I=1,33
      K=INSTAR(I)
      IF (K.EQ.5) GO TO 302
      IF (DAYDEG(I).LT.DEGTHR(K)) GO TO 302
      INSTAR(I)=INSTAR(I)+1
      IF (INSTAR(I).LT.5) GO TO 302
      IAGEAD(I)=I
302   CONTINUE
C.....AGE ALL APHIDS AND PARAMETERS  BY ONE DAY
      DO 303 J=1,32
      I=34-J
      ALATAE(I)=ALATAE(I-1)
```

```
      APTERAE(I)=APTERAE(I-1)
      DAYDEG(I)=DAYDEG(I-1)
      IAGEAD(I)=IAGEAD(I-1)
      INSTAR(I)=INSTAR(I-1)
303   CONTINUE
C.....COMPUTE TOTALS
      APTERAE(1)=BORN
      ALATAE(1)=0.
      DAYDEG(1)=0.
      INSTAR(1)=1
277   DO 309 I=1,5
 309  APT(I)=ALA(I)=0.
      TOTAPH=0.
      DO 310 I=1,33
      K=INSTAR(I)
      ALA(K)=ALA(K)+ALATAE(I)
      APT(K)=APT(K)+APTERAE(I)
310   TOTAPH=TOTAPH+ALATAE(I)+APTERAE(I)
C.....OUTPUTS PRINTED AND GRAFED HERE
      WRITE (6,544) IDAY, TOTAPH
 544  FORMAT(I4,100X,F10.0)
      STOT(IDAY)=TOTAPH
      SEMIG(IDAY)=EMIG
      IF (TOTAPH.LE.0.) GO TO 3
      TOTAL(1)=TOTAPH
      DO 2 K=1,5
      SAPT(K,IDAY)=APT(K)
      SALA(K,IDAY)=ALA(K)
      STAGE(K)=APT(K)+ALA(K)
      SSTAGE(K,IDAY)=STAGE(K)
      L=K+3
      TOTAL(L)=STAGE(K)
  2   CONTINUE
      TOTAL(2)=TOTAL(3)=0.
      DO 7 I=1,28
      IF (JDAYS(I)-IDAY) 7,8,7
 8    PRINT 603, AMEXPT(I),GMEXPT(I)
 603  FORMAT (1H+,116X,2F9.0)
      FMODEL(I)=TOTAPH
      TOTAL(2)=AMEXPT(I)
      TOTAL(3)=GMEXPT(I)
      GO TO 11
  7   CONTINUE
 11   CONTINUE
      ISTART=0
      DO 10 I=1,8
      CALL GRAF (TOTAL(I),I)
      IF(ISTART.EQ.7) ISTART=15
 10   CONTINUE
    1 CONTINUE
 3    CONTINUE
C.....REMOVE (GO TO 5) IF INSTAR STRUCTURE NEEDED
      GO TO 5
      PRINT 600
 600  FORMAT(/* DAY*,9X,*I*,8X,*II*,7X,*III*,
     +8X,*IV*,7X,*APT*,7X,*ALA*,4X,*TOTAPH*,6X,*EMIG*)
      DO 4 J=1,NDAYS
      PRINT 601,J,(SSTAGE(K,J),K=1,4),
     +SAPT(5,J),SALA(5,J),STOT(J),SEMIG(J)
 601  FORMAT(I4,8F10.0)
      IF(TOTAPH.LE.0.) GO TO 5
 4    CONTINUE
 5    CONTINUE
      PRINT 631
```

```
 631  FORMAT(//,11X,*COMPARE MODEL AGAINST CONTROL EXPT(AM)*)
      CALL CHISQ (FMODEL,AMEXPT,28)
      PRINT 632
 632  FORMAT(//,11X,*COMPARE MODEL AGAINST CONTROL EXPT(GM)*)
      CALL CHISQ (FMODEL,GMEXPT,28)
      STOP
      END
      SUBROUTINE GRAF(VALUE,ISYMBL)
      COMMON/DOG/ISTART
      DIMENSION IBLANK(100),IRT(16)
      DATA LBLANK/1H /
      DATA IRT/1H*,1HA,1HG,1H1,1H2,1H3,1H4,
     +1H5,1H6,1H7,1H8,1H9,1H.,1H0,1H+,1H^/
      ISTART=ISTART+1
      IF(ISTART.EQ.17)ISTART=1
      IF(ISTART.NE.1)GO TO 1
      DO 3 I=1,100
      IBLANK(I)=LBLANK
    3 CONTINUE
    1 CONTINUE
      IF (VALUE.LE.0.) VALUE=1.
