THE POPULATION DYNAMICS, PARASITES AND PREDATORS, WITH PARTICULAR REFERENCE TO THE PEACH-POTATO APHID, *MYZUS PERSICAE* (SULZER), ON BRUSSELS SPROUTS IN THE EDINBURGH AREA.

By

MARTIN AGYEN-SAMPONG, B.Sc. (Agric.), Dip. Rur. Sci.

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SUMMARY

Investigations were carried out on the seasonal changes of aphids, particularly Myzus persicae (Sulz.), on brussels sprouts and the importance of their natural enemies, from autumn 1968 to spring 1971 in the area around Edinburgh.

M. persicae overwintered anholocyclically on weeds, particularly on dock plants, but rarely on brassica crops. Plants in glasshouses also provided overwintering sites for M. persicae and Macrosiphum euphorbiae (Thomas).

These aphids started gradually to infest the brussels sprout plants during the end of June in a constant but irregular movement. Both M. persicae and M. euphorbiae have no fixed patterns of population changes throughout the field nor from year to year.

During early July the initially low densities of M. persicae and M. euphorbiae populations increased fast. By early August parasitism and predation increased; condensation of water droplets on the aphids also appeared in August and drowned some of them. Subsequently these mortality factors caused a sharp decline of the first peak of M. persicae abundance, and complete disappearance of M. euphorbiae from the field by mid-September. Favourable weather and reduced activities of natural enemies caused another peak of M. persicae to be reached in September. A slight drop in abundance occurred again, due mainly to parasitism; the third and last peak of a season appeared during late October and early November. The fall of this peak was attributed to the cold weather which reduced the rate of reproduction and hastened the abscission of bottom leaves which carried the aphid population.

Eighteen species in eight genera of aphid parasites and at least eight species in five genera of hyperparasites were recorded. All the eleven species of primary parasites and five genera containing at least eight species of

hyperparasites noted as parasites of M. persicae; and fifteen species of primary parasites and five genera of at least eight species of the hyperparasites listed under M. euphorbiae were first records of any such parasites in Scotland.

The M. persicae records as aphid host of seven species of primary parasites and two genera of at least three species of hyperparasites; and M. euphorbiae also as an aphid host of seven species of primary parasites and two genera of at least four species of hyperparasites were new records in Britain. Three and four species of primary parasites listed respectively under M. persicae and M. euphorbiae as aphid host were found to be new records in the general literature.

Praon volucre (Hal.) was the dominant species of the primary parasites followed by Diaeretiella rapae McIntosh and Aphidius picipes (Nees) which were about half and one third as numerous as the dominat species. Asaphes vulgaris Walker was the dominant species of the hyperparasites with cynipids about equally abundant.

Some aspects of the bionomics of hyperparasites and primary parasites, particularly P. volucre, were given.

Factors which limited the effectiveness of the parasites, particularly P. volucre, included :-

1. the fast developmental rate and the lower threshold of the aphid host (M. persicae) as compared to that of thep parasite (P. volucre).
2. hyperparasitism; - in 1969 and 1970 aphids on brussels sprouts were hyperparasitised respectively to the extent of 39.4% and 46.9%.
3. harvesting of brassica crops during autumn which destroyed some of the aphid mummies and the aphid populations which could be parasitised to increase the numbers of the overwintering mummies.

4. overwintering of the parasites which started during late summer and early autumn while the aphid hosts were reproducing.

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CONTENTS

INTRODUCTION

The economic importance of the peach potato aphid, Myzus persicae (Sulzer) in eastern Scotland, as in most countries, is as a vector of potato virus. In Scotland as a whole the seed potato is one of the most important crops. It forms 60% of the total acreage of certified seed potatoes in Great Britain and a considerable tonnage of the seed is exported each year to England, Wales and abroad (Hay 1969). This industry thrives primarily because of the low populations and the slow spread of the aphid-borne virus vector, and to stand the increasing competition from other seed producing areas with intensive healthy standards of seed crops, further research is needed on all aspects of the aphid-borne diseases.

Extensive ecological surveys by Fisken (1957) in eastern Scotland indicated that all the three species of potato-aphid, M. persicae, Macrosiphum euphorbiae (Thomas) and Aulacorthum solani (Kltb.), overwintered successfully as apterae on perrenial, glasshouse, heated frame and brassica crops primarily. He noted that M. persicae particularly migrated from the Edinburgh area, where there were high concentrations of brassica crops and heated frames, to the potato growing areas. The present work was carried out for the first time around Edinburgh from the latter part of 1968 to the spring of 1971, to add to our information on :-

1. The detailed population changes of the aphids, particularly M. persicae throughout the seasons on brussels sprouts in the Edinburgh area.

2. The influence of natural mortality factors on the aphid populations.

3. The occurrence of the primary aphid parasite and hyperparasite complex on the sprout crops in the study area.

4. Some aspects of the bionomics of the important and less important parasites.

5. The occurrence of predators, especially syrphids.

The present thesis is divided into the following main sections:

A. A general survey of the seasonal histories of M. persicae and M. euphorbiae and the experimental study of the effect of temperature on the development of M. persicae.

B. The population changes of M. persicae and M. euphorbiae on brussels sprout crops.

C. Some aspects of the bionomics, occurrence, and importance of the primary parasites and hyperparasites of aphids on brussels sprouts.

The sections are discussed separately and a concluding discussion is given at the end of the thesis.

- REVIEW OF LITERATURE -

GENERAL BIONOMICS OF MYZUS PERSICAE (SULZER) & MACROSIPHUM EUPHORBIAE (THOMAS)

Myzus persicae (Sulzer)

In the temperate regions, stages in the life history of Myzus persicae (Sulzer) normally alternate between a primary host and a secondary host with the production of complex polymorphic forms (Hille Ris Lambers, 1966). In autumn, eggs are laid to overwinter on peach and other Prunus species, (primary host). The eggs hatch from January to June and after a few apterous viviparous generations have appeared on the peach, alate spring migrants are formed which fly to the potato, a secondary host (Davis and Landis, 1951). Davidson (1925) found Myzus persicae on 52 host plants during the summer. However, during mild winters M.persicae may overwinter viviparously on crops, weeds, in glasshouses and on stored mangolds and sugar beet.

Davies (1934) found in Wales that Myzus persicae overwinters as apterous females on cabbages and other brassicas, especially of the variety Savoy. Jacob (1941) confirmed these findings and noted that Savoy cabbage (Brassica oleracea var.) is the most important winter host for M.persicae in North Wales. In England and Wales as a whole, brassica crops (Stanisland, 1943; Fidler 1949) and glasshouse crops (Doncaster and Gregory, 1948) are the most important overwintering sites for M. persicae while the less common places are mangold clamps (Broadbent, Cornford, Hull & Tinsley, 1949), lettuce and spinach crops (Broadbent, Tinsley, Buddin & Roberts, 1951). Heathcote et al. (1951) found M. persicae, Myzus ascalonius (Doncaster) and Macrosiphum euphorbiae (Thomas) on dock, Rumex species, and other weeds in early spring in England. Broadbent and Heathcote (1955) observed that most of the M. persicae migrating to potato

crops in the spring are virginogeniae. Of a total of 238 winged M. persicae they trapped before the end of June in England, only two were fundatrigeniae.

In Scotland, Shaw (1955) observed that it was not common for M. persicae and other potato aphids to overwinter successfully on brassica crops in north-east Scotland. Fisken (1959), finding how potato aphids, particularly M. persicae, overwinter in eastern Scotland and following the course of infestation of potato crops by aphids in different areas, stated that brassicas are the most important overwintering hosts of M. persicae followed by crops and plants in glasshouses and heated frames. He noted that peaches under glass and root clamps are less important.

On the Continent, peaches and nectarines are regarded as the most important winter hosts for the eggs of M. persicae. The apterous females also survive in glasshouses (Heinze & Profft, 1938; Heinze, 1948; Muller, 1949). Heinze & Profft (1940) considered that hibernation could occur on brassicas in milder parts of western Germany.

Macrosiphum euphorbiae (Thomas) (=solanifolii (Ashmead))

Doncaster and Gregory (1948) stated that overwintering eggs of M. euphorbiae could be found in small numbers among the colonies of Myzus persicae on cruciferous plants during the winter. According to Thomas and Jacob (1943), M. euphorbiae could appear as eggs on strawberries in North Wales.

Fisken (1959) recorded M. euphorbiae on species of Cineraria, Solanum capsicastrum, Hydrangea, Lilium and on lettuce under glasshouse in winter and suggested that in eastern Scotland it overwintered most commonly under glass.

SEASONAL FLUCTUATION OF APHID POPULATION

There is little in the literature concerning the dynamics of *M. persicae* and *M. euphorbiae* on sprout plants, but the following indicate the causes of aphid population changes on different host plants in the field.

Dicker (1952) studied the biology and seasonal changes of strawberry aphid, *Pentatrichopus fragaefolii* (Cock), in England and stated that the rapid fall in populations on plants over one-year old in June each year, was not due to climatic conditions, natural enemies or to any other causes; he concluded that the population decline was related primarily to the physiological state of the strawberry plant which led to a reduction in the number and quality of the young leaves produced at the time as a result of fruit development. The adults then move to another site and the reproductive rate was reduced.

Dunn (1951) and Dunn & Wright (1955) gave an account of the populations of pea aphid, *Acyrthosiphon pisum* (Harris), in England from 1948 to 1951 on legumes. They found that the aphid populations showed more or less similar trends each year - a sudden early seasonal increase to a peak between May and July followed by a sharp decline. The exact time of the peak depended on the type of crop, the planting time and the year. Dunn and Wright mentioned that hymenopterous parasites, syrphids, coccinellids and fungi have less effect in controlling the pea aphid than physical factors such as rain and hot summer conditions when the host plants were less attractive. They observed that the proportion of alatae produced in each spring varied, hence migration as a population reduction factor was variable.

Broadbent (1953) stated that typically in England *Myzus persicae* and *Macrosiphum euphorbiae* infestation of potatoes started with a few alatae

depositing nymphs which developed into apterae and increased in number until a peak is reached usually in July. The aphid populations then declined rapidly but occasionally rose again towards the end of the season or remained high throughout the summer. The decrease in numbers of aphids in the summer is attributed to high temperature and strong light inhibiting reproduction (Muller, 1952; Broadbent, 1953; Heinze & Profft, 1940).

Dunn (1949) discussed the bionomics of parasites and predators of aphids, M. persicae and M. euphorbiae, and population dynamics of the aphids on potatoes in England and estimated the abundance of some of the parasites and predators. He stated that Coccinella septempunctata L. could cause a total check on aphid numbers when it occurred in swarms during early August. The syrphid larvae and aphidiids appeared from about mid-July onwards and scarcely interrupted growth of the aphid populations until infestation was stable or declining.

Hughes (1963) worked on population dynamics of cabbage aphid, Brevicoryne brassicae, on kale in Australia during 1960 and 1961. He found that the population peak period occurred from the end of March to April and also noticed that migration and reduction of reproductive rate could be a means of averting food shortage. After emigration and density-induced decline in the reproduction rate, the aphidiids and syrphid larvae then caused further reduction of the aphid numbers. Under suitably warm and damp conditions dense infestations developed, and outbreaks of fungal disease limited the populations. Hughes (1963) occasionally found hemerobiid larvae and coccinellid beetles in the kale crop.

Broadbent (1953) mentioned a case in England where M. persicae population on potato in early summer was prevented from developing by

hymenopterous parasites. He added that in 1950 coccinellid predators checked a large apterous aphid population which was developing from a large May/June invasion of alate M. persicae.

In eastern England, during 1953 and 1954, George (1957) evaluated the control of cabbage aphid, Brevicoryne brassicae, exerted by predators and parasites on brussels sprouts. He found Diaeretiella rapae McIntosh the primary parasite of cabbage aphid on brussels sprouts, parasitising the aphid host to the extent of 7.2% during the peak aphid infestation. Syrphid larvae were recorded as important predators of cabbage aphid. He also found cecidomyiid larvae to be common on the brussels sprouts crop in certain areas while coccinellids were scarce.

Fielding (1953) recorded anthocorids feeding on B, brassicae and M. persicae in the cabbage field.

EFFECT OF TEMPERATURE ON THE RATE OF DEVELOPMENT AND REPRODUCTION OF MYZUS PERSICAE

Nymphal period:

Weed (1927), Sylvester (1954), both in the United States, Lal (1950) in India, MacGillivray & Anderson (1958) and Barlow (1962), both in Canada reared Myzus persicae on spinach, sugar beet and potato (last three workers) respectively. Weed determined the nymphal periods at different constant temperatures and relative humidities. At 10°C and 60% relative humidity, the nymphal period was 20.9 days and with increase in temperature to 28°C and relative humidity to 85%, the period decreased to 7.3 days. Lal (1950), Sylvester (1954) and MacGillivray (1958) rearing this species at average temperatures of 24.0°C and 20.1°C respectively, obtained nymphal periods

which were comparable to the results of Weed at about similar temperatures. On the other hand, the durations required to reach maturity as obtained by Barlow (1962) were shorter at temperatures of 10.0°, 20.0° and 25.0°C. His results indicated that at 5.0°C the nymphal period was 31.9 days, and also that development was incomplete at 30.0°C. At this same temperature in India, Lal (1950) reared this aphid to maturity. Weed (1927), Lal (1950) and Barlow (1962) observed that generally the nymphal periods decrease with increase in temperature.

Reproduction and longevity:

Weed (1927), Sylvester (1954), Lal (1950) and Barlow (1962) found that rate of fecundity of M. persicae increased with a rise in temperature. This declined after an average temperature of 25.0°C (Weed, 1927; Barlow 1962). In India, M. persicae reproduced at a temperature of 30.0°C (Lal, 1950), while in Canada, Barlow (1962), Weed (1927), Lal (1950) found that development was not completed at this temperature, the nymphal, reproductive and adult periods and total longevity declining with temperature increase. Lal (1950) stated that at any particular temperature the developmental and reproductive periods and total life span of the alatae were longer than the apterae. The alatae also reproduce less per female than the apterae.

THE APHID PARASITES AND HYPERPARASITES

Recent comprehensive reviews on aphid parasites have been prepared by the following: Mackauer and Stary (1967) on taxonomy, bionomics, geographical distribution and hosts of the world Aphidiidae; Stary (1970) on biology of aphid parasites with respect to integrated control; Hagen and van den Bosch (1968) on the effect of pathogen, parasites and predators on aphids and

Mackauer (1968) on insect parasites of green peach aphid, Myzus persicae, and their control potential.

The aphids and parasites have a complex and definite biological inter-relationship. All the most important aphid parasites belong to the hymenopterous families, Aphidiidae and Aphelinidae. The hyperparasites of the aphids which emerge through the aphidiids and aphelinids are also members of families from the Hymenoptera. Apart from Hymenoptera, only a few other species of insects, e.g. some species of Cecidomyiidae (Diptera) are found as parasites of aphids (Barnes, 1954).

The Primary Parasites

Aphidiidae: Ichneumonoidea

Most of the important parasites of aphids belong to the family Aphidiidae, formerly a subfamily of Braconidae. Today about 279 aphidiidae have been listed. The classification of the Aphidiidae into a separate family is done more because they are the sole parasites of aphids, than for phylogenetic reasons (Mackauer & Stary, 1967).

Aphidiidae are exclusive parasites of aphids; all the known species are endoparasitic, solitary and fairly constant in habit (Stary, 1970). Timberlake (1910), Vevai (1942) and Hafez (1961) recorded superparasitism or multiparasitism in the field. As many as thirteen first larvae of Diaeretiella rapae McIntosh in one aphid were recorded by Hafez (1961). In all cases, only one parasite completes its development.

Supernumerary larvae are generally eliminated by the most powerful competitor due to physiological suppression or mechanical injury. The larval development depends on temperature and host size.

Under optimum condition, a life cycle from egg to adult may be completed

within ten to twelve days, but under other conditions it may last from eight days to several weeks. Adult longevity depends on factors such as availability of food, hosts, temperatures and humidity, but under average conditions it lasts about two weeks (Vevai, 1942; Hafez, 1961; Mackauer & Stary, 1967; Stary, 1970).

The larval instars in the Aphidiidae seem variable. Spencer (1926) found four while Wheeler (1923) reported five for Aphidius matricariae Haliday. Schlinger and Hall (1960, 1961) recorded only three each for Praon exoletum (Nees) (=palitans (Muesebeck)) and Trioxys utilis Muesebeck. They believed there are only three larval instars in the family. The first larval instar is caudate type and subsequent larval instars are hymenopteriform (Clausen, 1940; Beirne, 1942; Schlinger & Hall, 1961).

The larval development consists of two separate phases. Phase one larva ingests the liquid contents of the giant cells. In the second phase, the parasite larva actively feeds on the body content of the host (Tremblay, 1966; quoted from Mackauer & Stary, 1967). The mature larva makes a slit opening in the ventral wall of the aphid abdomen and fastens the empty skin down to the substratum with silk. It then spins silk to line inside and pupates. The adult emerges from the shiny cocoon by cutting a circular opening at the anterior end of the abdomen between the cornicles (Hafez, 1961; Shands et al. 1965; Stary, 1970). The mature larvae of Praon (Haliday) and Dyscritulus (Hincks) species pupate differently. They cut a slit in the ventral wall of the dead host and spin a separate tent-like cocoon below the empty aphid skin and pupate inside it (Shands et al. 1965; Stary, 1970).

The female may oviposit immediately on emergence from the cocoon without mating and the offspring will all be males. Arrhenotoky is most common among Aphidiidae. In the laboratory the female has been found to mate only

once while the male mates many times. Mated females lay eggs which produce both sexes of approximately equal numbers. However, a constant sex ratio may be influenced by such factors as age of the parasite, number of available hosts and rate of oviposition. Oviposition may be into any stage of growth of the aphid host but the second and third instars are generally preferred (Sekhar, 1957 ; Hafez, 1961; Stary, 1970).

Praon volucre Haliday

This is a palearctic and a United States species. It has been reared from over 41 species of aphids, including Myzus persicae and Macrosiphum species. It is widely polyphagous but the host range is probably confined to subfamily Aphidinae (Mackauer & Stary, 1967).

Beirne (1942) working on the life history of P. volucre Haliday on Hyalopterus arundinus described ovipositional behaviour and found that the egg hatches in 3-5 days and the larva passes through five instar stages. Schlinger and Hall (1960) recorded only three for a similar genus, P. exoletum (=palitans).

Dunn (1949) found P. volucre scarcely parasitises potato aphids on potato in England. Similar observations were reported by George (1957) on aphids on brussels sprouts in England.

Beirne (1942) collected 291 mummified mealy plum aphids on plum at the end of July and beginning of August in Ireland, 77% of the number emerged as P. volucre; chalcidoid and cynipid hyperparasites emerged from 10% and 7% of the mummies respectively. In England, Fielding (1953) found P. volucre as the most dominant parasite of M. persicae. She further stated that Asaphes vulgaris Walker highly parasitised P. volucre and cynipids scarcely infested Praon species.

Dill (1937) reared a pteromalid, A. vulgaris, a cynipid, Charips cameroni and a ceraphronid, Dendrocerus (=Lygcerus) giraudi Kieff from P. volucre in the Swiss Midlands.

Praon myzophagum Mackauer

Mackauer (1968) reported that P. myzophagum Mackauer is distributed in Europe and recorded in Austria, Sweden, Germany, and England. Outside Europe it is found in Israel and was introduced into California, U.S.A. from the former (Fleschner, 1963). In England, it was originally distributed as a subspecies of volucre Haliday (Mackauer & Stary, 1967).

Myzus certus Walker and M. persicae are the only recorded aphid species hosts (Mackauer & Stary, 1967).

Diaeretiella rapae McIntosh

Diaeretiella rapae McIntosh has many aphid hosts, about 34. The host range includes most species of Aphididae with greater preference for the Myzus - Brachycaudus group. The species is cosmopolitan and very common in Europe and temperate North America (Stary, 1966; Mackauer & Stary, 1967).

Most of the work done shows D. rapae to be mainly a parasite of the cabbage aphid, Brevicoryne brassicae. Wheeler (1923), Broussal (1961) and Hafez (1961) described the stages of larval instars and Spencer (1926), Hafez (1961), Shand et al. (1965) and Broussal (1966) worked on the bionomics and aspects of the ecology of this parasite.

In the Netherlands, Hafez (1961) found that 60% of the parasites which emerged from cabbage aphid mummies collected in the field were females with longevity up to one week in summer and two weeks in spring. Parasitism fluctuated widely under field conditions and did not markedly affect the populations of the cabbage aphid.

In England, Dunn (1949) did not record D. rapae attacking M. persicae on potatoes. George (1957) confirmed this observation and stated that D. rapae parasitised M. persicae only in cages in the laboratory. However, Spencer (1926), Shands et al. (1965), Schlinger & Hall (1960), all in the United States, Hafez (1961) in the Netherlands, and Fielding (1953) in England recorded M. persicae parasitised by D. rapae. In the United States Pimentel (1961) stated that the effectiveness of D. rapae as a parasite of M. persicae or B. brassicae depended on the relative numbers of each aphid host. Hafez (1961) and Broussal (1966) have convincingly shown that B. brassicae is a preferred aphid host to M. persicae.

Hafez (1961) noted that hibernation of D. rapae starts in autumn and emergence begins in early spring in the Netherlands. However, there is sporadic emergence during the winter. There could be two peaks of emergence of the overwintered mummies at the beginning of April and in May. He further found that this parasite undergoes facultative diapause as hibernation could be terminated during the winter in the laboratory by subjecting the overwintering mummies to room temperature and long photoperiod.

In England, George (1957) estimated that overwintering starts about the end of August and there is no emergence until spring. He reared Charips species, Asaphes vulgaris and Dendrocerus (=Lygocerus) species through D. rapae. Fielding (1953) obtained similar hyperparasites through the same primary parasites. Hafez (1961) reared Charips ancylocera Cam., A. vulgaris, Pachyneuron minutissimum Fo, and Dendrocerus (=Lygocerus) aphidovorus K. from D. rapae.

Aphidius picipes Nees

Aphidius picipes Nees seems to be confined to Europe. It parasitises a number of various aphid groups with undefined host range (Stary, 1966),

but is possibly confined to the Myzus - Rhopalosiphum group (Mackauer & Stary, 1967). Mackauer, (1968) pointed out that Dunn (1949) gave a general account of A. picipes under the name of A. avenae Haliday. Dunn (1949) in England, found the life cycle during summer to be approximately three weeks. Most of the adults emerged five to six days after mummies were collected from the field and all emerged before the end of September. He speculated that hibernation starts in autumn and generations of A. picipes could reproduce throughout mild winter in unheated glasshouses.

Aphidius ervi Haliday

Mackauer & Stary (1967) stated that the host range is apparently restricted to certain Acyrthosiphon species feeding on legumes and other related aphids, but all other host records are questionable. They stated that this parasite is well distributed in the Palearctic region and that it has been introduced to Nearctic. The bionomics have been studied by Dunn (1949) and Stary (1966). In Czechoslovakia, Stary (1966) found A. ervi as an effective parasite of Acrythosiphon pisum on Trifolium species.

Aphidius rosae Haliday

The host range of Aphidius rosae Haliday is restricted to some Macrosiphum species. Its geographical distribution is Holarctic and some countries where it has been recorded are: England, France, Spain, Sweden, Germany, Russia, Canada, and the United States, (Mackauer & Stary, 1967).

In Czechoslovakia, Stary (1966) reported that it occurs mostly in the parks, gardens, and field shrubs infested by Macrosiphum species. The extent of their economic importance was insignificant.

Aphidius urticae Haliday

Mackauer & Stary (1967) noted that Marshall (1899) regarded this species

to be the same as avenae Haliday and ervi Haliday. Stary (1966) synonymised it with ervi Haliday. Mackauer & Stary (1967) rightly suggested that further taxonomic work was needed to determine the true identity of the species.

A. urticae is found only in Europe (Stary, 1966) and seemingly attacks mainly Microlophium species on Urtica (Mackauer & Stary, 1967).

Ephedrus plagiator Nees

Ephedrus plagiator is a Palearctic species and widely polyphagous with about 62 known aphid hosts, but it commonly parasitises the subfamily Aphidinae. The genus Ephedrus has a characteristic black mummy which is different from the rest of the Aphidiidae (Stary, 1966), Mackauer & Stary 1967).

Skriptschinskij (1930) described all the larval stages. He found the number of eggs laid by the female to be 133 and the longevity of adult males to be 8-15 days and that of females 13-18 days when fed on honey. He further stated that under conditions of 17°C and 85% relative humidity, development of the parasite takes 14-17 days. Hyperparasites reared through Aphis padi L. from E. plagiator, during studies in Russia, were the Chalcid, Pachycrepis clavata Walker, ceraphronid, Lygocerus testaceimanus Kieff and cynipids, Alloxysta species and Charips species.

Toxares deltger Haliday

This species is a parasite of Myzus persicae (Sedlag, 1959), and other hosts include Arythrosiphon and Dysaphis species (Mackauer & Stary, 1967). Its distribution is Holarctic. The only other species of the genus, shagai Takada, is found in Japan. Sedlag (1959) reported that T. deltiger Haliday was of little significance in controlling M. persicae.

Dyscritulus planiceps Marshall

Dyscritulus planiceps Marshall is found only in Europe. The only two aphid hosts recorded are Drepanosiphum species, and the parasite is economically unimportant (Stary, 1966; Mackauer & Stary, 1967).

Monoctonus pseudoplatani Marshall

Geographical distribution is confined to Europe (Mackauer & Stary, 1967). Seemingly the range is restricted to Drepanosiphum species on Aceraceae (Stary, 1966; Mackauer & Stary, 1967). Stary (1966) considered this parasite economically indifferent.

Aphelinidae: Chalcidiodea

A few genera of the subfamily Aphelinae are primary parasites of aphids and most of the species of the family Aphelinidae are parasites of homopterous families, Coccidae and Aleurodidae. Out of about seven Aphelinus species which are aphid parasites, A. mali (Haldeman) is the most effective one. It has been introduced into 50 countries, including Britain, to control woolly apple aphid, Eriosoma lanigerum (Hausman), (Clausen, 1956; Hagen & van den Bosch, 1968). As a parasite, Aphelinus has been recorded in Russia, United States, Hawaii, Australia, Italy, Switzerland, and Spain, (Thompson 1950). The impact of the species of Aphelinidae on the biological control of aphids, on the whole, has been inefective (Hagen & van den Bosch, 1968).

Aphelinus asychis Walker

This species has numerous hosts in Europe and the United States, mainly from species of Macrosiphum, Anuraphis, Toxoptera, Chaitophorus and Myzus. Ferriere (1965) synonymised A. semiflavus Howard with A. asychis while Mackauer (1968) thought they are conspecific.

A strain of A. asychis which parasitises Myzus persicae but not Therioaphis trifolii (Monell) was in existence in the United States. Another strain has been imported from the Middle East to California, United states, which attacks the latter aphid, T. trifolii, on alfalfa (van den Bosch et al. 1959). In California, the biology and the economic importance of A. asychis as a parasite of T. trifolii have been studied by van den Bosch et al. (1959), Force and Messenger (1964 a, b, 1965) and other workers.

Aphelinus flavipes Foerster

Aphelinus flavipes is found mainly in Europe being recorded in Austria, Germany, Switzerland, and Czechoslovakia. It has been little studied. A. flavipes parasitises aphids which include species of Siphonophora and Toxoptera (Ferriere, 1965). Rao (1968) reared this species from M. persicae in India.

Aphelinus tibialis Nees and Aphelinus daviola Foerster.

Both species are found in Europe and have many hosts especially among the species of Aphis and Toxoptera.

Peck (1963) synonymised A. tibialis with A. chaonia Walker while Ferriere (1965) considered it to be the same as A. varipes Foerster.

The Hyperparasites

In nature, primary parasites of aphids may be parasitised and these secondary parasites may also have parasites - tertiary parasites. The hyperparasites and tertiary parasites are found in three superfamilies of Hymenoptera, namely the Cynipoidea, Chalcidoidea, and Proctotrupoidea.

Cynipoidea: Cynipidae: Charipinae.

Charips, Alloxysta and Phaenoglyphis species are entirely hyperparasitic

on aphids through Aphidiiae and Aphelinus species. Haviland (1921) and Spencer (1926) gave accounts of the biology of the genus Charips. The species of the subfamily are solitary and endoparasites, and the female deposits her eggs into the larvae of primary parasites in a living aphid host. Both the primary parasite and the aphid host develop until the former attains maturity and the aphid host mummifies. Development of the primary parasite stops and the hyperparasite continues to thrive on the primary parasite. It pupates within the mummy. When fully grown, the adult hyperparasite emerges out of the mummy through the emergence hole.