      INPUT=INT(ALOG10(VALUE)*20.)
      INPUT=MOD(INPUT,100)
      INPUT=INPUT+1
      IBLANK(INPUT)=IRT(ISYMBL)
      IF(ISTART.LT.16) GO TO 6
      WRITE(6,543)(IBLANK(I),I=1,100)
 543  FORMAT(1H+, 5X,100A1)
    6 CONTINUE
      RETURN
      END
      REAL FUNCTION F(X,XVAL,YVAL,NDIM)
      DIMENSION XVAL(NDIM),YVAL(NDIM)
      IF (X.LE.XVAL(1)) GO TO 1
      IF (X.GE.XVAL(NDIM)) GO TO 2
      DO 3 I=1,NDIM
      IF (XVAL(I).LE.X) GO TO 3
      AM=(YVAL(I)-YVAL(I-1))/(XVAL(I)-XVAL(I-1))
      C=YVAL(I)-AM*XVAL(I)
      F=AM*X+C
      RETURN
3     CONTINUE
1     F=YVAL(1)
      RETURN
2     F=YVAL(NDIM)
      RETURN
      END
      SUBROUTINE CHISQ (O, E, N)
      DIMENSION O(N), E(N)
      DIMENSION X2(30)
      CHI2 = 0.0
      DO 1 I = 1,N
      DIF=O(I)-E(I)
      X2(I)=DIF*DIF/E(I)
    1 CHI2=CHI2+X2(I)
      NDF=N-1
      WRITE (6,103) CHI2, NDF
  103 FORMAT(  /,11X,13HCHI-SQUARED =, F10.3, 6H (WITH, I5, 6H D.F.)/)
      PRINT 4
 4    FORMAT(11X,*CHI SQ CONTRIBUTIONS*)
      PRINT 3,(I,X2(I),I=1,N)
 3    FORMAT(11X,I5,F10.2)
      RETURN
      END
```

Appendix 5.

```
      PROGRAM SYSTEM (INPUT,OUTPUT,TAPE5=INPUT,TAPE6=OUTPUT)
      DIMENSION IAGEAD(33),INSTAR(33),FECALA(14),FECAPT(14)
      DIMENSION APT(5),ALA(5),FALEM(33),DEGTHR(4)
      DIMENSION APTSURV (33),ALASURV(33)
      DIMENSION X1(4),Y1(4),X2(21),Y2(21),X3(4),Y3(4),X4(8),Y4(8)
      COMMON/ONE/TOTAPH,DAYDEG(33)
      COMMON /TREE/IDAY,TEMP
      COMMON/FIV/ABORN,PARASIT(4),PARAFID
      COMMON/NIN/PARALA(13),PARAPT(13),PAPT(5),PALA(5)
      COMMON/ATE/APTERAE(33),ALATAE(33)
      COMMON/FTN/DFEC
      COMMON/S21/UNPARA
      COMMON/A2/ALAPAR(30,21),APTPAR(30,21)
      DATA PARASIT/4*0./, PARAFID,ABORN/2*0./
      DATA
     +APT,ALA/10*0./,   ALATAE,APTERAE/66*0./,   INSTAR/33*1/,
     +DAYDEG/33*80./, DEGTHR/50.,100.,150.,200./,   FALEM/33*0./,
     +FECALA/.04,2.1,3.2,2.4,2.5,1.3,1.2,.8,.8,.6,.5,.2,.3,.2/,
     +FECAPT/.4,3.1,5.4,3.,3.2,3.8,3.5,2.2,1.5,.8,.6,3*.3/,
     +APTSURV/10*.945,23*.899/,ALASURV/10*.945,23*.924/
      DATA
     +X1/25.,60.,85.,450./,
     +Y1/0.,.015,.035,.42/,
     +X2/25.,36.,66.,125.,208.,239.,264.,292.,316.,339.,363.,385.,
     +   415.,420.,447.,495.,550.,620.,755.,920.,970./,
     +Y2/0.,.05,.13,.26,.42,.45,.51,.55,.58,.61,.63,
     +   .65,.67,.68,.69,.71,.73,.75,.77,.78,.782/,
     +X3/200.,315.,1000.,3160./,
     +Y3/1.,.86,.51,.04/,
     +X4/200.,700.,1200.,1700.,1950.,2200.,2450.,2700./,
     +Y4/1.,.968, .9,.815,.765,.705,.63,.55/
C.....INITIAL INTRODUCTION OF NYMPHS
      TOTAPH=APTERAE(5)=80.
      INSTAR(5)=2
      INSTAR(1)=1
      IAGEAD(11)=10
      INSTAR(11)=5
      NDAYS=108
      PRINT 545
 545  FORMAT(1H1,*DAY*,*   TOTAPH*,*   AVAILA*,*   FEMALE*,
     +*  PARAFID*,*   TODAYM*,*   TOTALM*,*  TODAYAD*,
     +*   DEADAD*,*   WEEKAD*,*   WEEK M*,*   MUMMY2*,*   ADULT2*)
      TEMP=20.
      DO 50 IDAY=1,NDAYS
      PRINT 101,IDAY,TOTAPH
 101  FORMAT (I4,F9.0)
**********************************************************
C.....TOTAL SUSCEPTIBLE APHIDS
      UNPARA=0.
      DO 550 I=1,13
 550  UNPARA=UNPARA+ALATAE(I)+APTERAE(I)
*******************************
      CALL PRIMARY
*******************************
C.....CALCULATE THOSE ESCAPED PARASITISM
      DO 66 I=1,13
      APTERAE(I)=APTERAE(I)-PARAPT(I)
      ALATAE(I)=ALATAE(I)-PARALA(I)
 66   CONTINUE
**********************************************************
```

```
C.....CALCULATE DAY-DEGREES EXPERIENCED
      DO 301 I=1,33
301   DAYDEG(I)=DAYDEG(I)+TEMP
C.....COMPUTE NUMBER BORN TODAY
      INSTAR(1)=1
      BORN=0.
      DFEC=F(TOTAPH,X3,Y3,4)
      DO 200 I=1,33
      IF (INSTAR(I).NE.5) GO TO 200
      K=I-IAGEAD(1)
      IF(K.GE.15) GO TO 201
      BORN=BORN+AINT(APTERAE(I)*FECAPT(K)*DFEC+.5)
      BORN=BORN+AINT(ALATAE(I)*FECALA(K)*DFEC+.5)
200   CONTINUE
201   CONTINUE
      BORN=BORN+ABORN
C.....CALCULATE FUTURE ALATES
      IF(TOTAPH.LE.35.) GO TO 500
      DIF=0.
      IF(APT(2).LE.0.) GO TO 500
      PROP2=F(APT(2),X1,Y1,4 )
      DO 501 I=1,11
      IF (INSTAR(I).NE.2) GO TO 501
      DIF=(APTERAE(I)*PROP2)
      APTERAE(I)=APTERAE(I)-DIF
      ALATAE(I)=ALATAE(I)+DIF
501   CONTINUE
500   CONTINUE
      EMIG=0.
      IF(IDAY.LT.10) GO TO 527
      IF(ALA(5).LT.25) GO TO 527
      PROPEM=F(ALA(5),X2,Y2,21)
      DO 5261 I=11,20
      EM=ALATAE(I)*PROPEM
      ALATAE(I)=ALATAE(I)-EM
      EMIG=EMIG+EM
5261  CONTINUE
527   CONTINUE
C.....COMPUTE DAILY SURVIVORS
      DSURV=F(TOTAPH,X4,Y4,8)
      DO 528 I=1,33
      APTERAE(I)=APTERAE(I)*APTSURV(I)*DSURV
      ALATAE(I)=ALATAE(I)*ALASURV(I)*DSURV
528   CONTINUE
C.....UPDATE INSTARS
      DO 302 I=1,33
      K=INSTAR(I)
      IF (K.EQ.5) GO TO 302
      IF (DAYDEG(I).LT.DEGTHR(K)) GO TO 302
      INSTAR(I)=INSTAR(I)+1
      IF (INSTAR(I).LT.5) GO TO 302
      IAGEAD(I)=I
302   CONTINUE
C.....AGE ALL APHIDS AND PARAMETERS  BY ONE DAY
      DO 303 J=1,32
      I=34-J
      ALATAE(I)=ALATAE(I-1)
      APTERAE(I)=APTERAE(I-1)
      DAYDEG(I)=DAYDEG(I-1)
      IAGEAD(I)=IAGEAD(I-1)
      INSTAR(I)=INSTAR(I-1)
303   CONTINUE
      APTERAE(1)=BORN
      ALATAE(1)=0.