Charips species were reared from Aphidius, Lysiphlebus, Praon, Trioxys and Aphelinus species by Haviland (1921), Dunn (1949), and George (1957) in England, Schlinger (1960), and Pimental (1961) in the United States and by Rosen (1967) in Israel. Hafez (1961) recorded that Charips species overwinters in the prepupal stage inside the mummy for a maximum duration of 259 days in the Netherlands. Phaenoglyphis species was reared from parasitised Rhophalosiphum insertum (Walker) in the Netherlands by Evenhuis (1966). Hagen and van den Bosch (1968) noted that this genus has been very little studied.

Chalcidoidea: Pteromalidae

The species of these genera, Asaphes, Pachyneuron and Coruna, are known to be hyperparasitic on aphids through Aphidiidae and Aphelinus species. They are ectoparasitic, solitary insects. The female oviposits on the last larval instar on the prepupa or pupa of the primary parasite or on other hyperparasites through a mummified aphid. The hyperparasitic larva feeds on the parasite and pupates inside the mummy (Haviland, 1922; Spencer, 1926; Sekhar, 1958). Hafez (1961) noted that during oviposition pteromalids

venomised the hosts to arrest development.

Asaphes and Pachyneuron have been reared from aphids through species of Aphidius, Diaeretiella, Praon and Aphelinus (Haviland 1922; Spencer, 1926; George, 1957; Sekhar, 1958; Pimental, 1961; Hafez, 1961; Shands et al. 1965).

Haviland (1922), Dunn (1949) in England and Shands et al. (1965) in the United States recorded that Coruna clavata Walker parasitises Ephedrus, Aphidius and Praon species.

Proctotrupoidea: Ceraphronidae

Ceraphronidae are common hyperparasites of many aphid species through Aphidiidae (Skriptschinskij, 1930; Dunn, 1949; George, 1957; Shands et al. (1965). They have the same life history as pteromalid being solitary and ectoparasitic; eggs are deposited on mature larvae or pupae of primary parasites or on hyperparasites inside mummified aphids. A detailed study of Dendrocerus (=Lygocerus) species as a hyperparasite was first made by Haviland (1921). She and Spencer (1926) gave an account of the bionomics of Dendrocerus (=Lygocerus) species; they found the species' eggs on their own larvae and pupae, thus being tertiary parasitic. Dendrocerus (=Lygocerus) have been reared from Aphidius, Praon (Fielding, 1953) and Diaeretiella (George, 1957; Hafez, 1961) and from Charips (Hafez, 1961).

Inter-relationships between primary parasites and hyperparasites

Sedlag (1959) studying Praon species and D. rapae and their hosts, Brevicoryne brassicae and Myzus persicae in West Germany, found that peak emergence of the primary parasites from the mummies always preceeded that of the hyperparasites, Asaphes, and Charips. Paetzold and Vater (1966), in East Germany, working on the parasite complex on B. brassicae, confirmed

Sedlag's findings and found the most numerous hyperparasites to be of the genus Charips followed by Pachyneuron and Asaphes; Dendrocerus (=Lygocerus) and Aphidencyrtus formed less than 1% of all emerging Hymenoptera.

Many workers have indicated that hyperparasites can reduce the effectiveness of primary parasites. In England, for example, Barnes (1931) collected 4366 mummies from a single brussels sprout plant heavily infested with B. brassicae and the parasite emergences were 12% primary parasites; 78% Charips species and 10% Asaphes species. Newton (1934), also in England, found that cabbage aphids on brussels sprouts were parasitised by 15% D. rapae, hyperparasitised 8% by Asaphes vulgaris and 1% by Charips brassicae (Ashmead).

Pimentel (1961), in the United States, found D. rapae and Praon species as the primary parasites of B. brassicae and Myzus persicae on cole crops; and Charips brassicae and Asaphes fletcheri (Crawford) as their hyperparasites. He noted that in 1957, the first year of the two years' study, hyperparasites were more numerous than the primary parasites. George (1957) mentioned that D. rapae, the primary parasite of the cabbage aphid, was more common compared to the hyperparasites, Charips, Dendrocerus (=Lygocerus) species and A. vulgaris.

In Maine, the United States, Shands et al. (1965) concluded from ten years study that hyperparasitation in potato-infesting species of aphids ranged from 0-53%; with Asaphes species as the most abundant followed by Dendrocerus (=Lygocerus), Coruna, Pachyneuron and Charips.
Sekhar (1958) found A. fletcheri deposited more eggs in the mummies of Aphidius testaceipes (Cresson) than in those Praon aguti (Smith).
Evenhuis (1964 and 1966) reported that each of the four main apple aphids

in the Netherlands is parasitised preferentially by one main primary parasite; three primary parasites were each parasitised by a different species of Charipinae. Gutierrez and van den Bosch (1970) found Aphidius smithi Sharma and Subba Rao as the most preferred primary host of Charips victrix (Westwood), out of the nine possible hosts.

SECTION A

THE BIONOMICS OF THE APHIDS ON BRUSSELS SPROUTS WITH PARTICULAR REFERENCE TO MYZUS PERSICAE

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OVERWINTERING OF MYZUS PERSICAE AND MACROSIPHUM EUPHORBIAE

As reported in the literature review Myzus persicae can overwinter outdoors in Scotland on brassicas and on un-named perennials and that both M. persicae and Macrosiphum euphorbiae can overwinter indoors on plants in heated frames and glasshouses. Also, because of the importance of overwintering and infestation of spring hosts with subsequent transmission of virus diseases to potatoes, it was considered necessary to study further the overwintering of both M. persicae and M. euphorbiae.

During the winters of 1968-69, 1969-70 and 1970-71 the overwintering habitats of M. persicae and M. euphorbiae in the Edinburgh area were studied, mainly on farms at Liberton, Newington and Musselburgh.

The Liberton and Newington farms are situated on the southern outskirts of Edinburgh while the one at Musselburgh is about 10 kilometres (6 miles) east of Edinburgh.

Overwintering of Myzus persicae on brassicas

To determine the extent to which M. persicae could survive the winter on brassica crops, 50 plants each of summer cabbage, brussels sprout and broccoli were marked with bamboo stakes at Liberton and Newington during the winter of 1968-69. In addition, 50 plants of spring cabbage were marked at the Newington site. The number of aphids on the plants at Newington was periodically counted and recorded from November 7 to

February 4, 1969, and from November 14 to January 22, 1969, at Liberton (Appendix 1). The alatae, apterae and nymphs were recorded separately. The condition of the plants were observed throughout the studies. Observations on similar crops were made at Musselburgh, except that 40 plants were randomly selected on each counting day, from November 22 to February 6.

During the 1969-70 winter, similar crops to those of the previous year were chosen for observation at the Newington site from December 12 to March 17. 30 plants of each crop were marked with bamboo stakes. In both years, the early frosty days and snowfalls in November generally caused the lower leaves of the brassica crops, which often sustained the aphids, to be flabby. By the middle of December most of the lower leaves were dead, and the infesting aphids died along with them (Plates I and II).

Tables 1 and 2 and Appendices 1 and 2 show that on each of the brassica crops the aphid population declined rapidly from November, and by the end of January no aphids were found on the crops. With the exception of spring cabbage, the other crops were harvested by the end of February. No aphids were found on the 100 plants each of spring cabbage and broccoli inspected at Newington and Liberton at the end of March 1969.

Overwintering of Myzus persicae on weeds

At Liberton, on 22nd January 1969, following the disappearance of the aphids on brassica crops, a thorough search was made among the weeds on the headlands for their overwintering sites. Dock weeds, Rumex species, were found for the first time to be an overwintering host plant for M. persicae. Fifteen infested plants carried an average number of four apterous aphids per plant. The aphids were in a comatose condition on the under surface

of the extreme lower leaves of the plants close to the ground, and occasionally in the partially opened terminal leaves. Most of the infested plants were inconspicuously hidden among dead weeds and grasses at the base of towering dock stems. This probably meant that there was a higher temperature under the leaves and that the aphids were protected from snow and frost (Plate III).

When the comatose M. persicae were collected and brought to the laboratory they became active and reproduced young apterous aphids. The overwintering apterous aphid appears pale yellowish green or deep green with yellow mottling around the cornicles and with the head darker than the rest of the body. The antennae, caudae and legs are dark, particularly at the extremities, and generally, the body of the summer apterae is light green in colour. Theobold (1926) gave a detailed description of the summer apterae. The colour of a newly born nymph in the winter is light yellowish green with faint dark colouration at the extremities of the antennae, legs and cornicles.

On January 27th 1969 at Newington, after a thorough search through the weeds of the headlands, (Plate IV), ten dock plants, Rumex species, were found with aphids on them. The plants were marked with bamboo stakes. Periodically, until April 29th, aphids on the docks were counted and recorded as follows:- alatae, apterae, alate 4th instar nymphs, advanced apterous nymphs (late 3rd instar to 4th instar), medium apterous nymphs (late 2nd instar to early 3rd instar) and young apterous nymphs (1st instar to early 2nd instar). The nymphs were divided into three groups since the four nymphal instars could not be distinguished under field conditions. Of the ten plants, eight had aphids on them during the second counting on 3rd March;

TABLE I

Estimated number of Myzus persicae per I0 plants at Liberton and Musselburgh during the winter 1968-69

Count	Sp. cabbage	Sm. cabbage	Br. sprouts	Broccoli
14/11/68	-	26.0 (0.4 al.)	I080.0	189.0 (0.6 al.)
20/11/68	-	17.8 (0.2 al.)	547.6	123.8 (0.2 al.)
22/11/68	5.5	38.5	271.8 (0.5 al.)	77.0 (1.0 al.)
27/11/68	-	2.8 (0.4 al.)	304.4 (0.8 al.)	48.2
29/11/68	3.5	26.5	183.3 (0.3 al.)	55.0 (0.5 al.)
4/12/68	-	0.8	212.2	22.4
13/12/68	1.5	11.5	134.5 (0.8 al.)	19.8 (0.3 al.)
18/12/68	-	0.2	19.2	2.0
27/12/68	1.5	5.5	24.3	I0.3
2/ 1/69	-	0	0	0.6
7/ 1/69	-	0	0	0
9/1/69	0.25	0	harvested	15.0
14/1/69	-	0	-	0
22/1/69	-	0	-	0
6/2/69	0	0	-	0

Sp. = spring; Sm. = summer; al. = alatae

TABLE 2

Estimated number of Myzus persicae per 10 plants at Newington during the winters of 1968-69 and 1969-70

Count	Sp. cabbage	Sm. cabbage	Br. sprouts	Broccoli
7/11/68	15.4 (0.4 al.)	45.4 (0.6 al.)	953.4 (1.6 al.)	192.8 (0.6 al.)
20/11/68	9.0	22.2 (0.2 al.)	378.6 (0.2 al.)	101.6
27/11/68	4.8	16.2	88.4	30.6
4/12/68	2.0	3.2	76.6	21.2
12/12/68	1.0	1.2	28.4	2.4
3/ 1/69	0.2	0.4	0.6	0.2
21/ 1/69	0.4	0.2	0	0
28/ 1/69	0.2	0	0	0
4/ 2/69	0	0	0	0
8/12/69	5.7 (0.3 al.)	9.7	10.7	10.3
22/12/69	4.3	4.0	7.3	10.3
7/ 1/70	3.7	0.6	5.3	5.0
21/ 1/70	1.6	0	4.0	3.0
3/ 2/70	0.6	0	0.3	0
17/ 3/70	0	0	0	0

Sp. = spring; Sm. = summer; al. = alatae

Plate I. Brussels sprout plant with flabbly leaves, particularly the bottom ones, during early December, 1969 at Lasswade.

Plate II. The experimental field of the brussels sprouts during early December, 1969 at Newington. Note the flabiness of the leaves.

Plate III. Rumex species infested with Myzus persicae during winter.

Plate IV. Headland of harvested brussels sprout field where Myzus persicae overwintered on Rumex species.

and two during the last two countings (Appendix 3). The alate form was first observed on April 29th when there was an overall increase in aphid numbers. Except for the alate forms, all stages of growth were found on the plants during winter and spring (Appendix 3).

On January 29th, 1969, mayweed, Matricaria inodora, and dandelion, Taraxacum officinale, were found infested with two adults and two nymphs; and two nymphs of M. persicae respectively. Two days later another dandelion plant growing close to the base of a wall along the road was found with three adults of M. persicae on it.

A survey similar to that at Newington was carried out from March 6th to June 20th at Musselburgh. Of the ten dock plants marked with bamboo stakes, only four had aphids on them by June 13th, and all the aphids had disappeared by June 20th.

During the winter docks produce fewer and smaller leaves per plant than in spring, usually 2-4 per plant. Leaf surface area is about 21.0 sq.cm., with petiole length of 4.0 cm., while the corresponding figures in late spring are about 4-5 leaves, 162.5 sq. cm., and 18.0 cm. The inflorescence started to appear in early June and the lower leaves which supported the aphids began to wither. The production of alate forms had by then increased (Table 3 and Appendix 3). These were first observed on May 24th, while all stages of aphid growth were found on the dock throughout the winter, as at Liberton and Newington.

At Gilmerton (approximately 2 kilometres or 1 mile, south of the Liberton site) on three occasions, March 4th, March 27th, and April 30th 1969, thorough searches were made through the weeds of the headlands. During the first survey, 25 dock plants were found with a total of nine adults and

40 nymphs of M. persicae on them; six adults and eight nymphs were found during the second survey; and the third search yielded three adults and 17 nymphs.

On November 27, 1969, at Newington six dock plants infested with M. persicae were marked on the headlands as before, and a similar method of counting and recording was used as in the previous year. The observations were terminated when no aphids were found on June 20, 1970. Two out of the six plants maintained various small numbers of the aphids throughout the observation. The alate fourth instar nymphs were first noted on May 19. 1970 (Appendix 4).

From November 27, 1970, to June 25, 1971, observations were made on four dock plants infested with M. persicae at Lasswade* and on three dock plants similarly infested at Newington. The alate fourth instar nymphs were first observed on May 14, 1971 (Appendix 5), and the aphid numbers on the dock plants declined to zero by June 25.

Overwintering of M. persicae in glasshouses

Occasional searches for aphids were made in twelve glasshouses in Edinburgh, Musselburgh, and Bush (Midlothian) during the winter and spring of 1968-69 and 1969-1970. Ornamental plants and other crops found infested with aphids in the glasshouses included species of Solanum, Lilium, Hydrangea Nicotiana, Chrysanthemums and radish carrot. Plants in five of the glasshouses were infested with M. persicae.

Overwintering of Macrosiphum euphorbiae

During the 1968-69 winter, a single dock plant wedged between a stone and the base of a glasshouse at Newington was found infested with two adults and one nymph of Macrosiphum euphorbiae. In March the aphids disappeared

* This site is described in detail on Page 52

TABLE 3

Estimated number of Myzus persicae on IO Dock plants during the winters of 1968-69, 1969-70 and 1970-71

Count	Newington No. of aphids	Count	Musselburgh No. of aphids
27/ 1/69	14.0	6/ 3/69	23.0
3/ 3/69	39.0	18/ 4/69	35.0
23/3/69	8.0	2/ 5/69	I08.0
1/ 4/69	28.0	16/ 5/69	268.0
23/ 4/69	3.0	24/ 5/69	202.0 (2.0 al.)
29/4 /69	114.0 (1.0 al.)	30/ 5/69	134.0 (4.0 al.)
		6/ 6/69	74.0 (4.0 al.)
27/11/69	70.0 (5.0 al.)	13/ 6/69	137.5
24/12/69	25.0	20/ 6/69	0
21/ 1/70	23.3	Newington and Lasswade	
30/ 1/70	I0.0	27/11/70	47.1 (2.9 al.)
24/ 2/70	8.3	18/12/70	28.6
17/ 3/70	65.0	7/ 1/70	21.4
8/ 4/70	53.3	22/ 1/71	17.1
5/ 5/70	30.0	5/ 2/71	15.7
19/ 5/70	23.3	26/ 2/71	21.4
1/ 6/70	13.3	12/ 3/71	24.3
8/ 6/70	95.0 (3.3 al.)	26/ 3/71	38.6
15/ 6/70	70.0 (3.3 al.)	15/ 4/71	38.6
22/ 6/70	0	30/ 4/71	52.9
		14/ 5/71	I05.7 (2.9 al.)
		28/ 5/71	80.0 (1.4 al.)
		11/ 6/71	70.0 (4.3 al.)
		25/ 6/71	0

al. = alatae

from the plant after all stages of growth were counted.

In the glasshouse, M. euphorbiae was found mainly on Lilium species during the winter.

Discussion on overwintering

In the Edinburgh area in eastern Scotland it seems that M. persicae has an anholocyclic life cycle on weeds, especially on dock plants, but rarely on brassica crops. Plants in glasshouses can also provide over-wintering sites for M. persicae and M. euphorbiae. If the host plants are able to withstand the winter temperatures, the peach-potato aphid can survive the outdoor conditions of the winter. During the five coldest months, temperatures are often at 0°C or below for short periods (Table 4). However, in the protected areas in the habitat, under leaves or under shelters, the temperatures may be higher than that of the air, even if the leaves are covered with snow or frost. The cold probably has little immediate effect on the aphids. Solomon (1967) showed that active M. persicae can undercool and survive a temperature of -20°C.

M. persicae hibernated during the winter on the undersurfaces of the older dock leaves, which often defoliated. However, sometimes the aphids were found on the stems and in the partially opened terminal leaves and movement up the plant and reproduction probably took place during the warm periods. M. persicae kept at a temperature of 1-2°C were able to reproduce. This behaviour helped some of the aphids to survive. Another of the survival factors is the winter hardiness of dock plants which resist break-down of the leaf cells. Dock plants were noted to have fresh succulent leaves in the winter while brassica leaves withered or became flabby.

TABLE 4

Monthly temperatures (°C) at Edinburgh* - November to March

Month	Year	Min.	Max.	Ave.	0° or below +
November	1968	-2.8	18.3	7.0	5
December	1968	-3.3	9.4	3.0	14
January	1969	-1.7	12.8	4.5	6
February	1969	-6.7	7.8	0.6	19
March	1969	-1.1	11.7	2.2	21
November	1969	-5.6	15.6	4.3	12
December	1969	-5.0	I0.6	3.3	15
January	1970	-6.7	11.1	3.0	I0
February	1970	-5.0	8.3	1.9	16
March	1970	-3.3	12.2	4.1	13
November	1970	-0.6	13.3	6.2	14
December	1970	-1.7	12.2	4.4	4
January	1971	-2.8	13.9	4.4	7
February	1971	-3.6	11.4	5.0	5
March	1971	-2.5	13.3	5.3	3

+ = number of days with minimum temperature of 0°C or below each month.

* = data for the Table were obtained from the Royal Observatory, Edinburgh.

An anholocyclic life cycle appeared to be predominant in south-eastern Scotland. All the 79 alate M. persicae trapped during late spring and early summer of 1969 and 1970 were virginogeniae. This suggested that all the M. persicae migrants overwintered on herbaceous secondary host plants. Fisken (1959) found no fundatrigeniae among the alate M. persicae trapped between spring and the end of July, 1954-56. In England, however, anholocyclic development is accompanied by minor holocycly. Broadbent and Heathcote (1955) found that two out of 238 alate M. persicae trapped during the springs of 1948-55, were fundatrigeniae.

Davies (1934) reported that M. persicae overwintered as the viviparous apterae in large numbers on winter brassicas in North Wales. Savoy cabbage with wrinkled leaves provided particularly favourable shelter for the aphids. Again, in North Wales, Jacob (1941) confirmed Davies' work and noted that leaf type was important to the survival of the overwintering aphids. Fisken (1959) reported that brassicas were the commonest overwintering host plants in eastern Scotland, particularly in the Edinburgh area with its higher concentration of suitable crops. The present work on spring cabbage, summer cabbage, brussels sprouts and broccoli did not confirm this. It was observed that the numbers of M. persicae on these brassicas began to decline during the November frosts which caused the lower leaves to be flabby. By the end of January the under surfaces of the bottom leaves which supported the aphids, together with some of the middle leaves, were withered. The aphids disappeared from the dead leaves (Tables 1 and 2).

Fisken (1959) counted apterous M. persicae on brassicas, broccoli, and spring cabbage, in January and March respectively. But no aphids were found on the crops until May. He reasoned that since apterous aphids were

again found in May, they overwintered on the brassicas, and suggested that his random sampling method did not reveal all the aphids. The present work has shown that M. persicae overwinters successfully on dock plants on headland and alatae can appear in late April or early May. Such early alatae could infest brassica crops in May. Shaw (1955) reported that M. persicae rarely overwinters on brassicas in north-east Scotland. The present work tended to confirm this. However, if leaves of crop varieties which can withstand the winter are grown, M. persicae would probably overwinter successfully on them. One of the reasons why M. persicae were not found on brassicas during winter might be that the varieties grown on the farms did not have all the required overwintering host plant characteristics - low growth habits, wrinkled leaves and winter hardiness. The last requirement at least was probably lacking.

Docks growing on waste land were also found to support M. persicae during the winter. Creeping buttercup, Ranunculus repens, like Matricaria species and dandelion, were occasionally found during the winter with M. persicae on them. Further work is needed on the importance of weeds as overwintering hosts for M. persicae.

It was observed that in protected environs M. euphorbiae could overwinter on outdoor plants.

SEASONAL HISTORIES OF APHIDS ON BRUSSELS SPROUT CROP

Theobold (1926) described the structures and life histories of Myzus persicae and Macrosiphum euphorbiae and both aphids are considered primarily as vectors of potato virus diseases.

M. persicae and M. euphorbiae were the important aphids found on brussels sprouts during the study in the Edinburgh area. They appeared

to be the commonest aphids on brassicas in Scotland (Shaw, 1955; Fisken, 1959) while Brevicoryne brassicae and to a lesser extent M. persicae infested brassicas in England (Barnes, 1931; George, 1957; Smith, 1969). During the whole study period, nine mummified aphids of B. brassicae were found at Newington, on November 26th 1968, and four living ones on October 19th, 1970. At Lasswade, only three individuals were found, on one date in October, 1970.

The alate M. persicae first appeared on the brussels sprout crops during mid-June and early July (Figures 8 and 9). p59 These migrants were small in number and usually reproduced parthenogenetic viviparous progeny. Some of the nymphs produced by this first generation of apterae were alatae which spread actively among the crop and the weeds and reproduced to increase the aphid population. M. persicae were most abundant during August and September. A decline in early October was followed by a further increase, but in November the aphid numbers declined again and by mid-January only isolated individuals of the apterae could be found, (Figures 10c, 11c, and 12c). No M. persicae were found on the brussels sprout crop in February, but dock weeds on headlands were infested with a few apterae during the winter. The complete disappearance of the aphids was probably due to the cold winter and the withering of crop leaves resulting in shortage of food and shelter.

M. euphorbiae appeared on the brussels sprout crops at the same time as M. persicae and rapidly increased in number to a peak at about mid-August. The numbers then declined to zero by early September.

MOVEMENT OF APHIDS AND DISTRIBUTION ON BRUSSELS SPROUTS

Myzus persicae could move from plant to plant by walking or flying, but dispersal by flight is essential for the survival, spread and build-up of the populations since most of the host plants are annuals.

The flight activities of M. persicae and M. euphorbiae in the brussels sprout crops were studied during the two years 1969 and 1970, at both Newington and Lasswade by means of water traps (Moericke, 1951).

Figures 8 and 9 show the levels of flight activity over the brussels sprout crops. The first alate M. persicae was trapped on June 16th in 1969 and on June 10th in 1970. During mid-August 1969 at both sites the flight numbers of both species of aphids increased in frequency to a peak and then declined by the end of the month. Later, in October, however, the flight magnitude of only M. persicae increased again and the cold weather in November probably reduced activity then. The average maximum temperatures for November in each of the two years were 6.3°C and 8.3°C. At 15.5°C flight of Aphis fabae is inhibited (Johnson, 1969). Dry and Taylor (1970) also found that none of the five species of aphids studied took flight below 14°C.

The first winged adult M. euphorbiae appeared in July and the numbers reached a peak in August, but the whole alate population disappeared by early September.

The data for both sites in 1970 (Figure 9) showed low fluctuating numbers of the alate M. persicae, but the trend of flight activity was similar to that of the previous year, except that at Lasswade the activity ended earlier in September due to the complete decline to zero of the whole aphid population at that time. Since no winged adult M. persicae

were trapped subsequently it is unlikely that mass aphid immigration occurred in the crop.

M. euphorbiae exhibited similar trends at both sites in both years. The actual numbers of M. persicae and M. euphorbiae trapped are considered later. The number of alate 4th instar nymphs counted in one week on a plant may give an indication of the number of alate adults which may be expected to occur on that plant the following week. Using this method estimates were made at Lasswade and Newington during 1969 and 1970, and Table 5 gives a summary of the relationships between these estimates and the number of alate M. persicae which remained to be counted on the brussels sprout plants. It also shows that comparatively few of the total number of alatae produced remained on the plant for any length of time. Johnson and Taylor (1957) found Aphis fabae to take flight immediately they are flight matured, and usually the peak flight period was in the morning. At Lasswade, 10.6% and 22.0% of the alatae produced in 1969 and 1970 respectively remained on the crop, while the corresponding figures at Newington were 6.5% and 12.8%.

It appeared that movement of the apterous aphids was limited. At both sites, occasionally aphids were observed moving to plants across touching leaves, i.e. leaf bridges were formed between weeds and brussels sprouts or among the sprouts, but movement up the stem was seldom observed. The peach-potato aphids were mostly found on the under surface of the lower leaves of the brussels sprouts. The senescent leaves usually defoliated with considerable numbers of aphids on them and it was determined that the aphids could walk across the soil to other plants.

During August, 1970, a number of circular plastic "barriers", (diameter, 22 cm., height 5cm.) were smeared inside with Stictite, and ten

of the "barriers" were placed firmly in the ground beneath brussels sprouts where the senescent leaves had fallen off. Aphids on the leaves were counted and recorded and the leaves were placed in the middle of the circular "barrier". Recording continued until all the aphids disappeared. Of the total of 351 aphids counted on the ten leaves only 9 adults were caught in the Stictite; the rest presumably died. Movement by apterae on the soil seemed less significant. It was observed that while the senescent leaves were on the ground the aphids stayed only at the succulent parts of leaves. They apparently moved away from the dried up parts. In the field, aphid infested leaves which defoliated and fell on host weeds were likely to be infested with the aphids.

M. persicae and M. euphorbiae showed preference for the under side of the extreme lower leaves of brussels sprout and cabbage plants. During the sampling periods of the two years, 1969 and 1970, no aphids were found reproducing on the upper surface of the brussel sprouts, except on leaves curved in or upside down. Upper surfaces of leaves touching under surfaces of other leaves were also occasionally found to be infested with aphids.

On the brussels sprouts overcrowding of the peach-potato aphids was not observed, and they rarely stayed in clusters on the leaves. The nymphs moved away from their mother and distributed themselves fairly uniformly. Again, it was observed that M. persicae tended to orientate themselves along the veins of the leaf.

TABLE 5

Relative numbers of alate Myzus persicae which remained on one brussels sprout plant.

Month	Lasswade				Newington			
	1969		1970		1969		1970	
	1	2	1	2	1	2	1	2
July	53.8	1.3	17.4	21.3	64.7	3.4	63.6	1.1
August	12.9	39.4	27.0	37.8	57.2	22.2	18.9	12.9
Sept.	14.0	30.8	0	4.0	4.0	487.4	4.8	I0.4
Oct.	11.0	82.6	-	-	4.7	280.8	57.2	7.0
Nov.	5.3	54.4	-	-	7.6	329.7	-	-
Total	I0.6	208.5	22.0	63.1	6.5	1123.5	12.8	31.2

1 = percentage of alate adults of alate 4th instars counted the previous week

2 = cumulative mean number of alate 4th instars counted the previous week.

EFFECT OF TEMPERATURE ON THE DEVELOPMENT OF EXPERIMENTAL POPULATIONS OF MYZUS PERSICAE

INTRODUCTION

Temperature is known to be one of the most important factors influencing insect population growth by affecting fecundity, longevity and the rate of development of individuals. The observed rate of development of insects at any particular time is the result of their physiological characteristics and the effects imposed by environmental factors such as temperature on these innate capacities for increase. Experiments were therefore set up to determine how temperature might affect Myzus persicae populations in the field.

The developmental rate, reproductive potential amd longevity of M. persicae have been studied in different parts of the world but with variable results (Weed, 1927; Fenjves, 1945; Lal, 1950; Barlow, 1962). To study the local population dynamics of the aphid it is therefore necessary to obtain similar data with local strains of M. persicae.