```

```
      DAYDEG(1)=0.
      INSTAR(1)=1
C.....COMPUTE TOTALS
277   DO 309 I=1,5
 309  APT(I)=ALA(I)=0.
      TOTAPH=0.
      DO 310 I=1,33
      K=INSTAR(I)
      ALA(K)=ALA(K)+ALATAE(I)
      APT(K)=APT(K)+APTERAE(I)
 310  TOTAPH=TOTAPH+ALATAE(I)+APTERAE(I)
      TOTAPH=TOTAPH+PARASIT(1)
      IF(TOTAPH.LT.1.) TOTAPH=0.
      DO 88 K=1,5
      APT(K)=APT(K)+PAPT(K)
 88   ALA(K)=ALA(K)+PALA(K)
      IF(TOTAPH.LE.0..AND.PARASIT(2).LE.0.) GO TO 3
 50   CONTINUE
 3    CONTINUE
      STOP
      END
      SUBROUTINE PRIMARY
      REAL MALPAR,MSURV
      DIMENSION FEMPAR(5),MALPAR(5)
      DIMENSION PDAYDEG(21)
      DIMENSION FPAR(5)
      DIMENSION FECPAR(5),FECAFID(2)
      DIMENSION PREFAL(13),PREFAP(13)
      DIMENSION ALAPREF(13),APTPREF(13)
      DIMENSION X5(6),Y5(6)
      DIMENSION X6(2),Y6(2)
      DIMENSION X9(5),Y9(5)
      DIMENSION
     +FSURV(5),MSURV(5),PARSURV(16),THRESPH(4),
     +THRESPA(2),ISTAGE(30,21),INSTAR(30,21),IAGEAFI(30)
      COMMON/ONE/TOTAPH,DAYDEG(33)
      COMMON /TREE/IDAY,TEMP
      COMMON/FIV/ABORN,PARASIT(4),PARAFID
      COMMON/ATE/APTERAE(33),ALATAE(33)
      COMMON/NIN/PARALA(13),PARAPT(13),PAPT(5),PALA(5)
      COMMON/FIN/DFEC
      COMMON/S21/UNPARA
      COMMON/A1/DRAPAE,REMAINP
      COMMON/A2/ALAPAR(30,21),APTPAR(30,21)
      COMMON/A5/L
      DATA DPARF,DPARM,FRESHAD,FRESHM,TOTALF,L/6*0./
      DATA X5/4.,8.,16.,32.,64.,128./,  Y5/1.,.995,.945,.8,.52,.31/
      DATA  X6/2.,256./,  Y6/1.,.837/
      DATA X9/10.,20.,40.,80.,160./,  Y9/2.,6.,14.,29.,55./
      DATA Q/.7865/, CM/.5954/
      DATA
     +FEMPAR,MALPAR/10*0./,
     +PREFAP/12.,17.,19.,25.,33.,34.,33.,31.,30.,27.,16.,5.,5./,
     +PREFAL/0.,0.,19.,25.,33.,34.,33.,31.,30.,6.,3.,1.,1./,
     +FECPAR/11.9,12.7,11.,11.4,7.6/,
     +FECAFID/1.,1./,
     +ISTAGE/630*1/,    INSTAR/630*1/,
     +APTPAR/630*0./,    ALAPAR/630*0./,
     +MSURV/4*.95,.01/,    FSURV/5*.95/,
     +PARSURV/11*.95,5*1./,
     +THRESPH/50.,100.,150.,200./,
     +PDAYDEG/21*0./,
     +THRESPA/200.,300./
C.....INTRODUCTION OF PARASITES
```

```
      IF(IDAY.NE.1) GO TO 20
      FEMPAR(1)=MALPAR(1)=1.
 20   CONTINUE
C.....FIND AVAILABLE HOSTS
      AVAILA=UNPARA+PARAFID
      IF(AVAILA.LT.1.) AVAILA=0.
C.....TOTAL ADULT PARASITES
      PARASM=0.
      PARASF=0.
      DO 61 I=1,5
      PARASF=PARASF+FEMPAR(I)
      PARASM=PARASM+MALPAR(I)
 61   CONTINUE
C.....CALCULATE NUMBER OF APHIDS PARASITISED
 62   PAHOST=EGGMAX=0.
      IF(IDAY.GT.1) GO TO 701
C.....THIS IS FOR FINDING MUMMIES FORMED AT THE
C.....START OF THE RUN,DATA FROM EXPTS
      PAHOST=F(AVAILA,X9,Y9,5)
      GO TO 702
 701  CONTINUE
      IF(IDAY.LE.5) GO TO 63
      IF (AVAILA.LE.0.) GO TO 63
      IF (PARASF.LE.0.) GO TO 63
C.....MODEL USES INTERFERENCE AND QUEST CONSTANTS
      B=(1-CM)
      Z=-Q*(PARASF**B)
      PAHOST =AVAILA*(1-EXP(Z))
 702  CONTINUE
C.....INTRODUCE EGG LIMITATION
      DO 60 I=1,5
      FPAR(I)=FEMPAR(I)
      IF(FPAR(I).GT.0.AND.FPAR(I).LT.1.) FPAR(I)=1.
 60   EGGMAX=EGGMAX+(FPAR(I)*FECPAR(I))
      IF (IDAY.EQ.1) GO TO 63
      PAHOST=AMIN1(PAHOST,EGGMAX)
 63   CONTINUE
      DO 72 I=1,13
      ISTAGE(I,1)=1
 72   CONTINUE
      INSTAR(1,1)=1
C.....FIND PARASITISED APHIDS FOR TODAY
      TODAYPH=0.
      SUPERPH=0.
      IF(PAHOST.LT.1.) GO TO 663
      IF(PARAFID.LE.0.) GO TO 671
      SUPERPH=(PARAFID/AVAILA)*PAHOST
 671  TODAYPH=PAHOST-SUPERPH
  672  CONTINUE
 67   CONTINUE
C.....PREFER=PREFERENCE OF APHIDS AVAILABLE FOR ATTACK
      PREFER=0.
      IF(TODAYPH.LT.1.) GO TO 663
      DO 800 I=1,13
      APTPREF(I)=ALAPREF(I)=0.
      IF(ALATAE(I).LE.0.) GO TO 8001
      ALAPREF(I)=ALATAE(I)*PREFAL(I)
 8001 IF(APTERAE(I).LE.0.) GO TO 800
      APTPREF(I)=APTERAE(I)*PREFAP(I)
      PREFER=PREFER+ALAPREF(I)+APTPREF(I)
 800  CONTINUE
      IF (PREFER.LE.0.) GO TO 663
      DO 66 I=1,13
      IF(ALATAE(I).LE.0.) GO TO 661
```

```
      ALAPAR(I,1)=TODAYPH*ALAPREF(I)/PREFER
      ALAPAR(I,1)=AMIN1(ALAPAR(I,1),ALATAE(I))
 661  CONTINUE
      IF(APTERAE(I).LE.0.) GO TO 66
      APTPAR(I,1)=TODAYPH*APTPREF(I)/PREFER
      APTPAR(I,1)=AMIN1(APTPAR(I,1),APTERAE(I))
 66   CONTINUE
 663  CONTINUE
      DO 82 I=1,13
      PARALA(I)=ALAPAR(I,1)
      PARAPT(I)=APTPAR(I,1)
 82   CONTINUE
*****************************************************
C.....SUM DRAPAE MUMMIES AVALABLE
      DRAPAE=0.