MATERIALS AND METHODS

In all the experiments, the viviparous parthenogenetic aphids were kept under artificial daylight at six controlled temperatures of 5°, 10°, 15°, 20°, 25°, and 30° C. These comditions were obtained by using Gallenkamp cooled incubators fitted with one Phillips 8-watt fluorescent light. The lights were connected to a Londex Rotaset (time switch) and a 16-hour photoperiod was simulated. The incubator has a built-in dial thermometer attached to the cabinet door, but the temperature in the incubator was constantly checked with a mercury-in-glass thermometer, scale -10° to 110°C, during the experiments.

The aphid populations of M. persicae were the progeny of apterous viviparous parthenogenetic females from colonies reared on brussels sprouts under glasshouse conditions at 20° - 25°C, and approximately 70% relative humidity and with a 16-hour photoperiod. The plants were grown in plastic pots in John Innes Potting Compost No.3.

On each of five leaves, about ten adult aphids were kept and each leaf petiole was inserted in a 2.5 cm. plastic vial which was filled with water and plugged with cotton wool. The leaves were kept at the temperature and humidity at which the nymphs were to be reared and the parent aphids were allowed to reproduce for 12 hours. But nymphs reared at 5°C were reproduced at 10°C. The parent aphids were removed from the leaves with a fine camel hair brush.

Johnson & Birks (1960), Hughes (1963) and Hughes & Woolcock (1965) successfully reared various aphids including M. persicae on leaf discs floated on water of culture solutions. The present method is a modification of aphid rearing on leaf discs. Each young nymph was reared on brussels sprout leaf disc in the apparatus described below (Plate V). Two moist 9 cm. filter papers were placed in a 9.3 cm. plastic petri dish. A circular flat plastic sheet with four holes of 2.7 cm. diameter each fitted the petri dish. This was placed on the filter paper. The holes in the sheet held the four plastic tubes (diameter 2.5 cm.; height 1.7 cm.) loosely in position. Perfectly fitting discs were cut from fresh turgid leaves of brussels sprouts with 2.5 cm. diameter leaf disc cutter (Figure 1) and inserted in the tubes. The young nymphs were each carefully placed on one disc and covered with blind rings with nylon organdie tops. 72 nymphs were used at each particular temperature. Three of the above described

Plate V. Apparatus for rearing Myzus persicae on leaf discs.

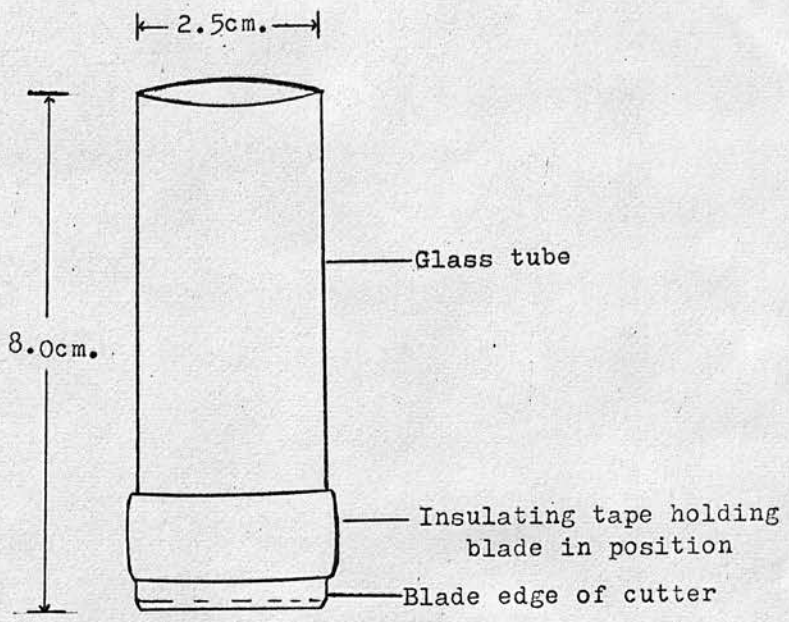

Fig. 1. Diagram of leaf-cutter in aphid studies.

sets were placed on inverted petri dishes in a round transparent plastic container (diameter 23.0 cm.; height 8.5 cm.). A saturated solution of sodium chloride was poured into the container to a height of 1.0 cm. to maintain a relative humidity of 75-80%. The edge was then smeared with soft paraffin and covered with a circular plastic sheet (Solomon, 1952).

The leaf discs were changed every other day from leaves of similar size and age. The brussels sprouts from which the leaves were collected were grown in the glasshouse under conditions described above. The aphids were checked every 12 hours until the first young were reproduced and then they were inspected every 24 hours. Nymphal development, reproductive potential and mortality were determined.

Some aphids were lost or killed accidentally and were not recorded.

The 24 hour inspection period avoided unnecessary disturbance of the experimental aphids. Twice a day handling would probably have increased the mortality rate of the aphids, (Sylvester, 1954).

Leaf discs were used to make space available in the cabinet for more experimental aphids and to standardize the nutrition and physiology of the host plant, as these factors could influence rates of development and fecundity of aphids (Kennedy & Booth, 1951; Way & Murdie, 1965). The intensity of lighting (350 lumens) within the incubator might not be enough for whole plants but was sufficient for aphid rearing. Lees (1959) successfully reared the aphid Megoura viciae Buckton under light intensity of 50-100 lumens.

Under normal working conditions the relative humidity of the incubator was very low for the experimental work; and to use whole or single leaves would mean raising the relative humidity in the incubator. Earlier

observations in the present work showed that this led to frequent ice forming which affected the efficiency of the incubator, and the necessary defrosting disturbed the aphids. The leaf discs kept standard nutrient for the aphids, giving a more uniform nutrient level for the different experiments than if whole plants grown in the soil were used.

However, the rearing of the aphids in isolation might have reduced the developmental rate, suppressed the development of winged forms, (White, 1968), or decreased reproductive stimulation due to absence of the same species (Way, 1968).

RESULTS

1. Nymphal period

Table 6, Appendix 6, and Figure 2, show the lengths of the nymphal period of M. persicae at various constant temperatures, between 5° and 30°C. The period ranged from a mean of 5.4 ± 0.13 days at 25°C to 43.9 ± 0.72 days at 5°C. The mean of 6.5 ± 0.13 days at 30°C was not significantly greater than at 25°C.

All the aphids studied at the various temperatures went through four instars. The mean of the instar periods indicated that the fourth instar tended to require the longest time at each particular temperature. (Table 6, Appendix 6.).

The developmental threshold was estimated graphically using the developmental rate - temperature curve. The method assumes that the relationship between development and temperature follows an equilateral hyperbola ($xy = c$); the relationship of developmental rate (1/time) with temperature is therefore linear, (Bodenheimer & Swirski, 1957). The temperature, below which no development occurs, is determined by

TABLE 6

The mean duration of development stages (± SE) of Myzus persicae in days at various constant temperatures (Relative humidity 75-80%)

Temp °C	1st Inst.	2nd Inst.	3rd Inst.	4th Inst.	Nymphal period
5	I0.9±0.44	I0.1±0.27	I0.9±0.24	11.9±0.25	43.9±0.72
I0	4.6±0.13	5.3±0.14	5.6±0.14	6.9±0.08	21.3±0.33
* I0	4.3±0.12	5.7±0.25	7.2±0.72	8.9±0.43	26.1±1.10
15	2.8±0.08	2.6±0.07	2.8±0.09	3.4±0.I0	11.6±0.22
* 15	3.0±0.08	2.8±0.07	3.2±0.12	5.6±0.09	14.7±0.19
20	1.7±0.06	1.6±0.04	1.8±0.07	2.2±0.04	7.5 ± 0.14
* 20	1.8±0.13	1.7±0.19	1.8±0.82	2.8±0.24	9.2±0.25
25	1.3±0.05	1.2±0.05	1.4±0.52	1.6±0.05	5.4±0.13
30	1.2±0.04	1.2±0.05	1.5±0.08	2.2±0.18	5.6±0.13

* = alatae

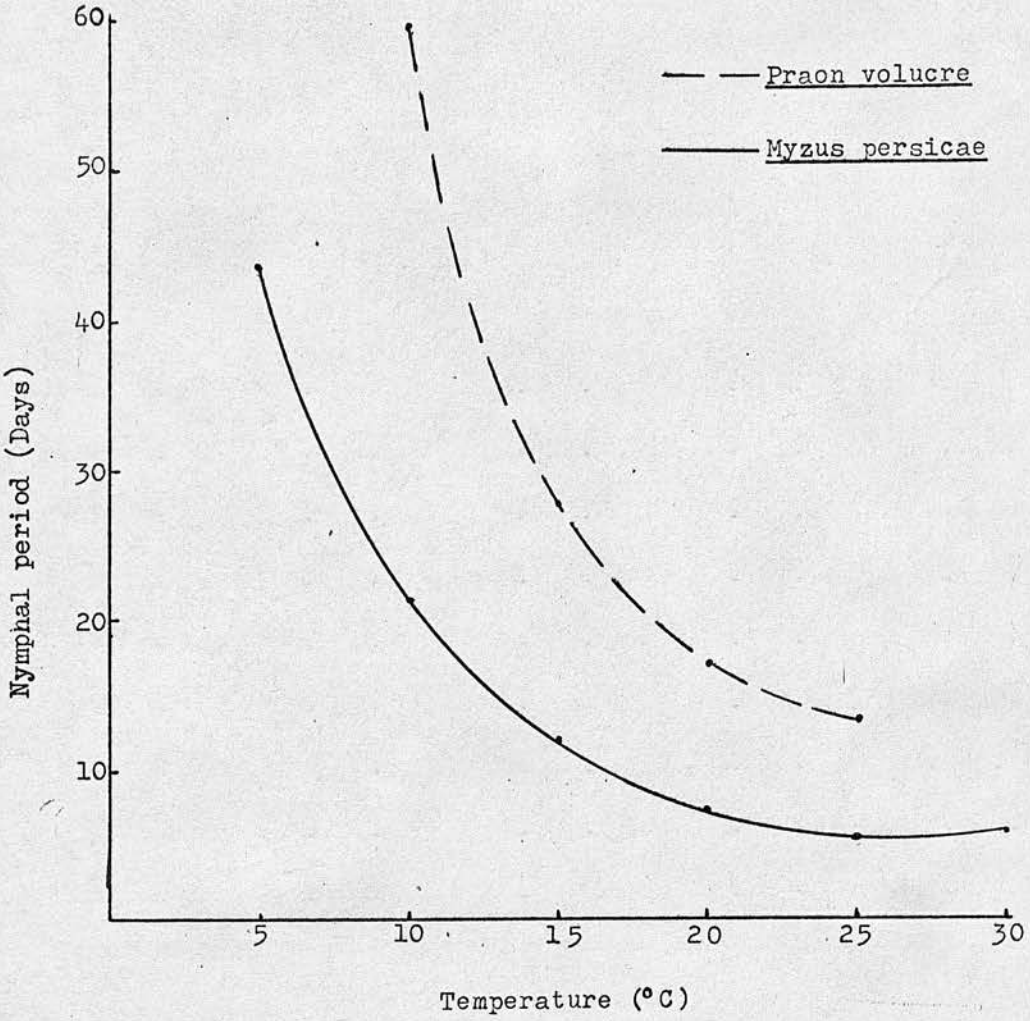

Fig. 2. Effects of different constant temperatures on the duration nymphal development of Myzus persicae and Praon volucre (Relative humidity 75-80%)

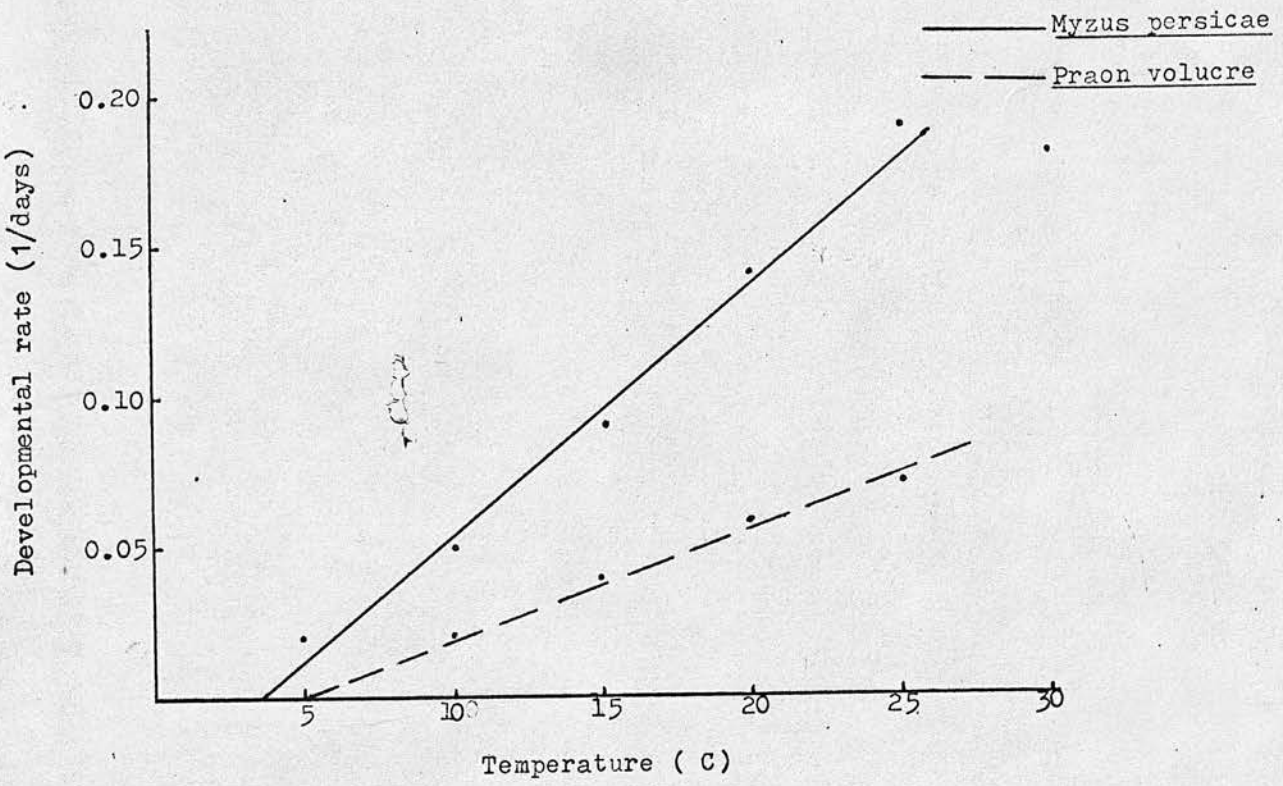

Fig. 3. Effects of different constant temperatures on nymphal development of Myzus persicae and Praon volucre (Relative humidity 75-80%)

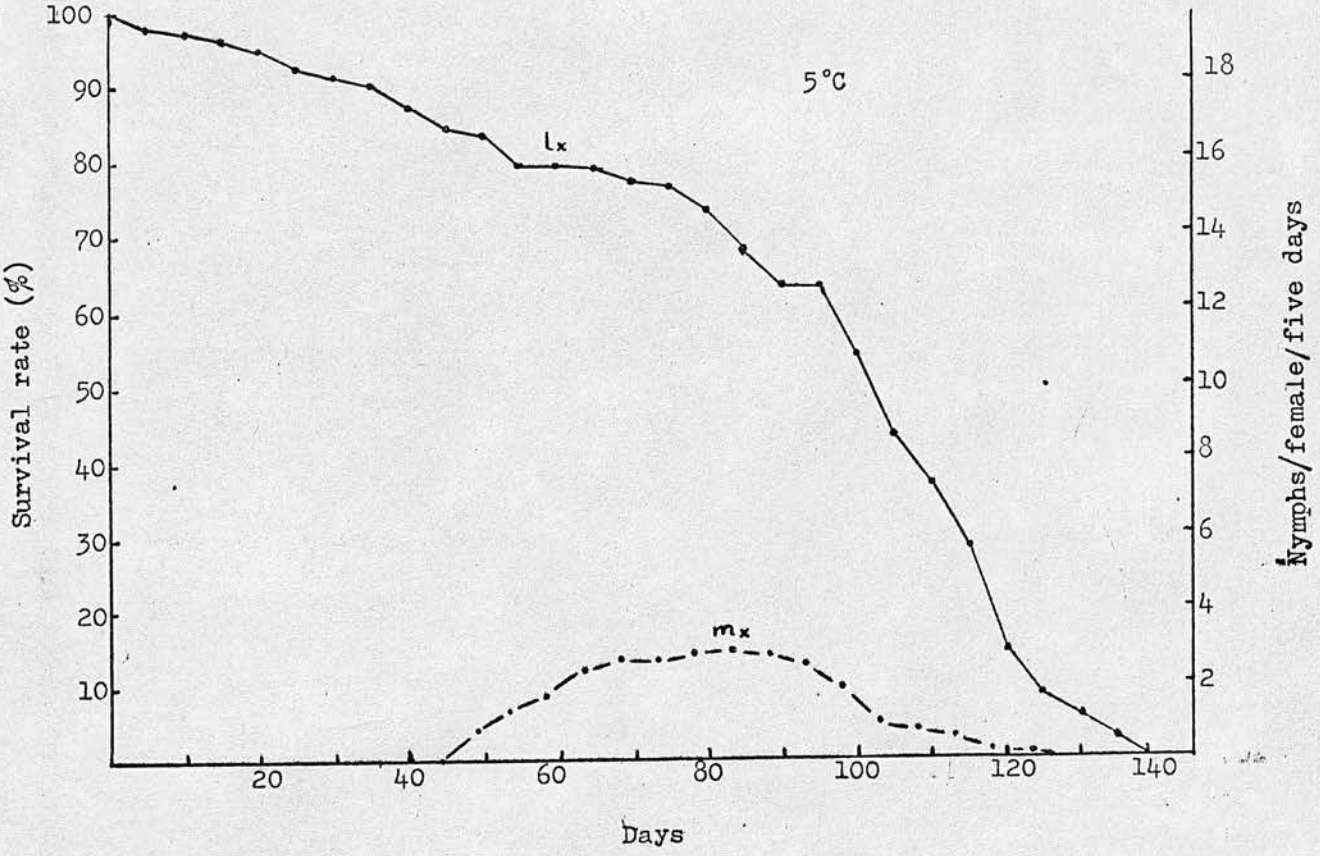

Fig. 4. Age-specific survival and fecundity rates of Myzus persicae reared on on brussels sprouts at constant temperature of 5°C

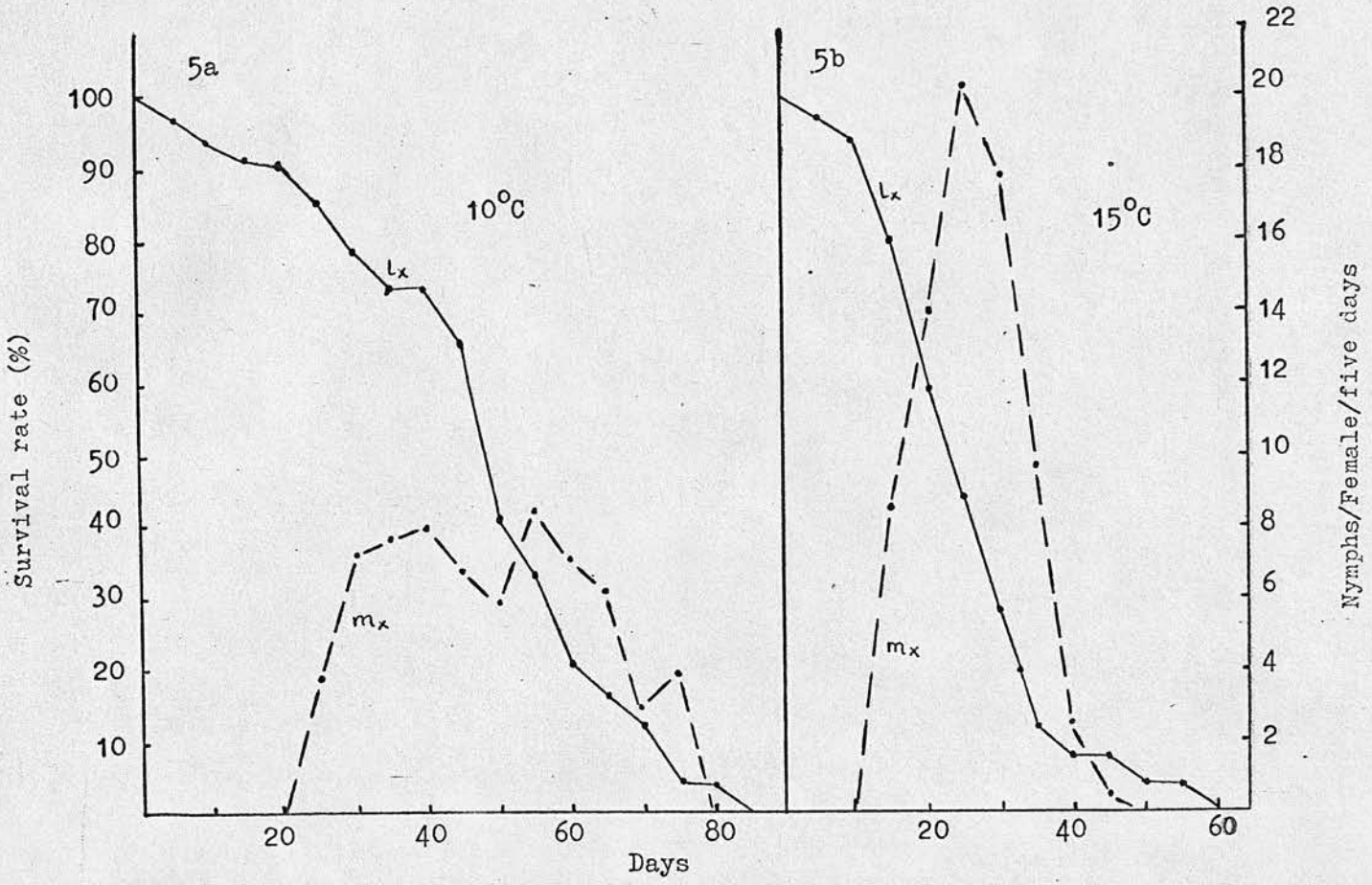

Fig. 5. Age-specific survival and fecundity rates of Myzus persicae reared on brussels sprouts at constant temperatures of 10°C and 15°C.

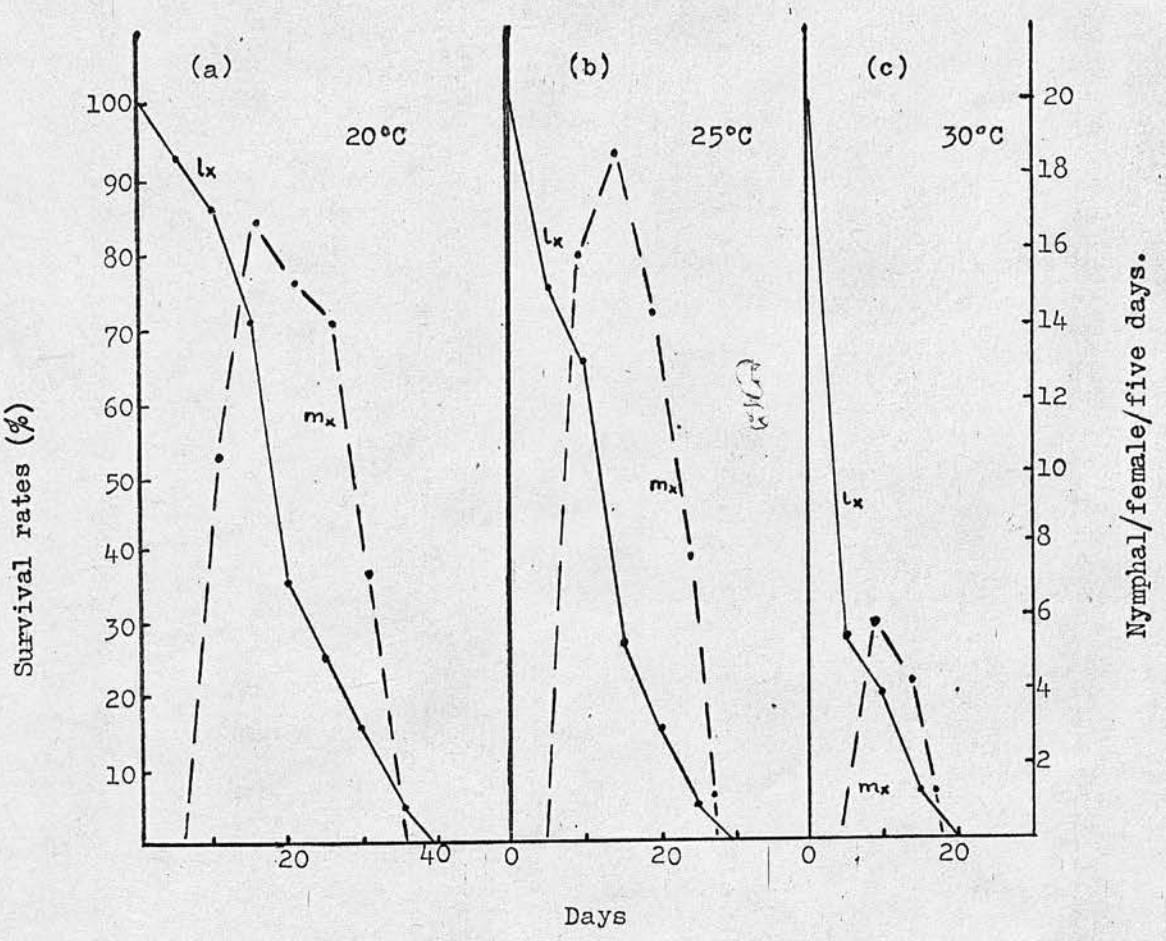

Fig. 6. Age-specific survival and fecundity rates of Myzus persicae reared on brussels sprouts at constant temperatures of 20°, 25° and 30°C.

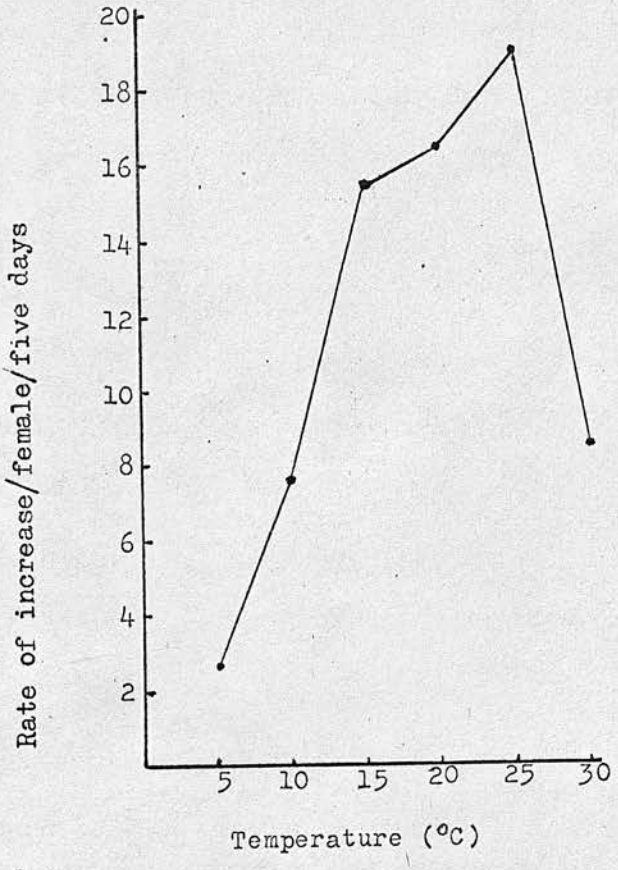

Fig. 7. Effect of different constant temperatures on fecundity rates of Myzus persicae

extrapolating the regression line of rate of development on temperature back to intercept it on the temperature axis. Figure 3 shows the regression line for nymphal development at constant temperatures of 5°, 10°, 15°, 20°, and 25°C. The threshold temperature was approximately 3.5°C. This is not the exact value since, like most other insects, the developmental period - temperature curve is not a true equilateral hyperbola (Bodenheimer & Swirski, 1958). In the present work, the developmental rate at 30°C was excluded from the regression line determination because of extreme divergence.

The effect of constant temperatures on the pre-reproductive period - the length of time from the final moult to the deposition of the first nymph - is shown in Appendix 6. The highest mean duration of the pre-reproductive period was at 5 °C and it decreased with increase in temperature up to 25°C, but at 30°C it started to rise again.