      DO 87 I=8,30
      DO 87 J=8,13
 87   DRAPAE=DRAPAE+ALAPAR(I,J)+APTPAR(I,J)
*****************************
      CALL SECOND
*****************************
C.....CALCULATE MUMMY ESCAPE SEONDARY ATTACK
      DO 88  I=8,30
      DO 88 J=8,12
      ALAPAR(I,J)=ALAPAR(I,J)*REMAINP
      APTPAR(I,J)=APTPAR(I,J)*REMAINP
 88   CONTINUE
*****************************************************
      DO 83 J=1,21
 83   PDAYDEG(J)=PDAYDEG(J)+TEMP
C.....J2-11=LARVA,J1212-16=MUMMY,J17-21=ADULT
C.....CALCULATE NYMPS BORN TO PARASITISED APHIDS
      ABORN=0.
      DO 75 I=1,23
C.....APHID=MUMMY LATEST TIME BY 23
      DO 75 J=1,11
      IF(INSTAR(I,J).NE.5) GO TO 75
      AFID=APTPAR(I,J)+ALAPAR(I,J)
      K=I-IAGEAFI(I)
      IF (K.GT.2) GO TO 75
      ABORN=ABORN+AINT(AFID*DFEC*FECAFID(K)+.5)
 75   CONTINUE
 751  CONTINUE
C.....FIND SURVIVORS OF PARASITISED APHIDS
C.....APHID REMAINS MUMMY LONGEST BY I=29
      DO 68 I=1,30
      DO 68 J=2,16
      IF(IDAY.LE.15) PARSURV(J)=1.
      APTPAR(I,J)=APTPAR(I,J)*PARSURV(J)
      ALAPAR(I,J)=ALAPAR(I,J)*PARSURV(J)
 68   CONTINUE
C.....MORTALITY EFFECT FROM EXCESSIVE PROBING
      IF (PARASF.LT.4.) GO TO 682
      SURVJAB=F(PARASF,X5,Y5,6)
      DO 681 I=1,6
      DO 681 J=2,3
      APTPAR(I,J)=APTPAR(I,J)*SURVJAB
      ALAPAR(I,J)=ALAPAR(I,J)*SURVJAB
 681  CONTINUE
 682  CONTINUE
C......UPDATE
      DO 70 I=1,30
      DO 70 J=1,21
      IF(J.GE.12) GO TO 69
```

```
C.....THIS REMOVES ALL MUMMIES AND ADULTS
      KA=INSTAR(I,J)
      IF(KA.EQ.5) GO TO 69
      IF(DAYDEG(I).LT.THRESPH(KA)) GO TO 69
      INSTAR(I,J)=INSTAR(I,J)+1
      IF(INSTAR(I,J).LT.5)  GO TO 69
      IAGEAFI(I)=I
 69   CONTINUE
      KP=ISTAGE(I,J)
      IF(KP.EQ.3) GO TO 70
      IF(PDAYDEG(J).LT.THRESPA(KP)) GO TO 70
      ISTAGE(I,J)=ISTAGE(I,J)+1
 70   CONTINUE
C.....AGE BY ONE DAY
      DO 71 II=1,29
      I=31-II
      M=I-1
      IAGEAFI(I)=IAGEAFI(M)
      DO 71 JJ=1,20
      J=22-JJ
      N=J-1
      APTPAR(I,J)=APTPAR(M,N)
      ALAPAR(I,J)=ALAPAR(M,N)
      INSTAR(I,J)=INSTAR(M,N)
      ISTAGE(I,J)=ISTAGE(M,N)
 71   CONTINUE
      DO 85 I=1,20
      J=22-I
 85   PDAYDEG(J)=PDAYDEG(J-1)
C.....CALCULATE ADULT PARASITE SURVIVORS
      DO 50 I=1,5
      PFLIVE=FEMPAR(I)
      PMLIVE=MALPAR(I)
      MALPAR(I)=MALPAR(I)*MSURV(I)
      FEMPAR(I)=FEMPAR(I)*FSURV(I)
      DPARM=DPARM+PMLIVE-MALPAR(I)
      DPARF=DPARF+PFLIVE-FEMPAR(I)
 50   CONTINUE
C.....SUM UP DEAD PARASITES (DP) WEEKLY
      DPARF=DPARF+FEMPAR(5)
      DPARM=DPARM+MALPAR(5)
      DEADAD=DPARF+DPARM
C.....AGE ADULT PARASITES ONLY
      DO 54 J=1,4
      I=6-J
      FEMPAR(I)=FEMPAR(I-1)
      MALPAR(I)=MALPAR(I-1)
 54   CONTINUE
C.....SUM PARASITISED(UNMUMMIFIED)APHIDS,PARASITES
      DO 81 I=1,13
      ALAPAR(I,1)=0.
 81   APTPAR(I,1)=0.
 998  CONTINUE
      DO 77 I=1,4
 77   PARASIT(I)=0.
      DO 73 I=1,5
      PALA(I)=0.
      PAPT(I)=0.
 73   CONTINUE
      PDAYDEG(1)=PDAYDEG(2)=0.
      PARAFID=0.
      DO 74 I=1,30
      DO 74 J=1,21
      IF(ALAPAR(I,J).LT.1.)ALAPAR(I,J)=0.
```

```
      IF(APTPAR(I,J).LT.1.)APTPAR(I,J)=0.
      IF(J.GT.6) GO TO 742
      PARAFID=PARAFID+ALAPAR(I,J)+APTPAR(I,J)
  742 CONTINUE
      IF(J.GE.12) GO TO 741
C.....APHID=MUMMY WHEN 16≥J≥12
      KA=INSTAR(I,J)
      PALA(KA)=PALA(KA)+ALAPAR(I,J)
      PAPT(KA)=PAPT(KA)+APTPAR(I,J)
C.....PARASIT(2)=MUMMY
  741 CONTINUE
      KP=ISTAGE(I,J)
      PARASIT(KP)=PARASIT(KP)+ALAPAR(I,J)+APTPAR(I,J)
   74 CONTINUE
      IF(PARAFID.LT.1.) PARAFID=0.
      TODAYAD=0.
      TODAYM=0.
      DO 86 I=1,30
C.....CALCULATE ADULTS EMERGED TODAY
      TODAYM=TODAYM+ALAPAR(I,12)+APTPAR(I,12)
      TODAYAD=TODAYAD+ALAPAR(I,17)+APTPAR(I,17)
   86 CONTINUE
C.....CALCULATE FEMALES AND MALES EMERGED TODAY
      FEMALE=0.5
      FEMPAR(1) =TODAYAD*FEMALE
      MALPAR(1)=TODAYAD-FEMPAR(1)
      PARASIT(3)=PARASF+PARASM
      FRESHM=FRESHM+TODAYM
      FRESHAD=FRESHAD+TODAYAD
      PARASIT(4)=PARASIT(1)+PARASIT(2)+PARASIT(3)
      PRINT 102,AVAILA,PARASF,PARASIT(1),TODAYM,
     +PARASIT(2),TODAYAD,DEADAD
  102 FORMAT(1H+,12X, 7F9.0)
      L=L+1
      IF(IDAY.EQ.1) GO TO 108
      IF(L.NE. 8) GO TO 500
  108 PRINT 107,FRESHAD,FRESHM
  107 FORMAT(1H+, 75X,2F9.0,//)
      L=1
      DPARM=DPARF=0.
      FRESHAD=FRESHM=TOTALF=0.
  500 CONTINUE
      RETURN
      END
      SUBROUTINE SECOND
      DIMENSION FEC2(7)
      DIMENSION ALBRAF(23),ALBRAM(23)
      DIMENSION SURV2M(23),SURV2F(23)
      COMMON/A1/DRAPAE,REMAINP
      COMMON /TREE/IDAY,TEMP
      COMMON/A2/ALAPAR(30,21),APTPAR(30,21)
      COMMON/A5/L
      DATA DEAD2M,DEAD2F/2*0./
      DATA SURV2M/16*.99,6*1.,1*.4/
      DATA SURV2F/16*.99,3*1.,2*.9,2*.4/
      DATA ADULT2/0./
      DATA THRESH2/300./
      DATA CM2/.55/,   Q2/.074/
      DATA FEC2/6.,9.5,13.5,2.,10.5,9.,7./
      DATA ALBRAM,ALBRAF/46*0./
C.....INTDAY=DAY WHEN ALLOXYSTA IS INTRODUCED
      INTDAY=12
      TOTDEAD=ADSEC=YGSEC=0.