2. Effect of temperature on fecundity

Figures 4, 5, 6, and Appendix 7, show the effects of five different constant temperatures on the age-specific fecundity rates of the apterous M. persicae expressed as m_x (the mean number of nymphs produced per day by a female aged x) (Birch, 1948). All the values of m_x were calculated from a 5-day period pooled data. Reproduction started at 5°C on the 44th day after birth and as the temperature increased this period shortened to the fifth day both at 25°C and 30°C. The peak rates at 5°C and 10°C were reached at about the middle of the reproductive period while the rest occurred at earlier times. At 10°C three peaks occurred at about the 40th, 55th, and 75th days from birth. With increase in temperature, the peak was reached at an earlier age and the subsequent decline was more rapid;

at 30°C the peak was reached within the first four days of reproduction and afterwards declined very rapidly. It was also noticed that from the lowest temperature, 5°C, the peak age-specific fecundity rate increased with rise in temperature, but at 20°C the peak was lower. It was highest at 15°C. However, the fecundity rate started to rise again at 25°C and at 30°C the adverse effects of high temperature upon reproduction were clear, for at this point the peak rate was far below that reached at 25°C.

Effects of the six temperatures on the mean fecundity rate (nymphs per female per five days of reproduction) are illustrated in Figure 7. The optimum temperature was 25°C with the fecundity rate at 19 nymphs per five days of reproduction. There was considerable variation in the number of nymphs reproduced daily by individual aphids and at all six temperatures the range started from zero. The greatest variability among the individuals, (0-10), occurred at 25°C, and the least, (0-3), at 5°C (Appendix 6).

The mean number of nymphs reproduced per female at the various temperatures, shown in Table 7, indicates that the optimum temperature for the peak fecundity rate occurred at 25°C. It was noted from the ranges of the fecundity that there was a considerable amount of variability in the number of nymphs produced by the aphids.

The duration of the reproductive period of M. persicae has an inverse relationship with temperature. The period extended from a mean of 4.4 ± 0.58 at 30°C to 53.2 ± 1.77 days at 5°C, as shown in Appendix 8.

3. Effect of temperature on longevity

Figures 4, 5, and 6, show the survival rates expressing the longevity of M. persicae at the six experimental temperatures. They were obtained by plotting the number of aphids alive at every fifth day as a proportion

of all the aphids which died naturally during the course of the experiments. The curve 1_x gives the probability at birth of a female being alive at age x (1_o = 100%). As temperature rises, longevity decreases, thus the rate of survival also declines. The mean total longevity or generation started from 13.9 ± 1.11 days at 30°C to 110.6 ± 2.22 days at 5°C. The longest generation (birth to death) observed was 133.0 days at the latter temperature and the shortest 11.0 days at the former temperature, (Table 7 and Appendix 8).

Mortality in the immature stages was as follows: 15.3% at 5°C, 9.8% at 10°C, 6.9% at 15°C, 8.6% at 20°C, 25% at 25°C, and 72.7% at 30°C. A higher mortality at 25°C and particularly at 30°C might have been due to the unfavourable effect of the temperature.

At the high temperature of 30°C (Figure 6c) the population declined at a fast rate. Presumably, the rate of metabolism was high enough for ageing to take place in the entire population within a short period. As shown in Figures 5b and 6a, the survival rates at 15°C and 20°C were gradual and then most of the population died within a shorter period, but at 15°C the population lived longer and at 25°C the decline was similar to that of 30°C, although at a slower rate.

DISCUSSION

1. Apterae

Changes in temperature have direct influence on the rate of development of M. persicae. The mean developmental periods,-i.e. the time between birth and production of the first young by females of any population - from 10°C to 25°C varied from 23.3 ± 0.33 days down to 6.2 ± 0.15 days and then rose again to 7.9 ± 0.31 days at 30°C (Appendix 6). These periods agreed closely with

TABLE 7

The mean reproduction (±SE) of Myzus persicae, in days, at various temperatures (Relative humidity 75-80%)

Temp. °C	Nymphs reproduced daily		Total nymphs reproduced/female
	Based on reprod've period	Based on adult longevity	
5	0.52 ± 0.02	0.41 ± 0.01	27.8 ± L.01
I0	1.50 ± 0.05	1.30 ± 0.05	48.4 ± 3.66
*I0	0.75 ± 0.65	0.53 ± 0.47	18.8 ± 4.59
15	3.50 ± 0.26	2.80 ± 0.33	57.7 ± 7.24
*15	1.60 ± 0.13	1.40 ± 0.13	21.0 ± 2.75
20	3.30 ± 1.88	3.20 ± 0.20	55.0 ± 4.88
*20	2.80 ± 0.56	2.40 ± 0.62	50.3 ± 5.36
25	3.80 ± 0.23	3.50 ± 0.25	53.9 ± 3.58
30	1.70 ± 0.19	0.90 ± 0.13	7.5 ± 0.64

* = alatae

TABLE 8

The mean longevity (± SE) of Myzus persicae, in days, at various constant temperatures (Relative humidity 75-80%)

Temp. °C	Adult longevity	Total longevity
5	67.2 ± 2.47	110.6 ± 2.22
10	35.8 ± 2.69	58.0 ± 2.89
*10	36.9 ± 10.66	62.8 ± 10.38
15	20.1 ± 4.44	30.2 ± 4.22
*15	21.2 ± 2.28	32.8 ± 2.24
20	17.0 ± 1.44	25.0 ± 1.51
*20	20.7 ± 6.25	31.0 ± 4.24
25	15.6 ± 1.63	21.2 ± 1.38
30	8.2 ± 0.20	13.9 ± 1.11

* = alatae

the results obtained by Weed (1927) working with M. persicae in the United States. Fenjves (1945) got similar results with M. persicae in Germany who showed that with a rise in temperature from 9.9°C to 25.°C the mean duration of development fell from 24.5 to 8.0 days. He further calculated the threshold of development to be 4.3°C while that obtained in the present work was about 3.5°C.

Weed (1927) in the United States, Fenjves (1945) in Germany and Barlow (1962) in Canada reared M. persicae on spinach, potatoes, and tobacco. The mean number of progeny produced per day was slightly lower in Scotland. In Barlow's (1962) experiments all the aphid population died at 30°C. Fenjves (1945) observed that temperatures above 28°C were harmful to development. Weed (1927) reared some of the species at 28°C to maturity and obtained a fecundity rate (number of young produced per day of reproduction) of 3.1. Lal (1950) found a similar fecundity rate in India at 30°C, but the result in the present work at the same temperature was lower. Weed (1927) and Barlow (1962) reported reproductive periods and longevities which were longer than those in the present results. The difference may be due to the level of humidities as discussed by Weed (1927). Other factors may have been the differences in host plants and strains of aphids in the various studies.

2. Alatae

Of the original 432 nymphs in the whole set of experiments, only 29 developed into alate adults - 5 alatae at 10°C, 20 at 15°C and 4 at 20°C. The reasons for such low numbers are not known. However, it might have been due to lack of 'crowding effect', that is, the proximity of one aphid to another (Bonnemaison, 1951).

As indicated in Tables 6, 7, and 8, the mean nymphal periods* and the mean total longevity* were longer at the above three temperatures than for the apterae, while the mean total fecundity was lower at the same temperatures. Lal (1951) in India made similar conclusions when working with M. persicae.

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* The statistical significances - mean nymphal periods at 10°C ($P<0.001$), 15°C ($P<0.001$), 20°C ($P<0.001$); mean total longevity at 10°, 15°, and 20°C (not significant at each of the temperatures); mean total fecundity 10°C ($P<0.01$), 15°C ($P<0.001$) and 20°C ($P<0.05$).

SECTION B

POPULATION STUDIES OF APHIDS ON BRUSSELS SPROUTS

METHODS

1. Site

The investigations were carried out under field conditions on experimental plots at Newington on the south eastern outskirts of Edinburgh, and at Lasswade about 13 kilometres (8 miles) away.

Lasswade

The 1969 experimental area measured 13 hectares (32 acres), and was sandy clay loam soil with a pH of 7.7 and it usually carried brassicas. The whole brussels sprout crop (variety Thor F1 hybrid) was directly sown during the first week of April on small ridges of 66 cm. (26 ins.) rows. To control weeds, on May 15th to 20th, the soil was drawn down the ridges. From 28th May to 4th June, the crop was thinned within the rows so that the remaining plants were about 46 cm. (18 ins.) apart. The experimental plot of 200 plants was marked out in this crop and it was about 9 m. x 6 m. (30 ft. x 20 ft.). The plants were numbered consecutively with the numbers on white garden pegs.

The experimental work was repeated at the same two sites for two years with the same number of brussels sprout plants and sampling procedures. In 1970, as in the previous year, the same farming practices were used. Direct sowing of the brussels sprouts, variety Thor F1 hybrid, was carried out during the second week of April. The drawing of soil down the ridges and crop thinning were done during the last and first weeks of May and June respectively.

Newington

In 1969, the experimental area was on a 6 hectare (15 acre) plot of land, with the southern side sheltered by a wall. The soil was loamy with pH of 7.3 and brassica, root and potato crops had often been grown on this land.

The experimental plot of 200 brussels sprout plants (10.0 m. x 9.1 m.) (32.7 ft. x 30.3 ft.) was marked out in the middle of a 1 hectare (3 acre) field of brussels sprouts (variety Dalmar 21). In 1968, this piece of land carried a potato crop.

The brussels sprouts were transplanted on 5th May, 1969, with spacings of 71 cm. x 71 cm. (28 ins. x 28 ins.). During the season, the plot was weeded and the soil stirred once. On 21st May, 1969, the hand hoes were used in weeding the plants and on 10th June the soil was stirred with tractor mounted cultivator, thereby killing the weeds and encouraging crop growth. On the 12th June SAI Hortus 4 fertilizer (10.5,N; 7.5 insoluble P; 10.5,K) was applied by broadcasting. The numbering system of the plants was similar to that of the experimental plot of Lasswade.

In 1970, the field was prepared and the brussels sprouts, variety Dalmar 21, were transplanted on 14th May, with the spacings as for last year (Plate VI). The plot was weeded on the 25th June. In the previous year the site was used for cabbage cultivation.

During the two years of the field investigation, no insecticides were used on any of the experimental plots.

2. Sampling of aphids on the brussels sprouts

During the first seven weeks of 1969 sampling period, fifty plants were sampled per week. Forty plants were sampled weekly on each of the two

Plate VI. Two months old brussels sprouts at Newington - 1970.
Note the two water traps - one in the foreground,
the other behind.

experimental plots at different dates during the remainder of the sampling period. The group of plants to be sampled on each particular week was determined systematically. The plant numbers were arranged thus:

1	2	3	4
5	6	7	8
9	.	.	.

to 200. A group of plants with numbers in each column was sampled weekly, and the group to be sampled during each week was picked at random. After the end of sampling in the fourth week, the group of plants sampled during the first week was sampled again, thus maintaining a systematic order of samples. The systematic arrangement was changed to the following after the seventh week:

1	2	3	4	5
6	7	8	9	10
11	.	.	.	. to 200.

The number of plants sampled per week was reduced from fifty to forty because the amount of work involved was too time-consuming for one person.

During the first seven weeks, all leaves on the fifty plants were sampled but in subsequent weeks, two of the six lower leaves and two from the remainder were sampled at random. As Shaw (1955) discovered in south east Scotland, the usual "three-leaf method" of sampling peach-potato aphids, that is, one upper, middle and lower leaf, might lead to considerable error because of the low densities, especially on the middle and upper leaves.

During sampling the following were counted and recorded carefully:

1. Myzus persicae and Macrosiphum euphorbiae

   Since the counts were done in the field, it was not possible to separate the four nymphal stages. Consequently the nymphs were

arbitarily divided into three groups and the following stages were recorded:

- alate adults
- alate 4th instar nymphs
- apterous viviparae
- advanced apterous nymphs (late 3rd instar to 4th instar)
- medium apterous nymphs (late 2nd instar to early 3rd instar)
- young apterous nymphs (1st instar to early 2nd instar)
- mummies

2. Syrphidae

   eggs

   larvae and pupae

3. Acarina

   Anystis species (predatory mite)

4. Other predators

   Cecidomyiidae

   Neuroptera

   Anthocoridae

Two local farms were chosen to determine any differences in the aphid population changes, as they do occur from place to place under farming conditions. Small units of plots were acquired in order to have absolute control and so avoid disturbances of the ecological system.

Aphids are known to have a high reproductive potential which necessitates frequent sampling time intervals, and the regular visits to the selected plants during the sampling period resulted in the estimation of the aphid population changes rather than the determination of absolute numbers of aphids per plant.

Sampling dates

Newington: Weekly sampling was done from 30:6:69 to 1:12:69, except on the 20:10:69; while in 1970 it began on 29:6:70 and ended on 19:10:70. No sampling took place on 21:9:70 or 12:10:70.

Lasswade: Except on 20:10:69, the 17th week, sampling was carried out from 2:7:69 until 26:11:69. In the following year the weekly sampling started on 1:7:70 and ended on 7:10:70. No sampling was carried out on 23:9:70.

3. Trapping of flying insects with yellow water traps

The yellow water traps consisted of plastic trays (33.0 cm. x 23.0 cm. x 9.0 cm.)(13 ins. x 9 ins. x 4 ins.) with the insides painted with enamel golden yellow (Moerieke, 1951).

The traps were filled to about six-sevenths volume with water containing some drops of formalin (preservative) with detergent. The added detergent reduced the surface tension and the trapped insects were drowned. The traps were supported to a height of 44.5 cm. (17.5 ins.) on metal cans half filled with water to prevent the traps from blowing off.

One trap each was placed about 3.0 m. (10 ft.) to the northern side of the experimental plot and another about the same distance to the south. All insects in the traps were collected weekly and put into 7.5 cm. x 2.5 cm. ((3 ins. x 1 in.) glass tubes and any aphids, syrphids, anthocorids and Neuroptera were sorted out, counted and identified. Of all the aphids, only M. persicae and M. euphorbiae were identified. The traps were refilled with clean solution to a constant level each week.

The weekly samplings were as follows:

Lasswade: From 9:6:69 to 10:11:69 inclusive.

From 10:6:70 to 18:11:70 inclusive.

Newington: From 4:6:69 to 19:11:69 inclusive

From 8:6:70 to 22:11:70 inclusive.

Except for the predatory mites, cecidomyiid larvae, Neuroptera and anthocorids, the mean numbers per plant of the other items recorded were calculated by a computer.

4. Meteorological data

At Lasswade throughout the two seasons temperatures and humidities were measured at about 183 m. (200 yds.) from the experimental plots with thermohygrograph. Thermograph was at Newington for recording the temperature.

Differences between the microclimate of the crops where insects are found and the free air above have been recorded by Broadbent & Hollings (1951), Long (1968), Fye & Benham (1969) and other workers. On a windy day of 1 st. September, 1970, at Lasswade, some measurements of the under surfaces of brussels sprout leaves, where the aphids usually stayed, and the free air in the crop were taken with Startronic Temperature Gauge Model 142. The under surfaces of the leaves were about 1.0°C colder than the free air.

The microclimate temperature of the under surface of the brussels sprout leaves where the aphids stayed was different from that recorded by either the thermograph or the thermohygrograph. However, it was not practically possible to obtain accurate measurements in the field. Nevertheless, temperature fluctuations at both places were the same, therefore the free air measurements could be regarded as a good indication of the conditions of the under surfaces of the brussels sprout leaves.

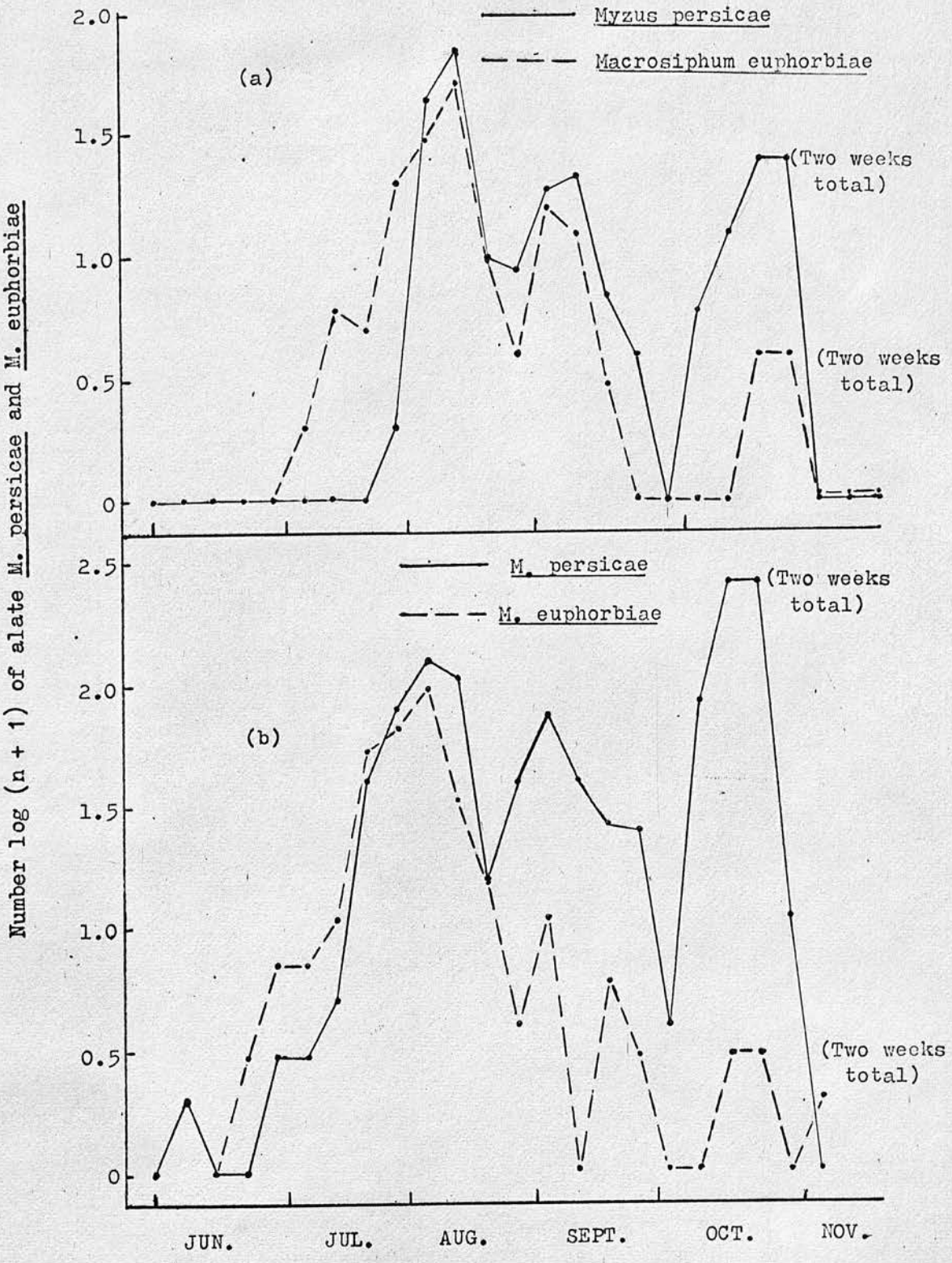

Fig.8. Year 1969. Weekly catches of alate M. persicae and M. euphorbiae in two water traps. (a) Lasswade (b) Newington.

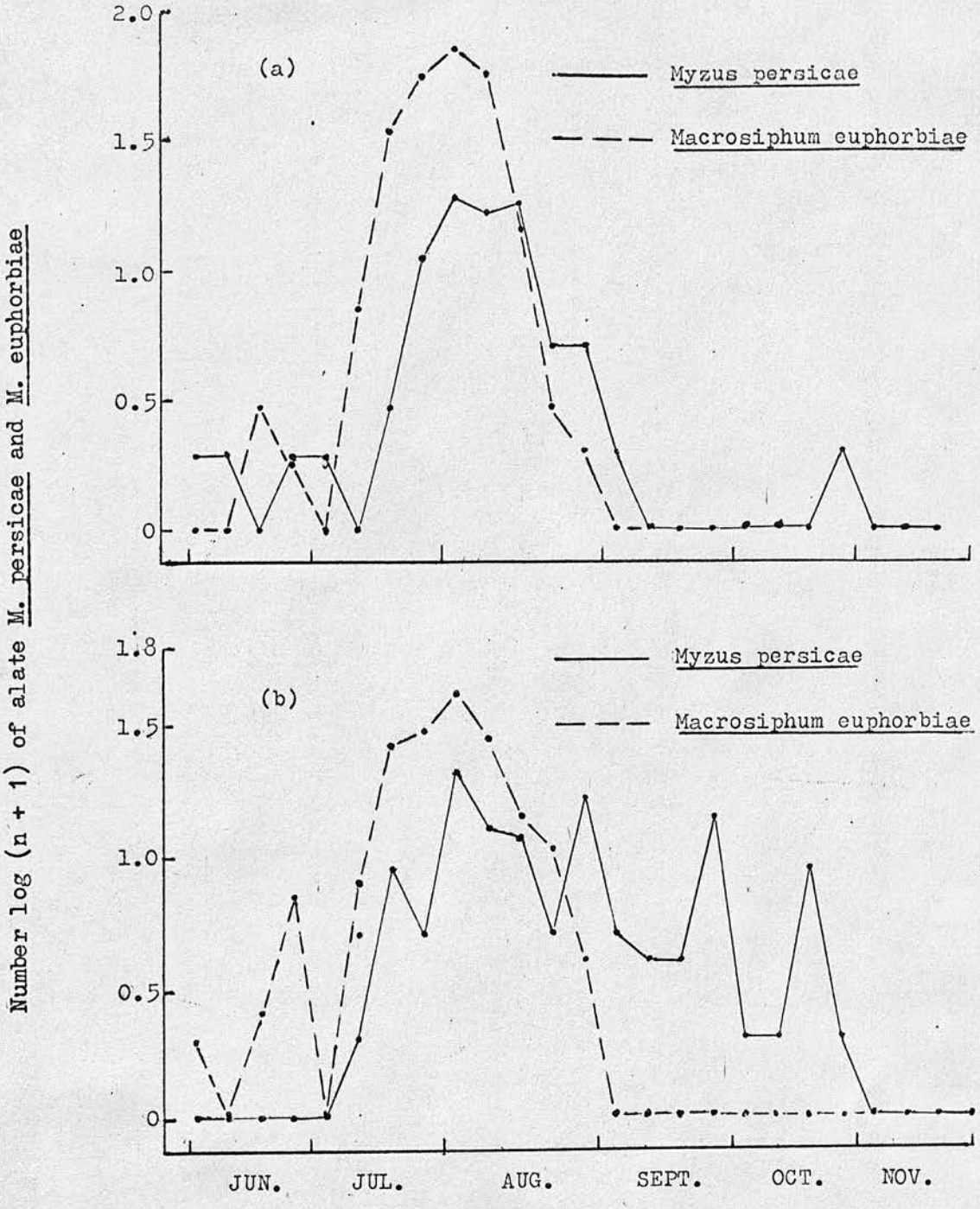

Fig. 9. Year 1970. Weekly catches of alate M. persicae and M. euphorbiae in two water traps. (a) Lasswade (b) Newington.

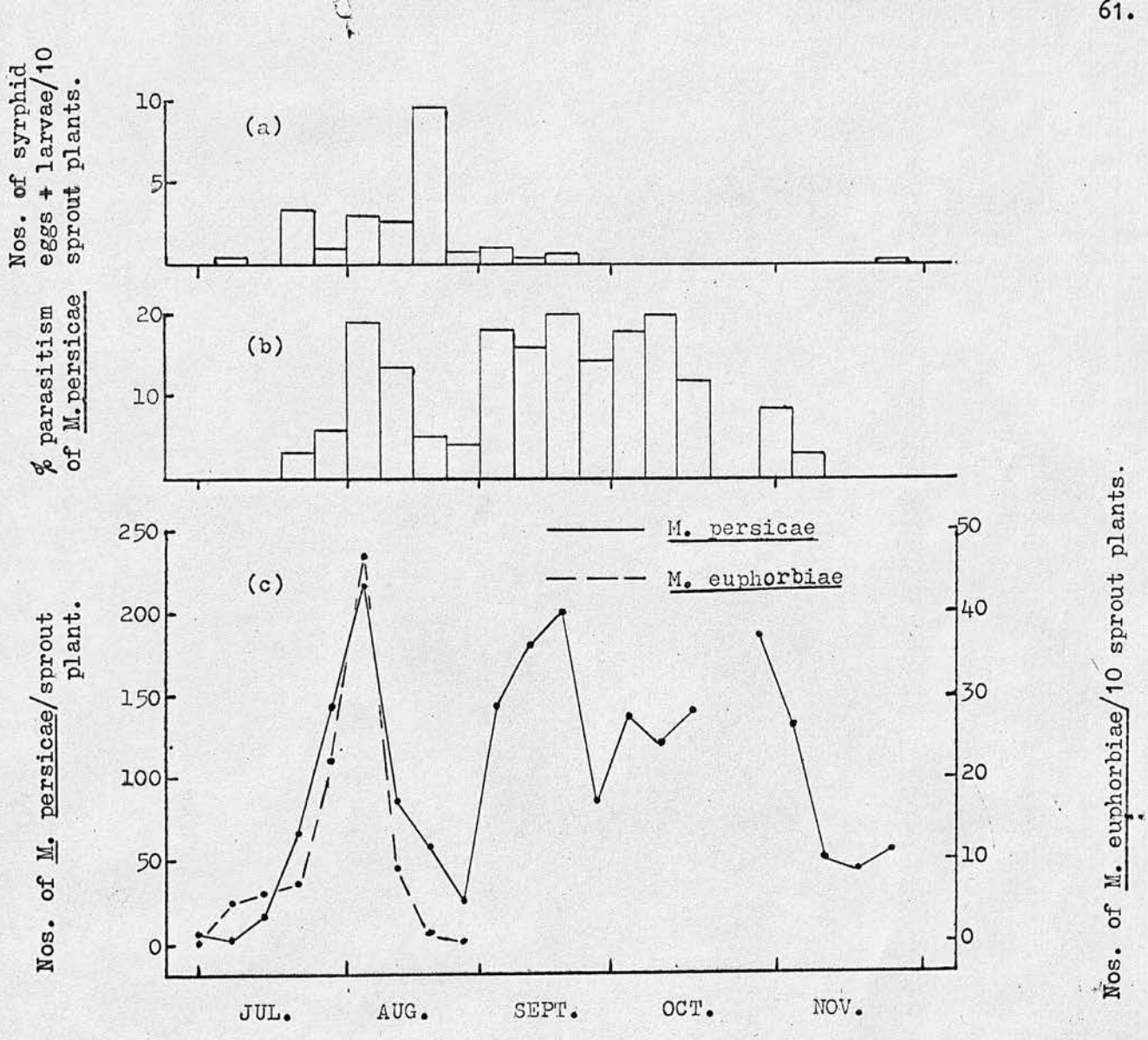

Fig. 10. Year 1969. Changes in Myzus persicae and Macrosiphum euphorbiae populations in relation to the natural enemies at Lasswade

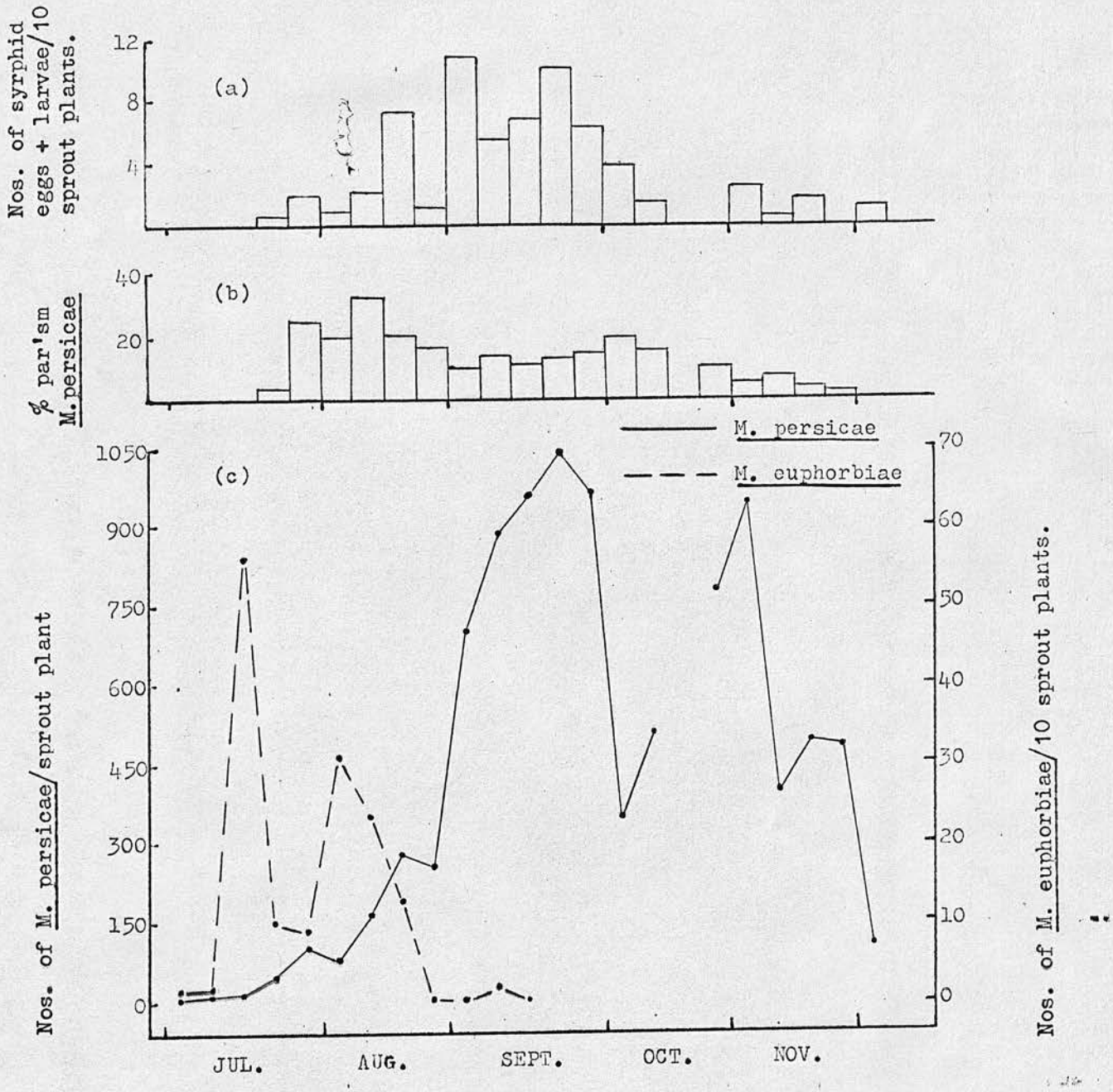

Fig. 11. Year 1969. Changes in Myzus persicae and Macrosiphum euphorbiae populations in relation to the natural enemies at Newington.

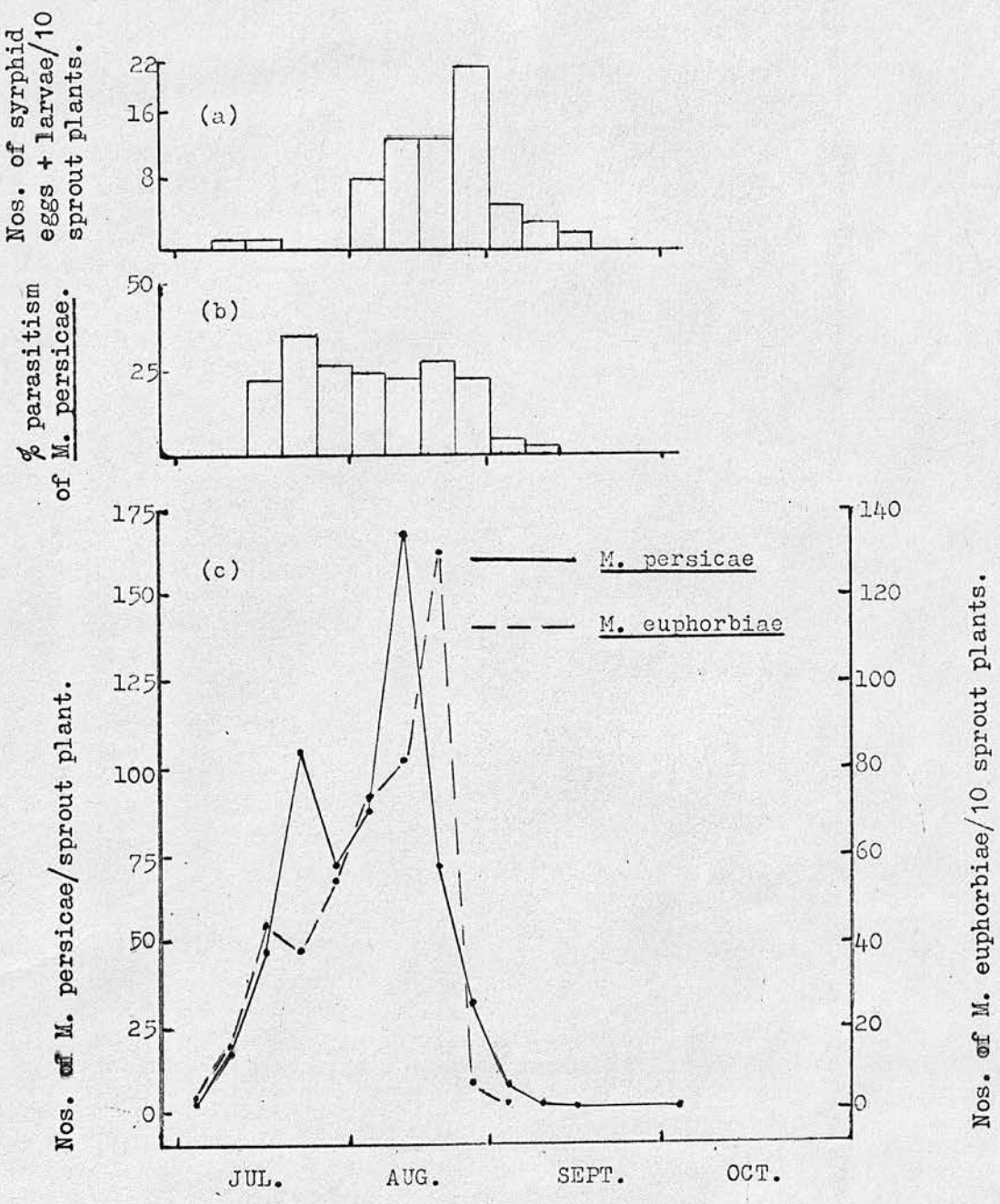

Fig. 12. Year 1970. Changes in Myzus persicae and Macrosiphum euphorbiae populations in relation to the naturnal enemies at Lasswade.

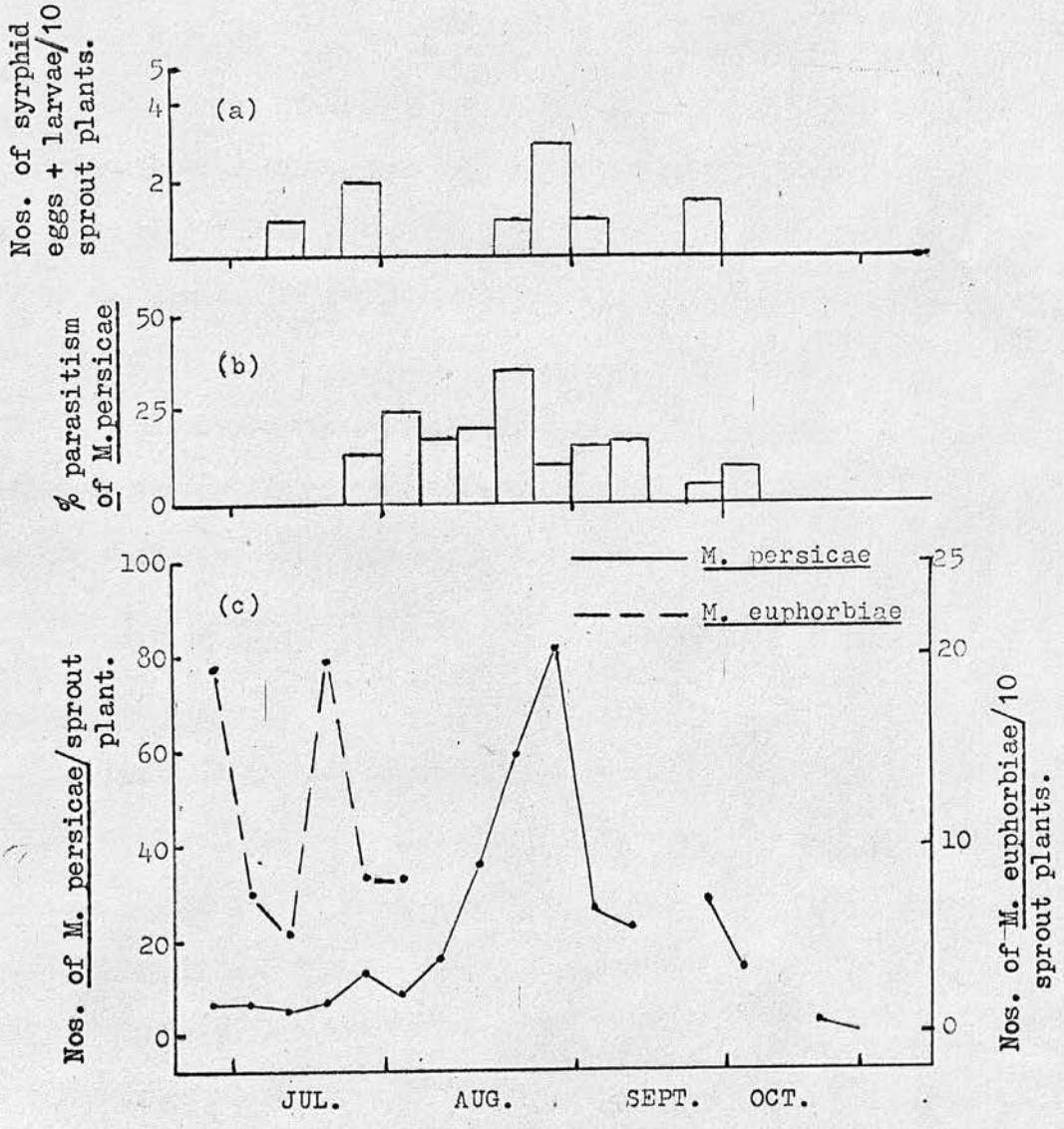

Fig. 13. Year 1970. Changes in Myzus persicae and Macrosiphum euphorbiae populations in relation to the natural enemies at Newington.

RESULTS

Aphid hosts

1. Water trap catches

The total number of aphids caught over the brussels sprout crops during the trapping periods during the two seasons was about 23,780. *M. persicae* and *M. euphorbiae* formed a small proportion of this number and the greater number of the aphids trapped included the *Aphis fabae* group (Appendices 9, 10, 11, and 12).

Table 9 shows the relative proportions of *M. persicae*, *M. euphorbiae*, and other aphids caught at Lasswade and Newington during 1969 and 1970. During the whole investigation period, at both locations, *M. persicae* formed 5.8% of the total aphids caught while *M. euphorbiae* formed 3.6%.

Myzus persicae 1969

At Lasswade, the first aphid was caught during the week ending 30th July, while that at Newington was caught during the week ending 16th June, (Appendices 9, and 10). There was then a sudden increase in numbers at Lasswade followed by a decline during mid-August. The numbers increased slightly at the beginning of September and tailed off again in early October. There was another slight rise in flight activity during October which lasted till the end of the month. Although the first aphid was trapped during mid-June at Newington, it was not until the end of July before sizeable numbers appeared. The flight activity of *M. persicae* from then onwards was similar to that at Lasswade, but the number caught per two traps at any time was higher (Figures 8a and 8b).

TABLE 9

The percentage of alate M.persicae and Macrosiphum euphorbiae of the total aphids trapped over sprout crops at Lasswade and Newington during 1969 and 1970

Aphid	Lasswade				Newington			
	1969		1970		1969		1970	
	Nos/2 traps	%	Nos/2 traps	%	Nos/2 traps	%	Nos/2 traps	%
M. per.	229	12.3	77	5.1	961	11.3	110	0.9
M. euph.	154	8.3	239	5.7	307	3.6	167	1.4
Others	1475	79.4	1204	79.2	7209	85.1	11645	97.7

M. per. = Myzus persicae

M. euph. = Macrosiphum euphorbiae

Macrosiphum euphorbiae 1969.

The first appearance of the alate M. euphorbiae in the brussels sprouts at Lasswade was in early July and the last one was caught about mid-September while the highest catch, 52 per two water traps, occurred in mid-August (Appendix 9 and Figure 8a).

At Newington, the flight activity started at the end of June, about the same time as at Lasswade; and the peak, 95 per two water traps, was reached in early August. The flight activity ended at the same time as at Lasswade (Appendix 10 and Figure 8b).

Myzus persicae 1970

At Lasswade, the flight activity started in the brussels sprout crop during the week ending 10th June. However, few aphids were trapped before the end of July when the number increased slightly. A peak of 18 aphids per two traps was reached in early August and the flight activity persisted at about this level for the greater part of the month. A decline then followed with the last catch in the week ending 9th September (Appendix 11 and Figure 9a).

At Newington the peak of 20 per two water traps, appeared during early August (as at Lasswade) but the flight activity started later in July than at Lasswade, and continued at lower magnitude until the end of October when no more were trapped, (Appendix 12 and Figure 9b).

Macrosiphum euphorbiae 1970

At Lasswade, the first aphid was trapped in mid-June. A peak of 70 aphids per two traps was reached in early August but completely tailed off in early September (Appendix 11 and Figure 9a).

At Newington, the flight activity started during the week ending 8th June and ended on August 31st. The peak of 41 per two water traps was at the end of July (Appendix 12 and Figure 9b).

2. Population on brussels sprouts

Myzus persicae 1969

a) Total population trends

The mean density of the aphids per plant at Lasswade varied from 3.2 ± 1.4 to 218.4 ± 51.3 with an average of 103.5 ± 15.0 during the sampling period, while the corresponding figures for Newington were 2.3 ± 0.6, $1,049.2 \pm 214.6$ and 435.5 ± 77.5.

Seasonal population trends at the two locations studied were almost similar although indices of population density at Newington were about four times as high as those at Lasswade. None of the populations at either location seemed stable. Peak population numbers were reached during early August, mid-September, early October and late October at Lasswade, and during mid-August, late September and early November at Newington. The first two and the fourth peaks occurring at Lasswade were nearly at the same level of abundance, but the third peak was much lower. At Newington, the peaks which occurred in September and early October were of about the same magnitude but higher than the one occurring in August (Appendices 13 and 14, Figure 10c and 11c).

b) Age specific population trends

As illustrated in Figures 14a and 15a, at both Lasswade and Newington, the numbers of young and medium nymphs increased steadily and the first peaks were reached in late July. There was a sharp decline, followed by

an abrupt increase to the highest peak in September. Another peak occurred at the end of October at Lasswade; at Newington there were two peaks, one in early November and the other later in the month.

The seasonal population changes of advanced and alate 4th instar nymphs followed similar patterns to those of the young nymphs at Lasswade and Newington (Figures 14a, b, and 15a, b)

The numbers of the winged and wingless adults (Figures 14b and 15b) increases in September and in early November at both locations. The winged adults counted on the brussels sprouts were usually small as most of them took to flight when fully developed.

c) Age structure

The age structure of M. persicae on the brussels sprouts were estimated for both locations. Of the total populations at Lasswade and Newington, the young nymphs formed 36.6% and 30.6%; medium nymphs 41.6% and 42.4%; advanced nymphs 9.6% and 8.0%; alate 4th instar nymphs 10.0% and 12.2%; apterous adults 7.1% and 6.0%; alate adults 1.0% and 0.8% respectively.

Macrosiphum euphorbiae 1969

The mean estimated density varied from 20 $\pm$ 2.0 to 48.0 $\pm$ 18.0 per ten plants at Lasswade and from 1.0 $\pm$ 1.0 to 57.0 $\pm$ 15.0 per ten plants at Newington. The greatest number of the aphids occurred in early August after a steady increase from early July. A decrease followed and by the end of August the species had completely disappeared at Lasswade. At Newington there were two peaks, mid-July and mid-August, each characterised by an abrupt rise and fall in numbers. The last aphid was found in early September (Appendices 15 and 16. Figures 10c and 11c).

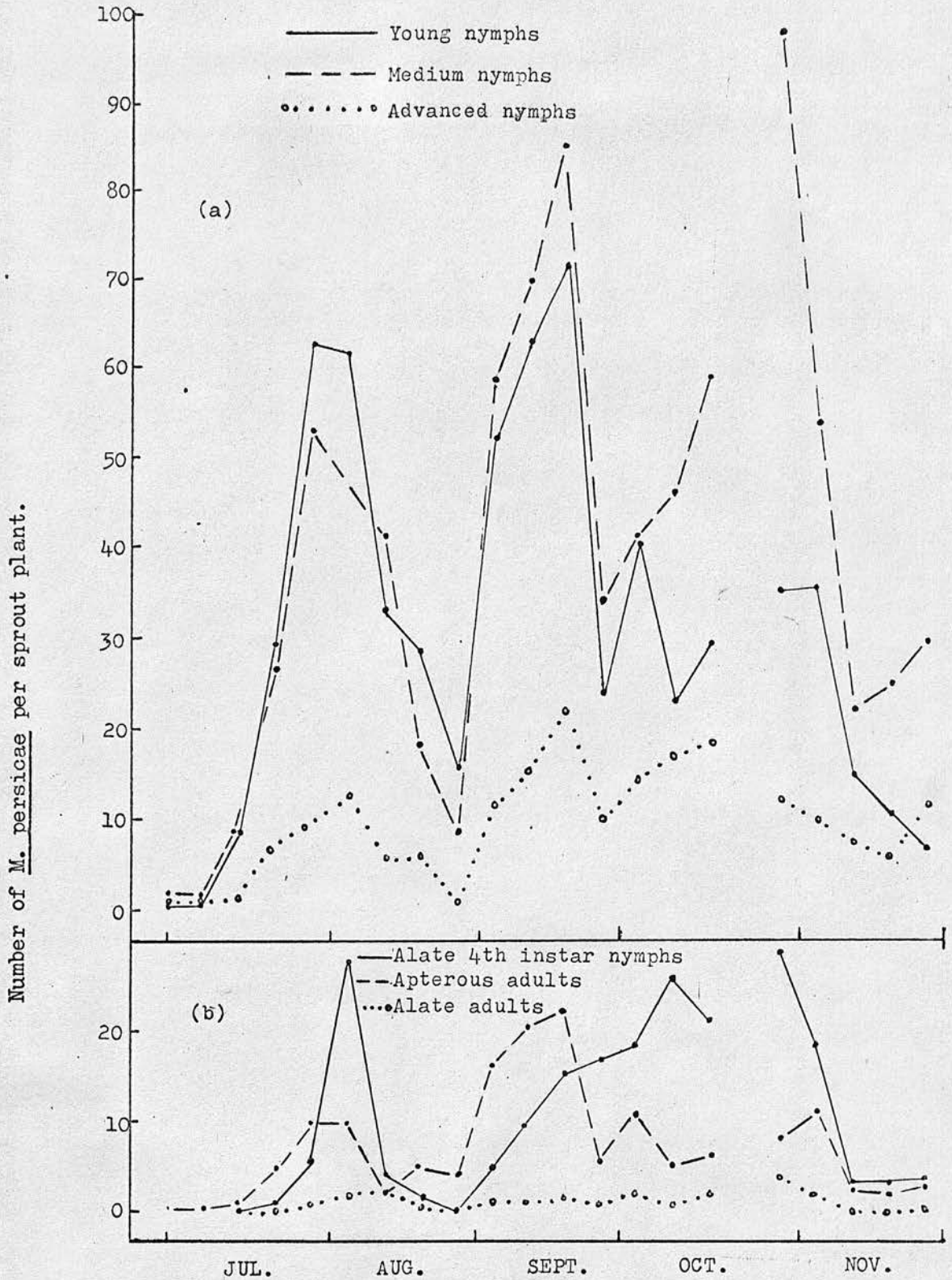

Fig. 14. Year 1969. Age specific population trends of Myzus persicae at Lasswade.

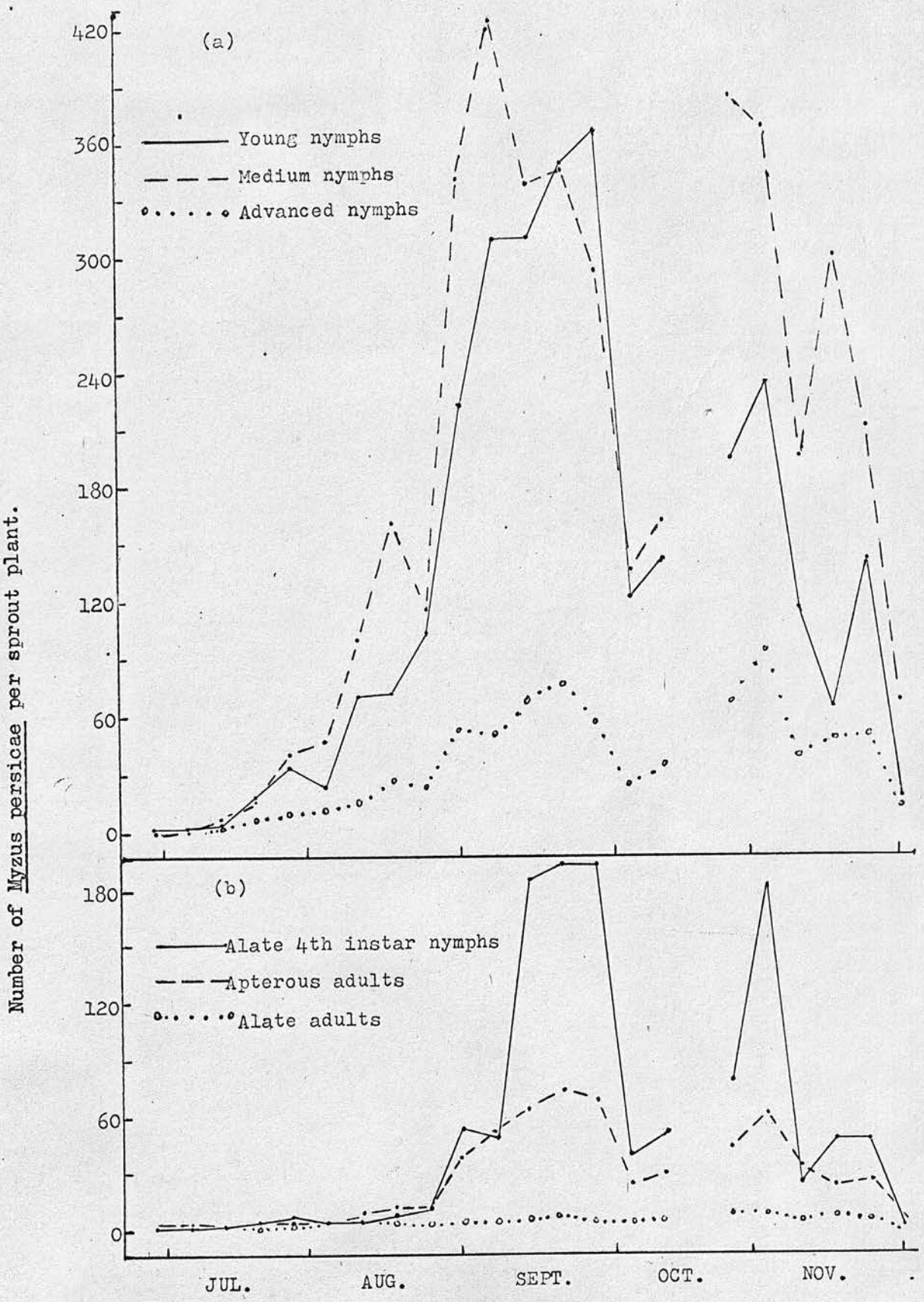

Fig. 15. Year 1969. Age specific population trends of Myzus persicae at Newington.

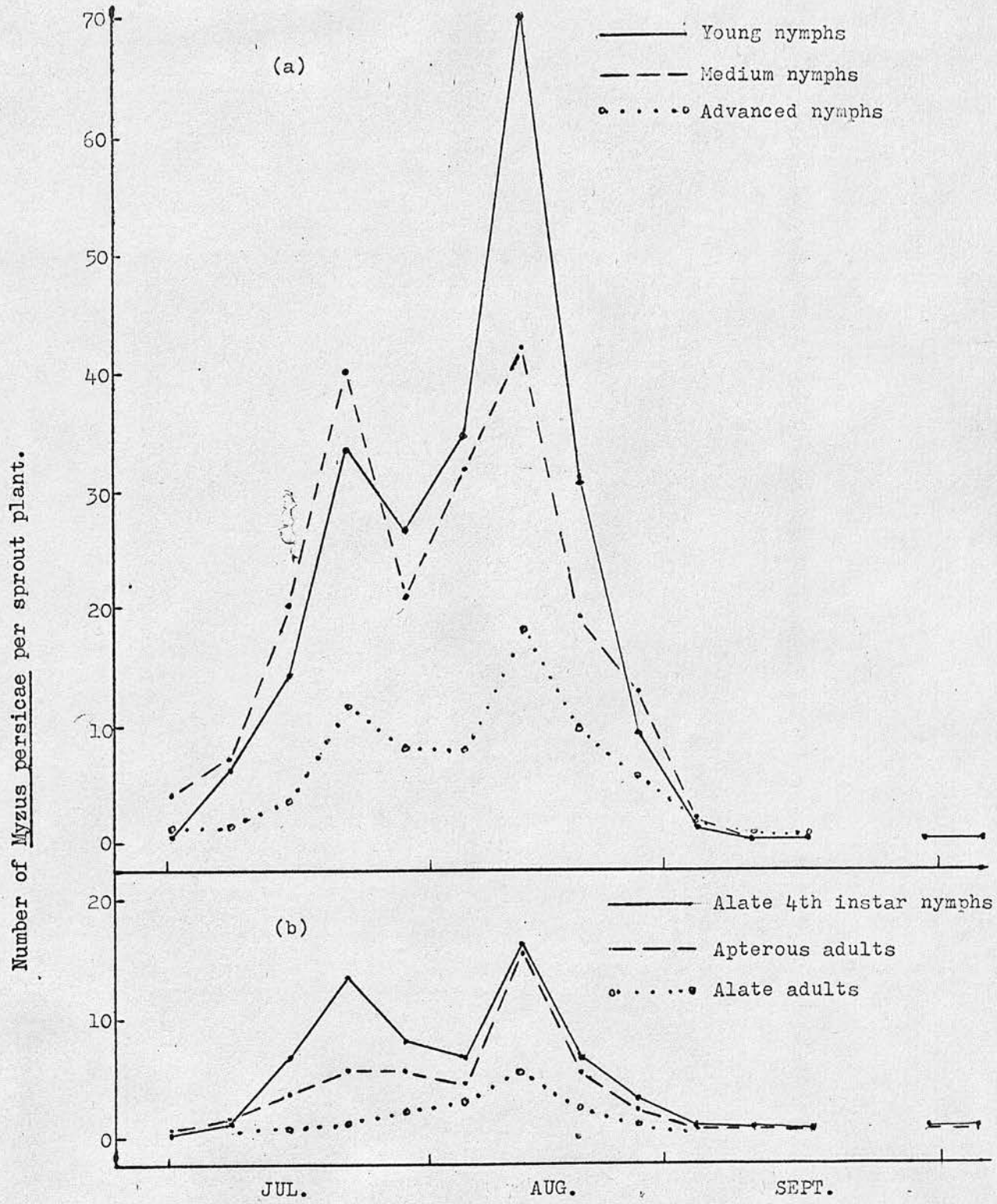

Fig. 16. Year 1970. Age specific population trends of Myzus persicae at Lasswade.