      REMAINP=1.
```

```
      IF(IDAY-INTDAY) 120,121,122
  121 ALBRAF(17)=ALBRAM(17)=1.
  122 CONTINUE
C.....TOTAL ADULT SECONDARY FEMALES
      PAHOST2=0.
      FEMALE2=EGGMAX2=0.
      DO 117 I=17,23
      FEMALE2=FEMALE2+ALBRAF(I)
      K=I-16
      EGGMAX2=EGGMAX2+FEC2(K)*ALBRAF(I)
  117 CONTINUE
      IF(FEMALE2.LE.0..OR.DRAPAE.LE.0.) GO TO 119
C.....SUM PARASITISED DRAPAE MUMMIES STILL SUSCEPTIBLE
      ALLOXYS=0.
      DO 118 I=1,3
      ALLOXYS=ALLOXYS+ALBRAF(I)+ALBRAM(I)
  118 CONTINUE
      HOSTS1=DRAPAE+ALLOXYS
C.....FIND DRAPAE MUMMIES PARASITISED
      TODAY2=SUPER2=0.
      B2=(1.-CM2)
      Z2=-Q2*(FEMALE2**B2)
      PAHOST2=HOSTS1*(1-EXP(Z2))
      PAHOST2=AMIN1(PAHOST2,EGGMAX2)
      IF(ALLOXYS.LE.0.) GO TO 123
      SUPER2=(ALLOXYS/HOSTS1)*PAHOST2
  123 CONTINUE
      TODAY2=PAHOST2-SUPER2
      REMAINP=(DRAPAE-TODAY2)/DRAPAE
      ALBRAF(1)=.5*TODAY2
      ALBRAM(1)=TODAY2-ALBRAF(1)
  119 CONTINUE
C.....FIND ALLOXYSTA SURVIVORS
C.....I2-16=YOUNG,I17-23=ADULT
      DO 111 I=2,23
      ALBRAM(I)=ALBRAM(I)*SURV2M(I)
      ALBRAF(I)=ALBRAF(I)*SURV2F(I)
  111 CONTINUE
C.....UPDATE
C.....AGE
      DO 114 J=1,22
      I=24-J
      ALBRAF(I)=ALBRAF(I-1)
      ALBRAM(I)=ALBRAM(I-1)
  114 CONTINUE
C.....SUM ALLOXYSTA,YOUNG AND ADULTS
      DO 115 I=2,23
      IF(I.GT.16) GO TO 116
      YGSEC=YGSEC+ALBRAF(I)+ALBRAM(I)
      GO TO 115
  116 ADSEC=ADSEC+ALBRAF(I)+ALBRAM(I)
  115 CONTINUE
      TOTSEC=YGSEC+ADSEC
      ADULT2=ADULT2+ALBRAF(17)+ALBRAM(17)
      ALBRAF(1)=ALBRAM(1)=0.
  120 CONTINUE
      PRINT 125,YGSEC
  125 FORMAT(1H+,93X,F9.0)
      IF(IDAY.EQ.1) GO TO 124
      IF (L.NE.7) GO TO 600
  124 CONTINUE
      IF(IDAY.EQ.INTDAY) ADULT2=ALBRAF(18)+ALBRAM(18)
      PRINT 103,ADULT2
  103 FORMAT(1H+,102X,F9.0)
```

```
      ADULT2=0.
      DEAD2F=DEAD2M=0.
  600 CONTINUE
      RETURN
      END
      REAL FUNCTION F(X,XVAL,YVAL,NDIM)
      DIMENSION XVAL(NDIM),YVAL(NDIM)
      IF (X.LE.XVAL(1)) GO TO 1
      IF (X.GE.XVAL(NDIM)) GO TO 2
      DO 3 I=1,NDIM
      IF (XVAL(I).LE.X) GO TO 3
      AM=(YVAL(I)-YVAL(I-1))/(XVAL(I)-XVAL(I-1))
      C=YVAL(I)-AM*XVAL(I)
      F=AM*X+C
      RETURN
    3 CONTINUE
    1 F=YVAL(1)
      RETURN
    2 F=YVAL(NDIM)
      RETURN
      END
```