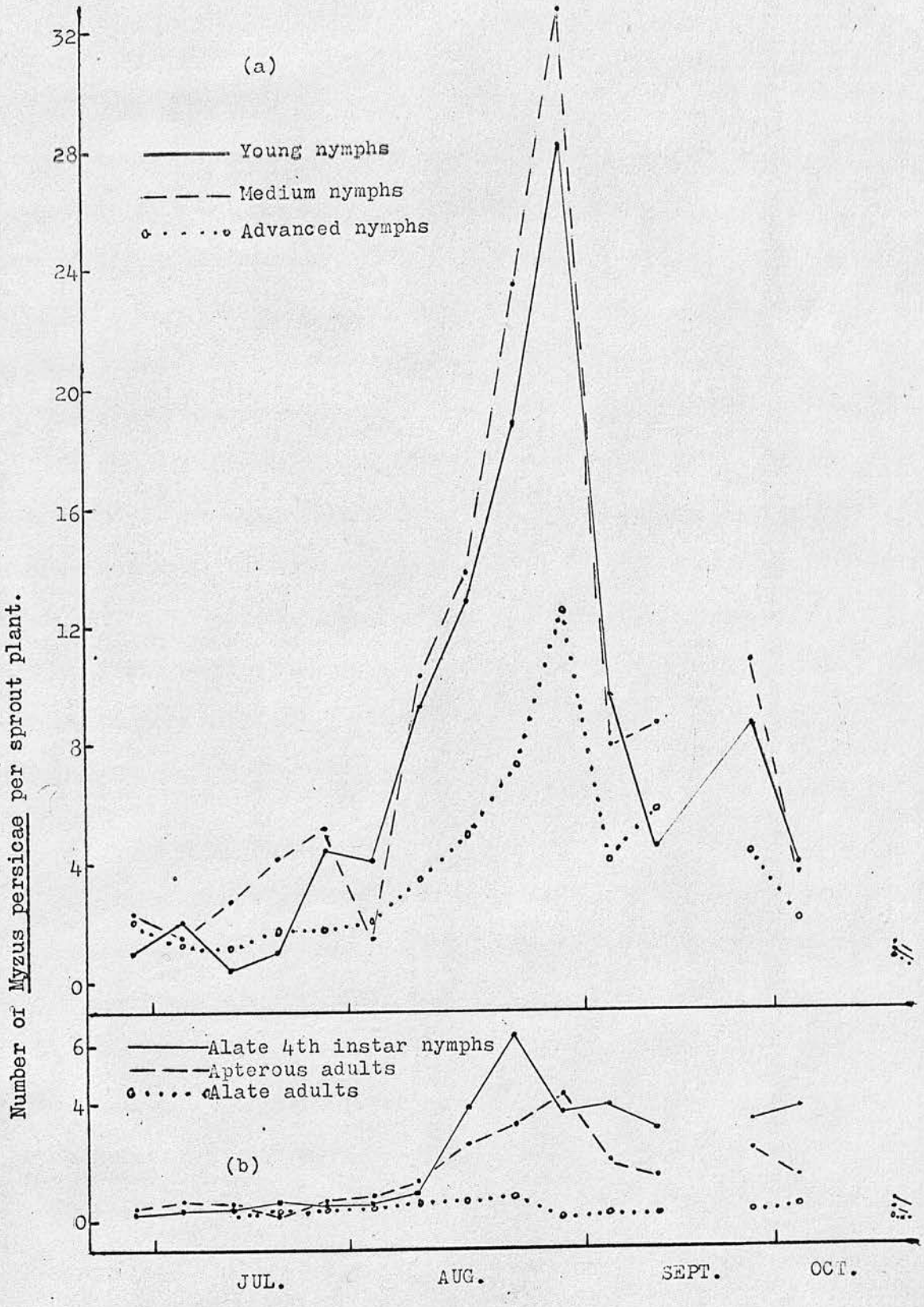

Fig. 17. Year 1970. Age specific population trends of Myzus persicae at Newington.

Myzus persicae 1970

a) Total population trends

At Lasswade there were numerous aphids on the brussels sprout crop during late July and mid-August and less during early July and early October (Figure 12c and 13c). The mean density varied between 1.1 ± 0.4 and 167.3 ± 54.9 aphids per plant with an average of 47.6 ± 14.3 over the sampling period. But at Newington the range density was 3.6 ± 2.8 to 81.3 ± 46.7, with an average of 23.4 ± 5.8 per plant (Appendices 17 and 18).

As shown in Figure 12c, at Lasswade, there was a rapid increase in the aphid numbers from early July to a peak during late July. A sharp short decrease occurred, followed by an abrupt rise to the highest peak in mid-August with a further decrease to almost zero in early October.

At Newington the rate of population growth was very slow. From early July the numbers gradually increased reaching a peak by the end of August and declining during October (Figure 13c).

b) Age specific population trends

The population fluctuations of the nymphs (young, medium, advanced and alate 4th instar) and the adult aphids at Lasswade showed two peaks, and that at Newington one peak (Figures 16 and 17). There was no time lag between the peak numbers reached by the different groups of the nymphs and the adults. The peaks occurred at the same time except that of the alate 4th instar nymphs which was a week earlier than the rest. The trend of population change, however, was similar to that of the total number. As in 1969, the young and medium nymphs seemed to determine the trend of the population changes at both sites.

c) Age structure

The relative proportions of the total populations of the various stages of growth found on the brussels sprout crops in 1970 at the two locations were as follows.

At Lasswade and Newington respectively the young nymphs represented 36.6% and 31.1%; medium nymphs 32.2% and 37.4%; advanced nymphs 11.4% and 15.6%; alate 4th instar nymphs 10.3% and 8.8%; apterous adults 7.1% and 5.9%; amd alate adults 2.3% and 1.2%.

Macrosiphum euphorbiae 1970

From the high level, 130.0 ± 38.0 aphids per ten plants, in mid-August at Lasswade, there was a rapid decrease in numbers and complete disappearance by early September. The lowest mean density, 6.0 ± 3.0 aphids per ten plants, was counted in early July at the beginning of the sampling period (Appendix 19, and Figure 12c).

At Newington, the numbers counted during sampling period were few. The mean density at the highest peak was 20.0 ± 8.0 aphids per ten plants in July, and by mid-August no aphids were found in the experimental plot, (Appendix 20 and Figure 13c).

Predators

Syrphidae - water trap catches

In addition to the aphidophagous syrphids, the non-aphidophagous ones were recorded to give an indication whether the aphidophagous adults were attracted to the brussels sprout crops to feed or to oviposit close to the larval food.

The aphidophagous syrphids formed 73.4% of all Syrphidae caught at

the two sites during the two seasons and they belonged to 18 species in six genera.

Syrphus ribesii (L.) was the most abundant of the aphidophagous species at all sites during the study period. S. ribesii alone accounted for 40.2% of all the apidophagous syrphids and, S. balteatus (Deg.) and S. corollae (Fab.) 24.9%. The rest made up 34.9% (Table 10).

The total of the three most numerous non-aphidophagous, Eristalis arbustorum L., Neoascia podagrica Fab., Eristalis tenax L., was not as great as that of S. ribesii. Together with the other non-aphidophagous species, their numbers reached a peak during September (Tables 11 and 12).

The first catch of aphidophagous syrphid over the brussels sprout crop was in early June (Appendices 21 and 25), although some had been seen flying late May. Numbers of syrphids increased gradually reaching a peak in September in each of the two years at both sites, and their numbers declined rapidly thereafter (Table 12).

The syrphid numbers trapped during the two seasons at the two experimental plots are shown in (Appendices 21-28; Table 13). At Lasswade 668 Syrphidae (29 species) were caught, whereas about half the number, 323 (22 species), were collected at Newington. The species found at Lasswade outnumbered or equalled those at Newington, except three aphidophagous (Platyceirus albimanus Fab., Melanostoma scalare Fab., and Xanthogramma citrofasciatum Deg.) and two non-aphidophagous (Neoascia podagrica Fab. and Syritta pipens L.) species.

The same six species of Syrphus were found at both sites but at Lasswade (368) about twice as many individuals were caught as at Newington (178). S. ribesii was the dominant species at both sites.

At Lasswade, 74 individuals of 6 species of Platycheirus species were trapped, whereas at Newington there were 28 individuals of 5 Platycheirus species. P. manicatus (Meig.) was the dominant species of this genus at Lasswade, with P. peltatus (Meig.) and P. tarsalis (Meig.) also being found at this site. At Newington, P. albimanus was the dominant species and P. scambus Staeg. was found there only once.

The two species of Melanostoma were not common, but were about equal in numbers at both sites. The only species of Pyrophaena and Sphaerophoria were caught at Lasswade. Xanthotrama citrofasciatum was trapped at both sites. The gravid females formed 37.7% of the female aphidophagous females. This was an indication that some of the adult insects were probably attracted to the brussels sprout crop to oviposit near larval food.

At *Lasswade, the weeds among the brussels sprout crop were more varied than at **Newington and provided a succession of flowers. This seemed to have attracted a greater abundance (X^2 = 120.0, d.f = 1, $P < 0.001$) and a non-significant variety of Syrphidae (X^2 = 0.96, d.f. = 1, $P > 0.05$) at Lasswade than at Newington. It was observed visually that the times of appearance and the abundance of the syrphids coincided with the flowering of the various weeds in the experimental plots. This was probably an influencing factor for syrphid oviposition. Dixon (1959) and van Emden (1965) found the peak activity of syrphids to occur at the same time as the peak flowering period while Chandler (1968) and Smith (1969) found to the contrary.

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*Flowering weeds at Lasswade :- corn poppy, Papaver rhoeas; groundsel, Senecio vulgaris; creeping thistle, Cardus arvensis; dandelion, Taraxacum officinale; charlock, Sinapis arvensis; sowthistle, Sonchus asper, and Matricaria species.

**Flowering weeds at Newington :- groundsel, dandelion and sowthistle.

TABLE IO

Totals of aphidophagous syrphid adults per two water traps at Lasswade and Newington

Species	Lasswade 1969	Lasswade 1970	Newington 1969	Newington 1970	Total
Syrhus ribesii (L.)	135	56	64	37	292
Syrphus balteatus (Deg.)	46	16	25	6	93
Syrphus corollae (Fab.)	26	52	3	7	88
Platycheirus manicatus (Meig.)	45	5	3	1	54
Syrph us vitripennis (Meig.)	18	7	12	12	49
Pyrophaena granditarsa (Fors.)	26	3	0	0	29
Platycheirus albimanus (Fab.)	7	1	6	13	27
Melanostoma scalare (Fab.)	4	7	3	11	25
Syrphus luniger (Meig.)	6	5	8	3	22
Melanostoma mellinum (L.)	7	5	7	0	19
Platycheirus scutatus (Meig.)	3	0	1	2	6
Platycheirus pelatus (Meig.)	1	5	0	0	6
Platycheirus clypeatus (Meig.)	2	2	1	0	5
Xanthogramma citrofasciatum (Deg)	0	1	0	4	5
Platycheirus tarsalis (Sch.)	3	0	0	0	3
Syrphus auricollis (Meig.)	1	0	0	1	2
Sphaerophoria menthastri (Meig.)	0	1	0	0	1
Platycheirus scambus (Staeg.)	0	0	1	0	1
Total	330	166	134	97	727

TABLE 11

Total of non-aphidophagus syrphid adults per two water traps at Lasswade and Newington

Species	Lasswade		Newington		Total
	1969	1970	1969	1970	
Eristalis arbustorum (L.)	71	20	6	1	98
Neoascia podagrica Fab.	5	0	11	40	56
Eristalis tenax L.	25	11	16	1	53
Syritta pipiens L.	7	0	4	5	16
Helophilus pendulus L.	7	2	1	3	13
Xylota segnis L.	3	5	0	0	8
Eristalis pertinax Scop.	1	5	0	0	6
Eristalis intricarius L.	4	0	1	0	5
Chilosia sp.	2	0	1	0	3
Xylota sp.	1	0	2	0	3
Chilosia variabilis Panz.	1	0	0	0	1
Eristalis nemorum L.	0	2	0	0	2
Total	127	45	42	50	264

TABLE 12

Combined monthly counts of aphidophagous and non-aphidophagous syrphid adults caught in two water traps, at both Lasswade and Newington. (1969, 1970)

Species	June	July	Aug.	Sept.	Oct.	Nov.	Total
Aphidophagous							
Syrphus ribesii	0	1	28	164	99	0	292
Syrphus balteatus	0	0	25	57	11	0	93
Syrphus corollae	1	2	15	64	6	0	88
Platycheirus manicatus	13	15	6	13	7	0	54
Syrphus vitripennis	0	0	2	24	23	0	49
Pyrophaena granditarsa	0	0	2	27	0	0	29
Platycheirus albimanus	1	0	2	19	4	1	27
Melanostoma scalare	1	0	5	13	6	0	25
Syrphus luniger	0	1	2	13	6	0	22
Melanostoma mellinum	0	0	11	8	0	0	19
Total	16	19	98	402	162	1	698
Non-aphidophagous							
Eristalis arbustorum	0	2	29	40	27	0	98
Neoascia podagrica	4	1	29	20	2	0	56
Eristalis tenax	0	4	2	12	29	6	53
Total	4	7	60	72	58	6	207

TABLE 13

Combined fortnightly counts of the more abundant species of aphidophagous syrphid adults at Lasswade and Newington (1969,1970)

Species	*Site	June		July		Aug.		Sept.		Oct.		Nov.		Total
Syrphus ribesii	L	0	0	0	0	1	5	35	69	72	9	0	0	191
	N	0	0	1	0	3	19	36	24	13	5	0	0	101
Syrphus balteatus	L	0	0	0	0	2	7	15	31	7	0	0	0	62
	N	0	0	0	0	1	15	6	5	4	0	0	0	31
Syrphus corollae	L	0	0	0	1	2	10	9	50	6	0	0	0	78
	N	0	1	0	1	1	2	3	2	0	0	0	0	10
Platycheirus manicatus	L	0	11	9	6	2	3	0	12	7	0	0	0	50
	N	0	2	0	0	0	1	1	0	0	0	0	0	4
Syrphus vitripennis	L	0	0	0	0	0	0	5	12	4	4	0	0	25
	N	0	0	0	0	0	2	5	2	8	7	0	0	24
Pyrophaena granditarsa	L	0	0	0	0	0	2	19	8	0	0	0	0	29
	N	0	0	0	0	0	0	0	0	0	0	0	0	0
Platycheirus albimanus	L	1	0	0	0	0	0	2	2	2	0	1	0	8
	N	0	0	0	0	0	2	10	5	2	0	0	0	19
Melanostoma scalare	L	1	0	0	0	0	4	4	2	0	0	0	0	11
	N	0	0	0	0	0	1	3	4	4	2	0	0	14
Syrphus luniger	L	0	0	0	1	0	1	2	3	4	0	0	0	11
	N	0	0	0	0	0	1	5	3	1	1	0	0	11
Melanostoma mellinum	L	0	0	0	0	0	5	2	3	2	0	0	0	12
	N	0	0	0	0	0	5	1	1	0	0	0	0	7
		2	14	10	9	12	85	163	238	136	28	1	0	698

* L = Lasswade; N = Newington

TABLE 14

Monthly means (±SE) of Syrphid eggs and larvae per ten sprout plants during the seasons of 1969 and 1970 at Lasswade and Newington.

	Lasswade		Newington	
	Syrphid eggs	Larvae	Syrphid eggs	Larvae
1969				
July	1.6 ± 0.6	1.4 ± 0.5	5.0 ± 2.1	0.8 ± 0.3
Aug.	31.3 ± 8.2	9.0 ± 3.1	22.8 ± 4.3	5.8 ± 1.2
Sept.	4.0 ± 2.8	2.8 ± 0.9	45.8 ± 11.4	35.2 ± 8.2
Oct.	0.5 ± 0.4	0.0	4.3 ± 1.2	18.0 ± 3.9
Nov.	0.0	0.5 ± 0.3	2.8 ± 0.8	9.8 ± 2.1
1970				
July	0.4 ± 0.1	0.0	0.0	0.8 ± 0.2
Aug.	5.3 ± 1.4	8.6 ± 1.8	0.2 ± 0.1	1.0 ± 0.3
Sept.	0.0	2.5 ± 0.8	0.7 ± 0.4	1.0 ± 0.6
Oct.	0.0	0.0	0.0	0.0

Syrphid eggs and larvae on the brussels sprouts

The results in Table 14 show that the female syrphids started to lay eggs on the brussels sprouts in July at both Lasswade and Newington during both seasons. At Lasswade, the peak numbers of eggs 31.3 $\pm$ 8.2 and 5.3 $\pm$ 1.4 per ten brussels sprout plants, were oviposited during August in 1969 and 1970 respectively, while at Newington the peak occurred in September of both years, 45:8 $\pm$ 11.4 and 0.7 $\pm$ 0.4 per ten brussels sprouts plants, and the numbers at both sites abruptly decreased during the succeeding months.

The numbers of the larvae followed similar trends of monthly number changes to those of the eggs, and there were no time lags between the peaks.

It appeared that the low numbers of syrphid eggs encountered during this investigation was related to the low density of the aphids. Chandler (1968) found that, in particular, Syrphus species showed greater preferences for ovipositing on plants infested with aphids than Platycheirus and Malanostoma species. Syrphus ribesii, the most abundant syrphid during the present investigation, was found to lay the optimum number of eggs of brussels sprouts infested with about 2,000 aphids per plant. The highest number of aphids recorded per plant during this study was at Newington, about 1,050 on 22:9:69.

Other predators

Syrphidae were the dominant predators; others were scarce during the study period.

1. Cecidomyiidae

The larvae were found on brussels sprouts at Newington during the two seasons but not at Lasswade. They appeared from September to

November. A total of 21 was recorded in 1969 and 30 in 1970.

An attempt was made to rear some of the larvae in the laboratory but all died. However, they appeared to be of the same species.

2. Coccinellidae

Coccinellidae were remarkably scarce. In 1969 only one Adalia bipunctata (L) was caught in the water trap at Newington early in the season. At Lasswade in 1970 two adults and one larva were found in July in the brussels sprouts; another adult, Adalia decempunctata (L.) was trapped in the water trap at the same time.

3. Anthocoridae

A few Anthocoridae of the genus Anthocoris were encountered. They were caught mainly in the adult form in the water traps. Eight were trapped during the season in 1969 at Newington and six at Lasswade. The only nymph found in the brussels sprouts during the two years study was at Newington in September, 1969. In 1970, one adult was caught in September and two early in the season at Newington.

4. Neuroptera

Only one hemerobiid adult, Nesomicromus pagnus (L.) was caught in the water trap at Lasswade early in the season in 1969, and five adults (2, N. paganus and 3, Sympherobius species) at Newington during early and middle part of the season. In 1970, four eggs of Chrysopa carnea Stephen were recorded on brussels sprouts in August and a single adult of the same species was trapped in July at Lasswade. No record of Neuroptera was made in 1970 at Newington.

5. Acarina

Anystis species (Order Prostigmata: Family Anystidae) was first found attacking M. persicae on brussels sprouts on July 21st, 1969, at Newington. The British fauna of the family has not been sufficiently studied to allow of species identification with any certainty (Macfarlane, per. comm. 1970). However, this observation appears to be the first record of predatory mites preying on aphid, in Scotland. In England Anystis species has been observed as a predator of strawberry aphid, Pentatrichopus fragaefolii (Dicker, 1952a) and all stages of aphids on broom, brussels sprouts, and broad beans (Baker, 1967).

Bachartia kuyperi Oud. and Thisumena lepida Thorek have been recorded in Israel (Bodenheinmer & Swirki, 1957) and in Germany (Borner & Heinze, 1957) as predators of M. persicae. Grobler (1962) found Anystis baccarum (L.) as one of the factors causing mortality of wooly pine needle aphid, Schizolachnus pini-radiatae (Davidson).

The Anystis species has a short, broad body and bright appearance with radial legs. Under dissecting binoculars, the body has a transparent medial band with mobile marks which are likely to be the contents of the gut. The species attacks aphids with great speed. During feeding the mouth parts are stuck in the prey and the predatory mite remains motionless except for occasional pulling of the victim closer to itself with the first pair of legs. The rhythm of the suction can be observed from the medial band as the sucking goes on. When the aphid content is exhausted, the empty exoskeleton is abandoned. Feeding takes about 10 - 15 minutes, and sometimes after feeding the mite cleans its mouth parts with its legs.

Under laboratory conditions of 17.5° - 23.0°C and relative humidity

75% each of eight mites was confined in a small petri dish with six nymphs and four adults of M. persicae on a brussels sprout leaf. The aphid number was kept constant in case of loss or predation by the mite. The feeding experiment went on for five days and it was found that a mite consumed 0 - 3 aphid nymphs daily.

Anystis species occurred at both Lasswade and Newington, usually during July and August, on brussels sprout plants. Between one and three mites per plant were found during 1969 and about two per plant during 1970.

DISCUSSION

The aphid population trends

The investigations showed that colonization by Myzus persicae and Macrosiphum euphorbiae of brussels sprout crops around Edinburgh appeared to be a gradual process rather than a sudden invasion. Very few alate adults were trapped in the crops by the end of June (Figures 8 and 9), although the crops were in the field before then. The gradual increases noted suggest that there were irregular movements into the crops. The immigrating adults were probably derived initially from a low density population on the surrounding perennial weeds, particularly Rumex species, and in the case of M. euphorbiae from sheltered plants.

There were no fixed patterns of population changes of M. persicae throughout the season in the fields and from year to year. In 1969, at both Lasswade and Newington however, there appeared to be some sort of general pattern of three peaks occurring in August, September and early November (Figure 10c and 11c). During 1970 however, there was no repetition of similar population trends at either locations. The rate of the population growth varied greatly from plot to plot and from year to

year. The mean number of M. persicae per plant in 1969 at Lasswade was 103.5 ± 15.0, while in 1970 the mean was 47.6 ± 14.3. This decline was significant at the 5% level probability. At Newington there was a correspondingly highly significant decrease in the aphid numbers at the 0.1% level of probability, from 435.5 ± 77.5 to 23.4 ± 5.8. A possible explanation for the 1969-70 decrease in the aphid numbers at Lasswade might be that the whole population finally declined earlier in September 1970, while in the preceding year it persisted until November (Figure 10c and 12c). At Newington in 1969, there were numerous self-sown aphid infested potato plants in the experimental plot which might have influenced the aphid populations on the brussels sprouts, while the aphid host plants were scarce in the plot the following year. The causes of the population changes are discussed later on.

In general, seasonal trends in the growth of M. euphorbiae populations on brussels sprouts had one peak from late July to mid-August, and the species disappeared from all the plots by mid-September. During both 1969 and 1970, M. euphorbiae were less numerous than M. persicae during the time they appeared in the fields and there was also variation in numbers from plot to plot and from year to year as indicated in Figures 10c, 11c, 12c and 13c.

Population studies of aphids on brussels sprouts made by other workers in England showed that mostly Brevicoryne brassicae and, to a lesser extent, M. persicae are found on this brassica crop (George 1957; Smith 1969). During the present study, however, only two individuals of B. brassicae were found in 1969 and seven in 1970. The scarcity of this aphid around Edinburgh and presumably in Scotland may be due to the cold weather as

compared to the relatively mild weather in England.

Analysis of seasonal population trends

An attempt is made here to analyse some of the causes of the numerical changes of M. euphorbiae and M. persicae as they occurred on brussels sprouts around Edinburgh during 1969 and 1970.

To understand the population dynamics of insects, Carke et al. (1967) suggested the making of conceptual models that linked the numerical changes with the causes. Such analysis or any other which is intended to determine precisely the causes of the aphid mortality is likely to be misleading due to:

1. the difficulties of distinguishing the various instar stages during sampling in the field.
2. extensive overlapping of stages and generations (Hafez, 1961).
3. polymorphism exhibited by the aphids (Van Emden et al., 1969).
4. the mortality factors which interacted in complex ways (Hafez, 1961).
5. the physiological conditions of the host plants that were beyond the scope of the present investigation. Kennedy & Booth (1951) and Kennedy & Stroyan (1959) showed that physiological conditions of aphid host plants affected their abundance.
6. the influence of migration which may unduly regulate the numbers of the aphids in the study area. It is therefore useful only to determine the part played by some of the mortality factors occurring during the population changes.

1. Climatic factors

Temperature is undoubtedly significant and Solomon (1967) showed that active stages of Myzus persicae could be undercooled and survive down to $-20^{\circ}C$.

It was found during the present study that M. persicae could reproduce at 1° to + 2°C and the developmental threshold for this aphid was found to be 3.5°C, and 4.3°C in Germany (Fenjves, 1945). Broadbent & Hollings (1951) obtained the upper thermal death point of 38.5°C after exposure for one hour. In an earlier section, the effect of temperatures within these extremes has been considered and it has been shown that the rates of development, survival and reproduction were influenced by the different constant temperatures - developmental and survival periods tended to decrease with a rise in temperature while fecundity increased with a rise in temperature.

During the two years sampling at the two field sites, the highest temperature recorded was 26.1°C and the lowest was -1.1°C. It was no where near the lethal points. The detrimental effects of the high temperatures on the aphids and the brussels sprouts were not observed in the fields. Temperatures encountered were not low enough to cause mortality. Violent and sudden changes in the temperature which could cause death of aphids were not recorded (Figure 18). However, towards the end of the 1969 season, the reproductive rate of M. persicae probably may have been reduced as a result of the low temperature at the two locations, thereby affecting population abundance.

Indirectly, temperature could exert influence on the aphid population, through its effect on the natural enemies. These were numerous during the warmer periods, July, August and early September, of the two seasons (Figure 10a, b, 11a, b, and 12a, b).

Rainfall is another important climatic factor. The sampling period in 1969 was drier than that of 1970, particularly in July (Table 15) and it was observed that by early August, 1969, the brussels sprout leaves

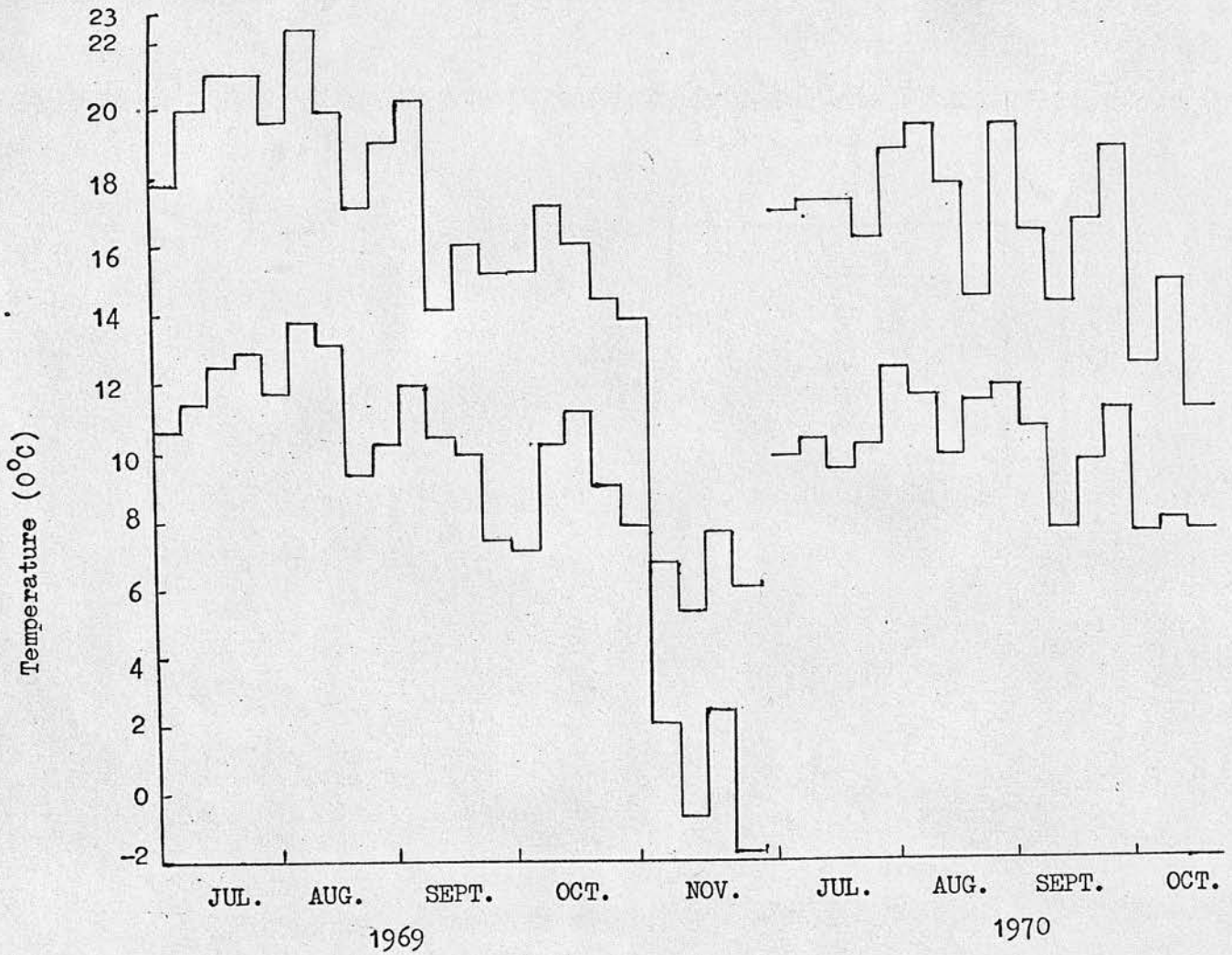

Fig. 18. Maximum and minimum mean weekly temperatures in 1969 and 1970 at Lasswade.

TABLE 15

Total monthly rainfall (mm) from July to November 1969 and 1970 in the Edinburgh area.

	1969	1970
July	309	738
August	461	444
September	487	632
October	175	550
November	855	768

Source of information:- the Royal Obervatory, Edinburgh

TABLE 16

The mean numbers of live and dead Myzus persicae per sprout plant at Lasswade and Newington during 1969

Site/sampling date	Mean (±SE) of dead aphids per plant	Mean (±SE) total of live aphids per plant
Lasswade		
30/7/69	0.2 ± 0.2	141.4 ± 21.4
6/8/69	8.6 ± 3.1	215.8 ± 48.9
13/8/69	17.6 ± 5.2	87.8 ± 25.5
20/8/69	24.3 ± 7.2	58.9 ± 19.5
27/8/69	9.2 ± 3.5	29.6 ± 13.6
3/9/69	7.2 ± 2.9	143.4 ± 36.4
10/9/69	1.3 ± 0.1	180.3 ± 39.5
Newington		
4/8/69	2.2 ± 0.1	88.4 ± 12.4
11/8/69	12.3 ± 4.2	204.1 ± 20.1
18/8/69	19.5 ± 7.5	281.9 ± 54.8
25/8/69	10.3 ± 4.3	268.6 ± 56.2
1/9/69	18 .9 ± 8.1	711.2 ± 223.6
8/9/69	3.3 ± 0.2	891.8 ± 141.2
15/9/69	0.5 ± 0.2	972.8 ± 165.0

TABLE 17

The mean numbers of live and dead Myzus persicae per sprout plant at Lasswade during 1970

Site/sampling date	Mean (±SE) of dead aphids per plant	Mean (±SE) total of live aphids per plant
Lasswade		
29/7/70	0.2 ± 0.1	71.2 ± 15.1
5/8/70	9.4 ± 3.1	88.4 ± 20.6
12/8/70	12.2 ± 3.2	167.3 ± 54.9
19/8/70	18 .8±6.8	72.9 ± 16.9
26/8/70	29.0 ± 9.1	32.4 ± 8.1
2/9/70	3.5 ± 2.1	6.0 ± 2.5
9/9/70	0	0

at Lasswade started to be less turgid. This condition of the leaves coincided with the sharp decline of both M. persicae and M. euphorbiae (Figures 9c and 10c) the latter reached zero by late August. Banks (1965) noted that the population of M. persicae on potatoes sharply reduced as the water content of the plant decreased and the foliage hardened. The flabbiness of the leaves was less marked at Newington, probably due to the differences in the variety of the brussels sprouts. In August of both years and in early September, 1970, rainfall was partially responsible for maintaining high humidity under the leaves for the water droplets on the aphids to persist, and this eventually drowned them. These droplets probably caused the whole aphid population at Lasswade in September, 1970, to be reduced to zero.

During August and September, the day temperatures were generally warmer followed by cooler nights with high relative humidities (Appendixes 29 and 30) and presumably since the soil retained its warmth during the cool nights, water vapour from the soil condensed on the under surface of the bottom leaves touching the soil where the aphids usually stayed. Owing to the high humidity at this part of the plant and lack of completely free air circulation, the water droplets persisted and probably drowned the aphids. According to Broadbent (1950, 1951) the aphids on the under surfaces of potato leaves were at a much higher level of humidity than the air between the plants. Measurements of relative humidity taken in the open air among the brussels sprout crops in bright sunlight with hand hydrometer averaged 67%, those at the under surfaces of leaves touching the soil were 27% higher.

All stages of growth were found dead during the periods of water droplet formation. Aphids which died as the result of old age and were counted among the dead ones on the leaves might have been negligible since dead old aphids

were not noted at other times. Since some of the dead aphids might have dropped off the brussels sprout leaves before recording, figures shown in Tables 16 and 17 are likely to be lower than the numbers of the aphids which might actually have drowned. In 1969 at Lasswade the highest numbers of the dead aphids were counted during the two weeks 13:8:69 and 20:8:69, when the total aphid population was on the decline. In 1970, at the same site, the effect of the dead aphids was apparent - during the three weeks 12:8:70 to 2:9:70 the aphid populations were drastically reduced. The numbers of the dead aphids per plant were 29.0 $\pm$ 9.1 on 26:8:70 and were almost the same as the total number of the live aphids per plant 32.4 $\pm$ 8.1. In effect, on September 9th, there was only about one aphid per plant.

At Newington, some of the aphids certainly died as a result of the water droplets but there was no apparent effect on the total aphid population (Table 16). Broadbent (1953) suggested that dew formation could affect aphid populations, but it was more likely that this mortality factor was enhanced by entomophagous fungi which might have infected individuals, but the high densities believed to be a contributive factor for the attack of entomophagous fungi (Theobald, 1926; Steinhaus, 1954; Hughes, 1953) were not reached during the investigations.

Closed crop planting probably may enhance the effectiveness of dew formation as an aphid mortality factor by creating a high humidity under the lower surfaces of the bottom leaves.

2. Biotic Factors.

The biotic factors are parasites and predators. In 1969, a peak of 1.8 $\pm$ 1.2 syrphid larvae per plant, at Lasswade (20:8:69) coincided with the population decline of both M. persicae and M. euphorbiae and the latter species

completely disappeared (Appendixes 13, 31. Figure 10a). In the following year at the same location a peak of 2.1 ± 0.8 syrphid larvae occurred when M. persicae numbers were declining during August (Appendixes 17,33.Figure 12a). Syrphid larvae are voracious feeders. Sundby (1966) found that Syrphus ribesii and S. corollae larvae consumed over 500 and 800 aphids during development. It therefore seems likely that the low numbers of syrphid larvae found on brussels sprouts during the present investigation could put pressure on the population which had a peak of about 220 aphids per plant at Lasswade in 1969. At Newington in 1969 three peaks of M. persicae which started to decline within a week of each other coincided with those of syrphid larvae at 6.8 ± 1.9, 1.7 ± 1.2 and 1.6 ± 0.6 per brussels sprout plant (Appendices 14,32. Figure 11a); in 1970, the larvae were too scarce to indicate any effect on the aphid population (Appendix 34. Figure 13a).

However in the present work where low aphid populations were usually encountered, the searching behaviour of the syrphid larvae was of considerable importance for effective predation. Syrphid larvae hatched on leaves with a few aphids or without any, may have had to search extensively for food in order to survive. Newly hatched larvae have low power of locomotion and occasionally, dead syrphid larvae were found on the brussels sprout leaves. They may have died of starvation. However, during the sampling periods, Aphis fabae found commonly on thistle,(Carduus arvensis), fat hen, (Chenopodium album) and nettle, (Urica urens) in the sprout crops were noted to be preyed upon by syrphid larvae, thereby sustaining the numbers of the natural enemies of all aphids in the field.

The numbers of Anystis species, Neuroptera, Anthocoridae, Coccinellidae and Cecidomyiidae were too few to exert any effective control on the aphid

populations by themselves. Other non-specific predators, carabids, staphilinids and families of Dermaptera and Heteroptera which may have preyed on aphids on the brussels sprout plants were found on the ground during July and August.

Both apterous and alate aphids were trapped in spider webs built across some aphid infested leaves, and Dunn (1949) recorded aphids caught in a spider's web in a potato crop.

Anystis species, a predatory mite, was observed early in May on dock weeds infested with M. persicae and although such early predation might not be of high density, or intensity, it could adversely affect the population of aphids which might subsequently infest brassica crops.

The numerous mummified aphids collected on the brassica crops around Edinburgh from late summer 1968 to autumn 1970, yielded primary parasites of eighteen species in eight genera and hyperparasites of at least eight species in five genera. The parasites and hyperparasites complex in relation to the seasonal changes of aphids on brussels sprouts and some aspects of their biological and ecological study formed a part of the present investigations to be considered.

Defoliation of senescent leaves

During the period of the investigation, it was noted that Myzus persicae and Macrosiphum euphorbiae stayed mostly on the undersurfaces of the lower brussels sprout leaves and defoliated senescent leaves which carried a number of the aphids which might also affect the population on the plant. To investigate this, aphids on five marked basal leaves of sprout plants at each of the two sites were recorded early in September 1969. Periodically, counting and recording was done on the five remaining (or less)

TABLE 18

Abscission of sprout leaves and its effect on Myzus persicae populations

	Lasswade				
	Plant 1		Plant 2		No. aphids per leaf
	L	A	L	A	
5/ 9/69	5	81	5	59	14.0
10/10/69	3	27	2	51	15.6
7/11/69	1	3	1	13	8.0
5/12/69	0	0	1	0	0
	Newington				
	Plant 1		Plant 2		No. aphids per leaf
	L	A	L	A	
5/ 9/69	5	363	5	341	70.4
10/10/69	4	79	2	60	23.2
7/11/69	2	39	2	51	44.0
5/12/69	1	8	0	0	8.0

L = number of infested brussels sprout leaves

A = total number of Myzus persicae on leaves

TABLE 19

The relationship between alate Myzus persicae and young nymphs trapped at Newington 1969

Sampling date	Alate M.persicae per two water traps	Mean number (±SE) of young nymphs per plant
2/ 7/69	0	0.8 ± 0.5
9/ 7/69	0	0.8 ± 0.7
16/7/69	0	8.3 ± 2.4
23/7/69	0	29.5 ± 5.8
30/7/69	1	62.7 ± 10.7
6/8/69	45	61.6 ± 16.9
13/8/69	76	32.8 ± 11.1
20/8/69	9	28.6 ± 12.2
27/7/69	8	15.5 ± 8.2
3/9/69	18	52.2 ± 14.5
10/9/69	22	62.9 ± 18.4
17/9/69	6	71.7 ± 22.5
24/9/69	3	23.8 ± 8.0
1/10/69	0	40.6 ± 11.4
8/10/69	5	23.4 ± 5.8
15/10/69	12	29.8 ± 7.5
22/10/69 } 29/10/69 }	24	35.5 ± 11.3
5/11/69	0	35.7 ± 14.3
12/11/69	0	13.3 ± 8.1
19/11/69	0	11.2 ± 6.9
26/11/69	-	-

TABLE 20

The relationship between alate Myzus persicae and young nymphs trapped at Lasswade 1970

Sampling date	Alate M.persicae per two water traps	Mean number (±SE) of young nymphs per plant
1/7/70	1	0.5 ± 0.4
8/7/70	1	6.2 ± 2.8
15/7/70	0	14.4 ± 3.1
22/7/70	2	33.9 ± 7.1
29/7/70	I0	26.5 ± 6.9
5/8/70	18	34.8 ± 8.8
12/8/70	16	70.2 ± 23.7
19/8/70	17	30.2 ± 7.4
26/8/70	4	9.2 ± 2.7
2/9/70	4	1.0 ± 0.8
9/9/70	1	0
16/9/70	0	0

leaves of each plant until early December. All the leaves on each of the whole plants were then inspected for aphids during the last sampling date.

Table 18 indicates that as the brussels sprout leaves matured and defoliated aphids on them still remained attached. This confirmed a similar observation by Fisken (1959) on spring cabbages in south-east Scotland. Another observation suggested that aphids on the defoliated leaves hardly moved away, thereby reducing the numbers on the sprout plants. It was noted during the present investigation that leaf abscission was common from October onwards when the brussels sprout buttons started to develop, and during the cold spell which followed. The frosty weather early in November caused flabbiness of the leaves and hastened abscission. The decline of the aphid populations as affected by maturation and defoliation of the leaves was common towards the end of the season.

Reproduction

It appeared that rates of reproduction did not act as a mortality factor. As shown in Appendices 13-20 at both sites during the study periods the young nymphs numbers per plant that followed a decline were far less than the numbers which preceded them. This was an indication that mortality factors other than reproduction were in operation. For retarded reproductive rate during any week to influence the aphid population, nymphs per plant in the following week would have to be about the same as the previous one.

Migration

It was suggested earlier that alatae which infested sprout leaves at the two sites were all virginogeniae which were reproduced by few apterous

M. persicae which had overwintered on perennial weeds. Later, the vagrant activities on both the brussels sprouts and aphid host weeds around and within the field seemingly influenced the size of the winged aphid population at any particular site. Johnson (1969) noted that M. persicae, like Aphis fabae, bred on secondary host plants would take flight a few hours after final moult. Therefore if mass migration was to affect the aphid population on the brussels sprouts, a sudden increase or decrease in the winged adult numbers trapped in any particular week should have led to a corresponding rise or fall of the young nymph population the following week. But from Tables 19 and 20, this did not happen as any increase or decrease in the winged adult M. persicae numbers trapped each week at any of the sites during the study did not determine the young nymph population that week, or the succeeding one.

SECTION C

APHID PARASITES AND THEIR HYPERPARASITES

INTRODUCTION

A number of aphid parasites are mentioned in the literature but only a few have been studied in detail. The biology of the parasites which attack aphids in Britain are mostly unknown, particularly in Scotland. The remainder of this work deals with the bionomics of the parasite and hyperparasite complex of the aphids on brassicas, particularly, on brussels sprout crops around Edinburgh. The data presented here although incomplete provides much new information on some of the aphid parasites in Scotland, which may be of great help in biological control studies as well as in studies relating to other members of the families Aphidiidae and Aphelinidae.

METHODS

In both 1969 and 1970, and at each of the two sites (Lasswade and Newington) an area of about 0.3 hectare (0.75 acre) was marked out with an experimental plot at or near the centre. Each week an hour's search was carried out to collect all types of aphid mummies on both mature and senescent leaves of the sprout plants. About 6 mm. square of leaf was cut and taken with the mummy, but some mummies were detached during handling. The collections were mostly done on the non-experimental sections to avoid upsetting the balance of the natural populations of the aphids and their parasites and hyperparasites.

In 1969, at Lasswade, similar collections were made on a plot of about 0.3 hectare (0.75 acre) demarcated on a 12 hectare (30 acre) cabbage crop near to the 32 acre brussels sprout crop across the road. The

collections were unbiased since the content of the mummies were not known during the sampling. Periods for mummy collection were mostly from 1st August to 7th November, 1969, at both sites. In 1970, at Lasswade, weekly collections were from 31st July to 18th September, and at Newington periodically from 31st July to 4th September due to scarcity of the mummies at the site.

Each week's collection of the mummies was brought to the laboratory and each mummy was placed in a 7.5 cm. x 2.5 cm. glass tube, the top was covered with white nylon organdie held in position with a rubber band. The mummies from each plot were separately counted, recorded, grouped and then kept in an open insectary. The air temperature of the open insectary was found to be approximately the same as that of outside.

However, the removal of the mummies from their individual micro-environments to a common environment could affect the time of the season of the adult emergence. Nevertheless, the present information on the aphid parasites and hyperparasites would not have been obtained without collecting the mummies from the field.

In the preliminary study of 1968 late summer and autumn, aphid mummies on brassica crops were collected from various parts around Edinburgh in less systematic order, however, they were handled as in the following years except that the glass tubes were cork-stoppered. The relative humidity might have been reduced inside the tubes but enough air was available.

The tubes were inspected daily for adult emergence during the summer, autumn and spring, and weekly during the winter. All emergence from the mummies were taken to the laboratory, identified, sexed, counted, recorded, and the species of aphid host noted. If the parasite of the aphid host

Plate VII. Pupated Praon volucre with Myzus persicae on their tops.

was Praon species, it was readily recognised by the parasite's tent-like structure attached to the leaf with dead aphid as roof (Plate VII).

RESULTS AND DISCUSSION

1. Records and occurrence of aphid parasites and hyperparasites

Tables 21 and 22 show parasites and hyperparasites of Myzus persicae and Macrosiphum euphorbiae recorded in Britain compiled from Thompson (1950), Fielding (1953), Mackauer & Stary (1967), and Hellen (1963). The parasite and hyperparasite complex reared from M. persicae and M. euphorbiae on brassica crops, mostly on brussels sprout crops, during the present investigation is also shown in Tables 23 and 24. In appendix 35 are the names of the specialists with the corresponding aphid parasites and hyperparasites they determined. The specimens are also kept in the museum of the Department of Agricultural Zoology, Edinburgh School of Agriculture. In this work names of parasites and hyperparasites mentioned are listed in Appendix 35 with any other synonyms or uncertainty expressed by the specialists. Owing to the poor taxonomy in the whole world (Hellen, 1963; Evenhuis, 1964; Quinlan, per comm. 1970) of the hyperparasites belonging to the family Cynipidae, sub family, Charipinae, only a few of the species could be identified. The cynipid specimens have been retained in the British Museum for a thorough study of the British Charipinae which might take a couple of years (Quinlan per. comm. 1970). In the present study, they were grouped together as cynipids.

Most of the 2,600 parasites reared from the aphid mummies during the present study - 18 species in 8 genera - are in three sub families, Aphidiinae, Prainae and Epherinae of one family, Aphidiidae. The small number of Aphelinidae (7) comprised five species. The 1,031 hyperparasites

represented at least eight species in five genera.

As far as it could be discovered all the eleven species of primary parasites and five genera containing at last eight species of the hyperparasites listed under M. persicae, and fifteen species of primary parasites and five genera of at least eight species of the hyperparasites under M. euphorbiae are the first records of any such aphid parasites in Scotland. Alloxysta species was the only Scottish record found in the literature (Hellen, 1963).

The M. persicae records as aphid host of seven primary parasites and two genera of at least three species of hyperparasites, and M. euphorbiae also as an aphid host of seven primary parasites and two genera of at least four species of hyperparasites are new records in Britain. Three and four primary parasites listed respectively under M. persicae and M. euphorbiae as aphid host were found to be new records in the general literature (checked from Mackauer & Stary, 1967).

As indicated in the addendum of Table 24, Aphelinus flavus was reared from Drepanosiphum species on Acer species. Aphis fabae commonly found on weeds, nettle (Urtica urens), thistle (Carduus arvensis) and fat hen (Chenopodium album), in the experimental plots mainly at Lasswade, was parasitised by Ephedrus plagiator, Diaeretiella rapae and Praon volucre.

Of the numerous primary parasites and hyperparasites reared from both M. persicae and M. euphorbiae mummies during the three years investigation period, Praon volucre was the dominant species (33.4%) (Figure 19). D. rapae and A. picipes were each about half and one third as numerous as the dominant species, while the rest of the primary parasites accounted for 4.3%. Asaphes vulgaris was the dominant species of the

hyperparasites (19.9%) with cynipids about equally abundant. The remainder represented 2.5% of all of the primary parasites and hyperparasites.

Table 25 shows the relative abundance of the various parasites and hyperparasites reared from M. persicae and M. euphorbiae during the whole study period. It was only in 1968 that D. rapae was the dominant primary parasite which emerged from the aphid mummies collected.

At Lasswade in 1969 thirteen of the eighteen species of the primary parasites reared during the study were found in the cabbage crop. Monoctonus pseudoplatani, Dyscritulus planiceps and Aphelinus sp.nr. davicola could be found only at this site. The experimental plot of the brussels sprouts yielded ten primary parasite species with Aphidius (Diaeretiella) species peculiar to the plot. The most abundant primary parasite species at the two sites of Lasswade and at Newington was Praon volucre. Toxares deltiger was found only at Newington. In 1970, at Lasswade, the relative abundance of the primary parasites was the same as the previous year. At Newington in the same year, the parasites were scarce but more of Praon volucre were found.

In 1968, A. vulgaris was the dominant hyperparasite with cynipids about a third as common as the former. The only other hyperparasite was Coruna clavata which was scarce. Apart from the hyperparasite species found in 1968, two additional species of Dendrocerus (=Lygocerus) were reared from the aphid mummies in the succeeding two years. The most common species of the hyperparasites at all the sites in 1969 and 1970 were A. vulgaris and Cynipids, in almost the same numbers each year.

TABLE 21

Previously recorded parasites and hyperparasites of Myzus persicae (Sulzer) in Great Britain

Species	Country
Primary parasites	
Aphidius matricariae Haliday	England
Aphidius lonicerae Marshall	England
Aphidius avenae Haliday	England
Diaeretiella rapae McIntosh	England
Aphidius sp. (possibly cardui Marshall)	England
Praon volucre (Haliday)	England
Praon flavipes sp. n.	England
Aphidius picipes (Nees)	England
Ephedrus plagiator (Nees)	England
Hyperparasites	
Alloxysta (=Charips) curvicornis (Cameron)	England
Alloxysta (=Charips) ancylocerus (Cameron)	England
Alloxysta (=Charips) victrix var. victrix (Westward)	England
var. luteiceps (Kieffer)	England
Alloxysta (=Charips) spp.	England, Scotland
Dendrocerus (=Lygocerus) aphidivorus Kieffer	England
Asaphes vulgaris Walker	England
Coruna clavata Walker	England
Encyrtid sp.	England

TABLE 22

Previously recorded parasites and hyperparasites of Macrsiphum euphorbiae (Thomas) in Great Britain

Species	Country
Primary parasites	
Aphidius matricariae Haliday	England
Aphidius avenae Haliday	England
Aphidius ervi Haliday	England
Aphidius urticae Haliday	England
Aphidius ulmi Marshall	England
Aphidius picipes (Nees)	England
Praon volucre Haliday	England
Hyperparasites	
Alloxysta (=Charips) victrix var. luticeps (Kieffer)	England
Asaphes vulgaris Walker	England

TABLE 23

Parasites and hyperparasites reared during the investigation

Aphid host Myzus persicae

Primary parasites

ICHNEUMONOIDEA
Aphidiidae
Prainae
Praon volucre Haliday
* *Praon myzophagum* Mackauer

Aphidiinae
Aphidiini
+* *Aphidius* (Diaeretiella) spp.
Diaeretiella rapae McIntosh
Aphidius picipes (Nees)
+ * *Aphidius urticae* ? group
+ * *Aphidius ervi* ? Haliday
* *Aphidius picipes* group

Epherinae
* *Toxares deltiger* Haliday ?
Ephedrus plagiator Nees

CHALCIDOIDEA
Aphelinidae
Aphelinae
* *Aphelinus flavipes* Kurdjumov

Hyperparasites

CHALCIDOIDEA
Pteromalidae
Asaphes vulgaris Walker
Coruna clavata Walker

PROCTOTRYPOIDEA
Ceraphronidae
* *Dendrocerus* (*Macrostigma*) *bicolor* (Kieffer)
* *Dendrocerus* (*Macrostigma*) *aphidum* (Rondani)

CYNIPOIDEA
Cynipidae
Charipinae
* *Phaenoglyphis* spp.
Alloxysta spp.
Alloxysta spp. ? *curvicornis*
Alloxysta victrix Westwood

* = new record in Britain as a primary parasite or hyperparasite

\+ = new record in the literature as a primary parasite or hyperparasite

TABLE 24

Parasites and hyperparasites reared during the investigation

Aphid host Macrosiphum euphorbiae

Primary parasites	
ICHNEUMONOIDEA	
Aphidiidae	
Prainae	
	Praon volucre Haliday
+*	*Praon myzophagum* Mackauer
+*	*Dyscritulus planiceps* Marshall
Aphidiinae	
	Diaeretiella rapae McIntosh
	Aphidius picipes (Nees)
	Aphidius ervi Haliday
	Aphidius urticae group ?
*	*Aphidius rosae* group ?
Tioxini	
+*	*Monoctonus pseudoplantani* (Marshall)
Epherinae	
+*	*Ephedrus plagiator* Nees
CHALCIDOIDEA	
Aphelinidae	
Aphelinae	
	Aphelinus asychis Walker
*	*Aphelinus* sp. nr. *davicola* Foerster
*	*Aphelinus flavipes* Kurdjumov
	Aphelinus sp. nr. *tibialis* Nees
	Aphelinus sp. ? *mali* (Haldeman)
Hyperparasites	
CHALCIDOIDEA	
Pteromalidae	
	Asaphes vulgaris Walker
*	*Coruna clavata* Walker
PROCTOTRYPOIDEA	
Ceraphronidae	
*	*Dendrocerus (Macrostigma) bicolor* (Kieffer)
*	*Dendrocerus (Macrostigma) aphidum* (Rondani)
CYNIPOIDEA	
Cynipidae	
Charipinae	
*	*Phaenoglyphis* spp.
	Alloxysta spp.
	Alloxysta sp. ? *curvicornis*
	Alloxysta victrix Westwood

* = new record in Britain as a primary parasite or hyperparasite

+ = new record in the literature as a primary parasite

TABLE 24 (Cont)

Addendum

Parasites reared from different aphid mummies collected from plants other than brassica crops

Primary parasite	Aphid host	Host plant
Aphelinus flavus	Drepanosiphum sp.	Acer sp.
*Ephedrus plagiator	Aphis fabae	Urtica urens (Nettle)
*Diaeretiella rapae	do.	Cardus arvensis (Thistle)
*Praon volucre	do.	Chenopodium album (Fat Hen)

TABLE 25

Numbers of primary parasites and hyperparasites emerged from mummified aphids of Myzus persicae and Macrosiphum euphorbiae on brassicas during the study

Species	Sites around Edinburgh	Newington experimental plot		Lasswade experimental plot		Lasswade cabbage plot	
	1968	1969	1970	1969	1970	1969	Grand total
Praon volucre	29 (7.1)*	322 (51.7)	9 (50.0)	281 (57.8)	111 (20.4)	115 (22.1)	867 (33.4)
Praon myzophagum	0 (0.0)	3 (0.5)	0	1 (0.2)	13 (2.4)	3 (0.6)	20 (0.8)
Aphidius urticae group	0	3 (0.5)	0	7 (1.4)	2 (0.4)	16 (3.1)	28 (1.1)
Diaeretiella rapae	249 (60.9)	47 (7.5)	0	19 (3.9)	63 (11.6)	27 (5.2)	405 (15.5)
Aphidius picipes	8 (2.0)	38 (6.1)	3 (16.7)	21 (4.3)	55 (10.1)	52 (10.0)	177 (6.8)
Aphidius ervi	1 (0.2)	0	0	0	0	1 (0.2)	2 (0.1)
Toxares deltiger		2**					
Ephedrus plagiator	1 (0.2)	6 (1.0)	0	4 (0.8)	25 (4.6)	14 (2.7)	50 (1.9)
Aphidius rosae group	0	0	0	1 (0.2)	0	2 (0.4)	3 (0.1)
Monoctonus pseudoplantani	0	0	0	0	0	1 (0.2)	1 (0.1)
Aphelinus species	0	0	0	3 (0.6)	1 (0.2)	3 (0.6)	7 (0.3)
Dyscitulus planiceps	0	0	0	0	0	1 (0.2)	1 (0.1)
Asaphes vulgaris	86 (21.0)	102 (16.4)	1 (5.6)	69 (14.2)	117 (21.5)	142 (27.3)	517 (19.9)
Coruna clavata	3 (0.7)	12 (1.9)	1 (5.6)	3 (0.6)	19 (3.5)	2 (0.4)	40 (1.5)
Cynipids	32 (7.8)	85 (13.6)	4 (22.2)	73 (15.0)	128 (23.6)	135 (25.6)	455 (17.5)
Dendrocerus bicolor	0	3 (0.5)	0	2 (0.4)	7 (1.3)	5 (1.0)	17 (0.7)
Dendrocerus aphidum	0	2 (0.3)	0	2 (0.4)	2 (0.4)	3 (0.6)	9 (0.4)
Total	409	623	18	486	543	520	2599

* = numbers in parentheses represent percentage of total numbers of primary parasites and hyperparasites

** = reared from aphid mummies which were first collected as alive aphids.

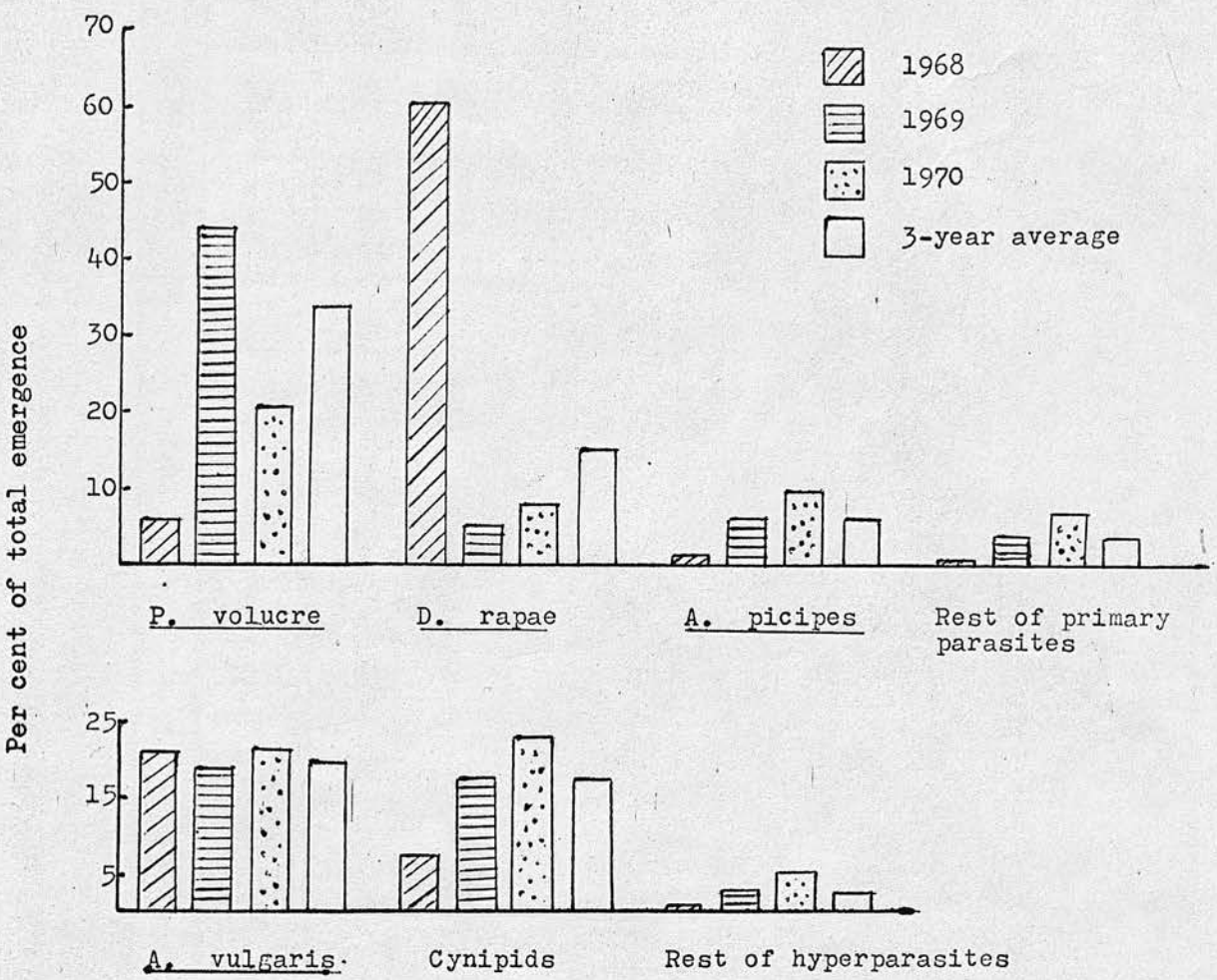

Fig. 19. Percentages of the primary parasites and hyperparasites reared from all aphid mummies collected from brassicas around Edinburgh during 1968, 1969 and 1970.

TABLE 26

Fortnightly totals of three common primary parasites and the hyperparasites reared from Myzus persicae mummies collected at Lasswade and Newington in 1969 and 1970

	1969							1970					Totals		
	8/8	22/8	5/9	19/9	3/10	24/10	7/11	7/8	21/8	4/9	18/9	2/10	1969	1970	Grand
P. volucre	18	46	107	246	105	101	32	8	9	14	0	0	655	31	686
As. vulgaris	1	9	29	17	33	31	16	2	3	1	0	0	136	6	142
Cynipids	5	12	9	9	10	7	0	4	2	4	0	0	52	10	62
C. clavata	0	0	6	4	1	1	0	0	0	1	0	0	12	1	13
Dend. spp.	0	0	0	3	4	1	0	0	0	0	0	0	8	0	8
D. rapae	12	6	11	20	11	17	15	40	11	9	3	0	92	63	155
A. picipes	5	14	9	10	13	23	10	14	4	1	0	0	84	19	103
As. vulgaris	0	6	12	4	9	4	10	22	5	4	0	0	45	31	76
Cynipids	11	24	7	2	11	16	6	12	0	4	0	0	77	16	93
C. clavata	0	0	2	0	0	0	0	1	0	0	0	0	2	1	3
Dend. spp.	2	0	0	0	1	0	0	4	0	0	0	0	3	4	7

P. = Praon; AS. = Asaphes; C. = Coruna; Dend. = Dendrocerus:

TABLE 27

Fortnightly totals of three common primary parasites and the hyperparasites reared from Macrosiphum euphorbiae mummies collected at Lasswade and Newington in 1969 and 1970

	1969							1970					Totals		
	8/8	22/8	5/9	19/9	3/10	24/10	7/11	7/8	21/8	4/9	18/9	2/10	1969	1970	Grand
P. volucre	8	10	20	14	6	5	0	9	48	27	4	0	63	88	151
As. vulgaris	1	8	16	3	12	7	8	2	7	5	6	0	55	20	75
Cynipids	3	10	10	2	12	3	4	2	11	2	3	0	44	18	62
C. clavata	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Dend. spp.	0	2	0	1	0	0	0	1	0	0	0	0	3	1	4
D. rapae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. picipes	2	6	6	11	0	1	0	10	24	5	0	0	26	39	65
As. vulgaris	8	10	4	4	6	8	6	8	6	13	5	0	46	32	78
Cynipids	21	30	21	5	13	1	4	7	9	18	12	0	95	46	141
C. clavata	1	0	1	0	0	0	0	0	0	1	2	0	2	3	5
Dend. spp.	1	0	0	0	0	0	0	2	0	1	0	0	1	3	4

P. = Praon; As. = Asaphes; C. Coruna; Dend. = Dendroserus; D. = Diaeretiella:

2. The primary parasites

(a) Praon volucre

Praon volucre was the most common primary parasite of both M. persicae and M. euphorbiae on the brassicas, constituting about 30% of the parasite complex. In the field, the first adult probably appeared in May (Figures 23 and 25) when low populations of the host could be found on weeds (Table 3), and scarcely emerged from the aphid mummy after November. On the sprout plants, earliest records of the pupa (mummy) was on 21st July, 1969.

M. persicae was parasitised to a greater extent than M. euphorbiae by P. volucre (Tables 26 and 27). The probable reason being the higher density of M. persicae (Figures 10, 11, 12, and 13) and possibly inter-specific competition and difference in host preference. The effectiveness of this parasite was reduced by its being attacked by A. vulgaris and cynipids (Tables 30, 31, and 32).

Effect of temperature on the rate of development of Praon volucre. It is generally known that temperature has some effect on the rate of development of insects. Since no records of such effect on the dominant primary parasite, Praon volucre, was available, it was determined experimentally.

Young fertilised P. volucre females were held with non-parasitised half-grown nymphs of M. persicae on a piece of sprout leaf in a glass tube (7.5 cm. x 2.5 cm.) cork stoppered. Each nymph observed to be parasitised was removed from the tube and placed on a sprout leaf, the petiole of which was inserted into a small plastic vial filled with water and stoppered with a plug of cotton wool. Each leaf with at least fifteen parasitised nymphs was placed into a rectangular plastic container

(height 6 cm. length, 24 cm. width, 11 cm.) with lid. Two of the containers were placed at six various temperatures (5°, 10°, 15°, 20°, 25°, and 30°C) in Gallenkamp incubators (described on Page 39); old leaves were changed by carefully transferring the parasitised aphids to the new leaves. The parasitised aphids were observed daily and the mummified aphids (indication of pupation) were collected by cutting a piece of the leaf (about 6 mm. square) with each mummy and each one was put into a glass tube closed at open end with nylon organdie. They were held at the various temperatures the parasites developed until the adult emergence from the mummies. The photoperiod and relative humidity in all cases were 16 hours and 75-80% respectively.

Table 28 shows the results of the effect of the various constant temperatures on the development of P. volucre. The egg and larval developmental period is the time from oviposition to mummification and the pupal period is mummification to adult emergence. The whole mean developmental period of P. volucre is the time from oviposition to emergence of the adult from the aphid mummy. It is evident from the results that temperature has some influence on the development of the parasite. However, since P. volucre is a parasitoid, it is apparent that the effect of temperature on the parasitic phase (oviposition to mummification) is determined through the need of the aphid, while after mummification the influence is direct.

At 5°C, none of the parasitised aphids reached the mummified stage and all died within 73 days. After 66 days of development one appeared to have partially built the characteristic tent-like structure between the aphid host and the substratum. It was removed and put into the

TABLE 28

Development rates of Praon volucre at different constant temperatures

Temp. °C	No. of aphids	Development time in days					
		Oviposition to mummification		Mummification to emergence		Oviposition to emergence	
		Range	Mean	Range	Mean	Range	Mean
5	34	None reached pupal stage (mummification) - all died within 73 days					
10	23	25 - 27	26.2 ± 0.22	31 - 36	33.3 ± 0.47	57 - 63	59.5 ± 0.46
15	30	12 - 13	12.1 ± 0.06	13 - 18	15.4 ± 0.21	25 - 30	27.6 ± 0.22
20	31	7 - 8	7.7 ± 0.09	9 - 11	9.6 ± 0.12	17 - 18	17.2 ± 0.09
25	20	5 - 8	6.4 ± 0.31	7 - 8	7.5 ± 0.17	13 - 15	13.9 ± 0.31
30	35	Within 10 days all were dead					

environment of 15°C for 60 days but there was no adult emergence. It was dissected and found to be a dead mature larva (prepupa). Other dead parasitised aphids dissected were found to contain various stages of larval growth.

Forty-two days after parasitisation, four of the parasitised aphids were removed from the 5°C environment to a 10°C cabinet. After eight to nine days all the aphids mummified and the adult parasites emerged with an average time of 34 days, normal pupal period (Table 26). The above evidence indicated that at this low temperature, developmental rate of the egg and the early larval stages of P. volucre go on slowly but the mature larval stages seemed to be detrimentally affected.

At 5°C there was no indication of stimulation of development of diapause. However, it must be noted that photoperiod partially influences induction of diapause in insects and that during these studies it was 16 hours, probably insufficient to induce diapause (Danilevskii, 1965). However, in some insects for example, Nasonia vitripennis, Hymenoptera: Pteromalidae, induction of diapause depends on external environmental conditions (e.g. temperature and photoperiod) incident on the maternal generation, that is, diapause is of maternal origin (Saunders, 1962). The P. volucre used in these studies were reared at 20°C with a photoperiod of 16 hours. Such external environmental conditions probably could not have induced diapause in their progeny. Further work on the diapause induction is needed.

The developmental period at 10°C was about twice that at 15°C but with increase in temperature the duration was further reduced until a minimum of about 13 days duration was reached at 25°C. At 30°C, all

the 35 parasitised aphids died within ten days. Dissection of the dead parasitised aphids showed that most of the parasites (25) died as mature larvae.

Mummy and emergence. Two types of mummies were observed during each season. The non-diapause type, white straw-coloured, were found early in the season and the diapause types, brown coloured, first appeared during mid-August. They are thick and more difficult to dissect than the non-diapause mummies. However, slightly different shades of colours and probably different construction appeared between the two main types. Schlinger & Hall (1960) described two types of mummies in related P. exoletum (=palitans) - a diapause and a non-diapause type. There are both white and brown in each type. The diapause mummy is strongly constructed. Force & Messenger (1964a) on the other hand, observed gradation in colour and construction from one type to the other in the same species. Schlinger & Hall (1960) thought that diapause of P. exoletum (=palitans) was induced indirectly through the effect of the autumn and early winter conditions on the alfalfa plant, and that this affected the aphid physiologically, hence the parasite. Force & Messenger (1964a) felt that plant condition had little or nothing to do with the induction of the diapause of P. exoletum (=palitans). In the present studies, however, ~~weekly~~ weekly live aphids in field were collected from July to November and reared in the laboratory under conditions of 20°C and 70-75% relative humidity. The parasitised aphids mummified. The diapause mummies were first observed during mid-August at the same time as those under natural conditions in the field. It seemed that the parasites destined to undergo diapause are induced before the egg stage;

presumably, the induction is of maternal origin.

In nature the adults do not emerge out of the diapausing mummies until spring (Figures 23 and 25). Preliminary study was therefore undertaken to determine the termination of diapause as affected by temperature and photoperiod. Samples of the diapausing mummies, probably in varying depths of diapause, were collected in November, 1969. The samples were randomised as the commencement time of the diapause was not known, and because they were collected from different brassica plants (cabbages and sprouts). The collection was kept in the open insectary and the experiment began when no more of the parasites were emerging in January, 1970.

Each of P. volucre mummy was placed in a glass tube (7.5 cm. x 2.5 cm.) closed at the top with nylon organdie held in position with a rubber band. Fifty of the tubes were placed in two circular plastic containers. Each container was maintained at relative humidity approximately 75% with a saturated solution of sodium chloride in a petri dish (as described on Page 42) and two containers were put in each of the two Gallenkamp cooled incubators (described on Page 39) at 18°C with a 12 hour photoperiod, and at 10°C with a 16 hour photoperiod. The tubes were checked daily for adult emergence for six months.

The results revealed that with the 18°C/12 hour photoperiod, and with the apparent effect of the high temperature, the first P. volucre emerged ten days after diapausing mummies were put in the incubator. The last of the twenty-five P. volucre which emerged from the mummies appeared 111 days after the first one. In the other incubator, the 10°C/16 hour photoperiod caused the first parasite to emerge twenty-nine days after the

mummies were kept in the incubator. In spite of the lower temperature, the emergence period for the thirty-five P. volucre was twenty-five days as compared to the 111 days at 16°C/12 hour photoperiod. The variance ratio of 55:1 of the two emergence periods was highly significant. The longer photoperiod at 10°C might have influenced the shorter emergence period. Both temperature and photoperiod seem to play a part in inducing termination of the overwintering P. volucre. Further work on the factors which induce termination of diapause in aphid parasites is needed.

The adult parasite emerged by cutting a circular opening with the mandibles in the tent-like structure surmounting the whole dead aphid (Plate VII), and pushed itself out with the head first. A small section of the cut is left as a hinge for the emergence hole lid which occasionally falls off. In relation to the mounted aphid, the exit hole is mostly at the posterior end. Of the 294 non-diapause aphid mummies examined carefully, 192 of the parasites emerged posteriorly, 82 anteriorly, and 20 laterally.

Mating. Observations on the mating behaviour of P. volucre were made in a glass tube (7.5 cm. x 2.5 cm.) on not less than twenty-five pairs. In a tube containing the virgin of both sexes, the male showed signs of awareness of the female when they were within a distance of about 3 cm. The male then opened its wings and moved towards the female waving the antennae in the air. When physical contact was made the male rapidly vibrated the wings periodically. Occasionally, the female walked away for a while to be pursued by the male. After a moment the female remained quiet while the male approached her posteriorly; or he might

climb the back anteriorly, grasped the female and moved gradually to the posterior end. He supported himself on the hind legs and might hold the wings of the female with the fore and mid legs. At the same time, he bent the abdomen forward and downwards to copulate with the female. The pair remained quiet during copulation which lasted 18–30 seconds (average 24 seconds). This is comparable to the time of copulation in P. exoletum observed by Schlinger & Hall (1960) but in contrast to the average time of 46 seconds in P. aguti (Sekhar, 1957). Immediately after copulation the male walked off while invariably the female stayed at the spot rubbing the last pairs of her legs against each other and occasionally cleaning the abdomen with these legs. On four occasions when mating had been going on for not less than 25 seconds the actions were terminated by the females cleaning the abdomen with the hind legs or deliberately warding off the males.

The females mated only once during their lifetime. Both virgin (n = 10) and mated (n = 10) males were isolated individually with mated females. The behaviours were varied; in some cases, they (virgin male or mated male and mated female) touched each other by the antennae and moved away unconcerned or both, or the female might jump off. In cases where the male jumped on the female, he was discouraged from mating by the female moving about and pushing him away with the hind legs.

Multiple matings were found among the males. Five males were each observed to mate with 4, 5, 5, 7, and 10 virgin females respectively. Although the number of matings during their life-time were not determined it was likely that they could mate more. Sekhar (1957) found that P. aguti could mate as much as 22 times in its life. The single and

multiple mating behaviours of the female and male respectively were also found among the related P. aguti (Sekhar, 1957) and P. exoletum (Schlinger & Hall, 1960).

Oviposition. Ovipositional habits of P. volucre were observed by confining a parasite in a glass tube (7.5 cm. x 2.5 cm.) containing a piece of sprout leaf infested with about thirty half grown M. persicae. More than twenty mated and unmated females of about 200 ovipositional acts were observed. It was found that generally the parasite was able to perceive the aphid host only by sensory contact. Some of the observations indicated that the parasites could walk alongside the aphid hosts within a distance of a millimetre without perceiving their presence. In one instance, a female parasite moved in a direction swaying her antennae from side to side which missed an aphid yet the parasite literally walked over it without showing signs of oviposition. A moment later, the same parasite touched the same host with her antennae and parasitised it.

The general ovipositional behaviour of P. volucre was similar to that observed by Beirne (1942) and the related P. aguti (Sekhar, 1957) and P. exoletum (Schlinger & Hall, 1960). When a female parasite searching for aphid hosts came into contact with one, she stopped and gently tapped her antennae on the host. She stood on the hind legs and usually put her front legs or sometimes her middle legs on top of the aphid. At the same time she bent the abdomen downward and forward and often used the ovipositor to search for an appropriate point on the host and rapidly thrusted the ovipositor in. The wings were normally raised vertically above the body in a V-shape.

The positioning of the fore legs on the aphid host during oviposition seemed typical of the Praon species. Schlinger & Hall (1960) reasoned that it could be an adaptation to overcome the jumping habit of the aphid, however, it might also be for the successful oviposition in Praon species.

During the ovipositional act, the aphid could be lifted off the leaf surface by the ovipositor until the latter was withdrawn. Older aphids tended to sway their abdomens or walked away when the parasites made the initial contact or attempted to oviposit. In such cases they were pursued by the parasites with the abdomens in the bent positions until the aphids were parasitised. Immediately after the oviposition, the parasite walked away from the aphid.

Ovipositional strikes were usually made at any part of the body and from any angle but greater preference was shown to the abdominal region. Location of the ovipositional strikes on the host body was carefully observed. Of 128 cases observed, 104 were in the abdomen, 12 on the thorax, 8 on the antennae and the head, and 2 on the legs. Occasionally the parasites were found orientating themselves to avoid strikes on the head region or on the legs. However, Schlinger & Hall (1960) found this behaviour contrary to that of P. exoletum.

The parasites observed individually in the small confinement of the glass tube with about thirty aphid hosts showed that they have a pattern of successive ovipositional strikes. Within a few minutes, the parasites were able to locate the host. Uninterrupted groups of 2 - 6 strikes went on within periods of rest, 2 - 25 minutes. The rest periods between successive strikes were longer and the number of

strikes diminished during each observation period of two hours per day. With advance in age, the above ovipositional activities were reduced. The old parasites often slowly initiated ovipositional strike but stopped in the middle of the action and moved away.

Sex ratio. Like other Aphidiidae, Praon volucre is parthenogenetic. The female deposited eggs when aphid hosts were available, whether mated or unmated. Six virgin females were allowed to oviposit for ten days in unparasitised aphids. All their progeny were males, indicating that P. volucre is arrhenotokous.

In 1969, the numbers of females slightly exceeded those of the males, while in 1970 the sex ratio was almost equal. Of the 376 adults of P. volucre reared in 1969 from all the aphid mummies collected, 226 (60.1%) were females. In 1970, 160 out of 308 (51.9%) were females.

Longevity. To determine the influence of temperature on the adult longevity of P. volucre, newly emerged parasites were kept in glass tubes (7.5 cm. x 2.5 cm.) provided with cotton wool soaked in dilute honey solution as food. The open end was covered with nylon organdie held in position with a rubber band. A number of such tubes containing both sexes were kept in a circular plastic container maintained at relative humidity of about 75% as described on Page 123. One or two of the containers were placed at various temperatures (5°, 10°, 17°, and 25°C) in Gallenkamp cooled incubators. The glass tubes were checked daily and mortality recorded. The results shown in Table 29 indicate that longevity of the adult P. volucre decreased with rise in temperature, as in other insects. Differences in the longevity of the sexes were apparent at the various constant temperatures. At all the temperatures the female

parasites lived longer than the males. On the contrary, Schlinger & Hall (1960) found that at certain different temperatures the males of P. exoletum showed greater longevity than the females. However, they varied the relative humidities with the various temperatures and the relative humidities were generally lower than those used in the present study. Secondly, the species of parasites were different.

Fecundity. The total fecundity - the total number of eggs deposited by the female parasite throughout life - was determined at constant temperatures of 5°, 15°, and 25°C. Ten newly emerged mated females of P. volucre were used at 5° and fifteen at each of the other two temperatures. The method and material used were the same as described under 'longevity' at Page 128 except that a fresh strip of sprout leaf infested with fifteen half grown M. persicae was provided daily until death of the female parasite.

The total number of eggs laid daily by each female parasite was determined by rearing the parasitised aphids removed from the tube in the laboratory at a temperature of about 20°C for two days before dissecting. Newly laid eggs were too small to be found easily among the internal tissues of the host, but after two days, the advanced eggs and early larval instars were easily recognised for recording.

At 5°C, the inhibiting effect of the low temperature on the activities of the parasites was apparent. During the average adult life time of 81.3 days, the mean number of eggs deposited was 3.8 eggs per parasite. With increase in temperature to 15°C, the total number of eggs oviposited by parasite ranged from 90 to 188 (average 121.6 $\pm$ 12.9), at 25°C the range was 108 to 208 (average 169.4 $\pm$ 13.7). Figure 20 shows the relationship of daily oviposition rate with the parental

TABLE 29

Effect of temperature on longevity of Praon volucre

Temp. °C	No. & sex	Longevity in days		Mean long'y ratio		P <
		Range	Mean	♂	♀	
5	10 ♂	28 - 56	40.0±2.42	1 :	1.5	0.001
	16 ♀	37 - 85	59.3±3.68			
10	11 ♂	19 - 45	29.8±2.17	1 :	1.6	0.001
	13 ♀	33 - 59	48.8±2.57			
17	7 ♂	13 - 20	15.1±0.91	1 :	1.5	0.01
	11 ♀	14 - 36	22.9±1.78			
25	14 ♂	3 - 12	8.1±0.62	1 :	1.3	0.001
	15 ♀	5 - 13	10.8±0.59			

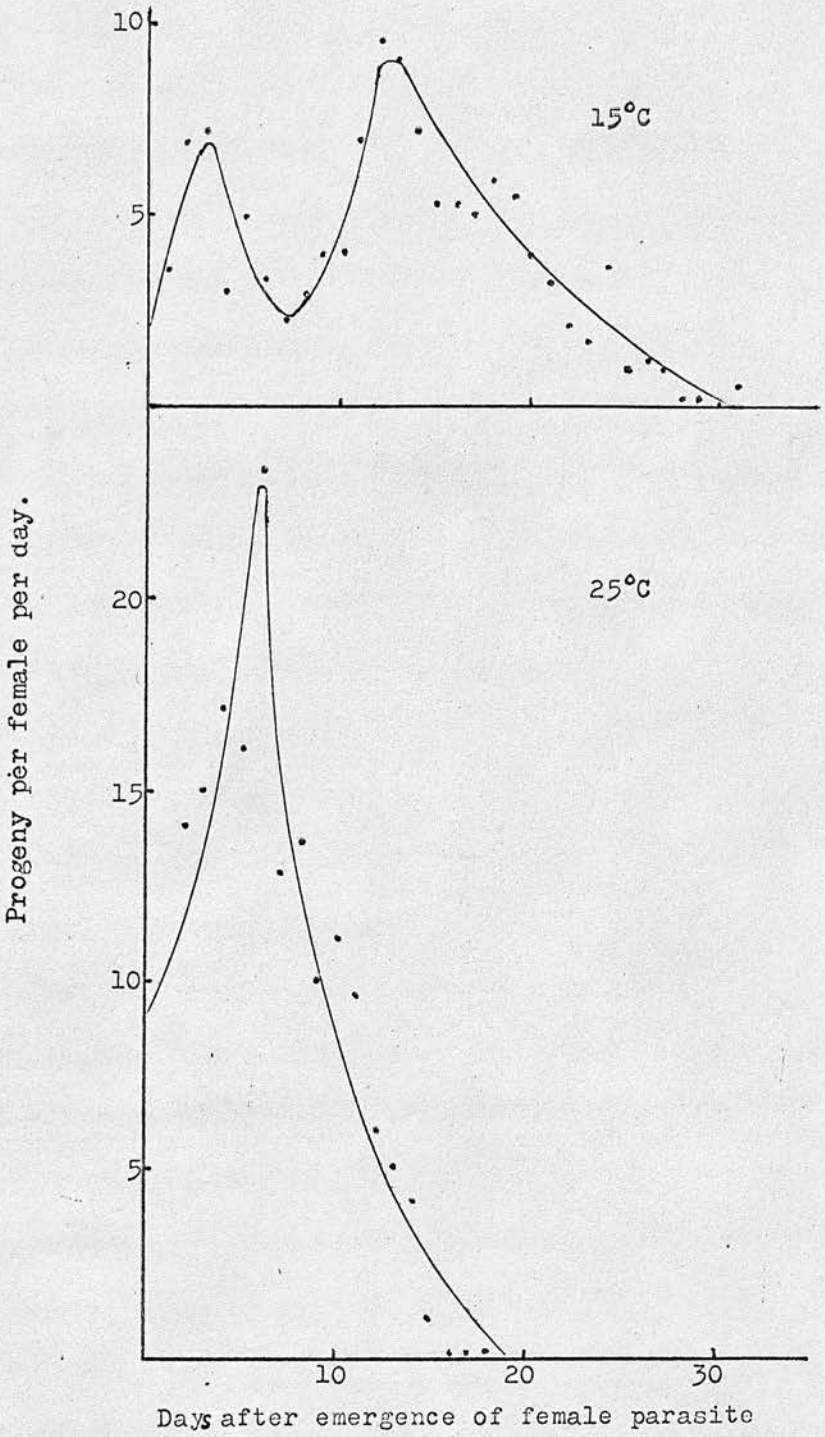

Fig. 20. Daily fecundity of Praon volucre at constant temperatures of 15° and 25°C.

age of P. volucre at constant temperatures of 15°C and 25°C. At 15°C there was an early smaller peak of the daily oviposition rate followed by a bigger peak about ten days later which tailed off steadily. At the higher temperature of 25°C, the daily fecundity rate rapidly decreased after the peak had been reached a few days from the beginning. The mean total fecundity of related P. exoletum appeared to be higher than that of P. volucre. Force & Messenger (1964b) stated that temperatures below 15.6°C induced diapause in P. exoletum so that studies of reproductivity could not be carried out while the mean total fecundity at 23.9°C was 299.9. The differences between their work and the present study at 15° and 25°C might be due to the physiological differences between the species and the experimental condition of 12 hour photoperiod and 40 - 60% relative humidity.

(b) Praon myzophagum Mackauer

This species was reared from both Myzus persicae and Macrosiphum euphorbiae. Twenty specimens emerged from mummified aphids collected during August, September and October of 1969 and 1970. All the specimens reared were found to be females and the species was thought to be unisexual. To confirm this another female which was reared later and thought to be of the same species was confined with a number of unparasitised half grown M. persicae. All the progeny were males and they appeared much darker than the females. Professor Mackauer of Simon Fraser University, Canada, who earlier on identified the female P. myzophagum, commented that these males differed in a number of characters from a typical P. myzophagum, for instance, in wing venation and in the chaetology of the thorax, apart from the differences in colour

which were not significant. To ascertain further, he needed to examine more material including female specimens. Unfortunately larger numbers of the required specimens were scarce and it was near the end of these studies when the request was made. However, it seemed that they could be a different species of Praon. The male P. myzophagum which was not recorded in the studies may have completely different characteristics from the female. This probably made it difficult to differentiate between the males of P. volucre and P. myzophagum. The latter were however, scarce considering the numbers of the females reared.

The abdomen of the female P. myzophagum is slightly darker compared to that of continental European specimens (Mackauer, per. comm. 1970).

(c) Diaeretiella rapae McIntosh

Diaeretiella rapae was reared mainly from M. persicae. Only eight of this species were reared from Macrosiphum euphorbiae during the whole study period (Tables 26 and 27) (Appendices 36 and 38). D. rapae formed 86.5% of the primary parasite complex in 1968 while at Lasswade and Newington together, in 1969, it constituted 9.3% and 17.0% in 1970 (Table 25).

Under laboratory conditions of 20° - 23°C and 50 - 60% relative humidity, the parasite had an average developmental period, oviposition to emergence of the adult, of 16.2 $\pm$ 0.7 days. The time from deposition to mummification and mummification to adult emergence from aphid hosts, respectively, took 10.6 $\pm$ 0.4 and 5.7 $\pm$ 0.3 days. The mature last instar larval stage makes a small hole at the ventral surface of the

aphid host and fastens the aphid, which has then turned into a hardened brown straw-coloured mummy, to a leaf. A circular emergence hole is cut, usually posteriorly at the dorsal side and the lid often remains hinged to it, (Plate VIII).

The sex ratio indicated a greater number of females during the study.

Female : male 1.7 : 1 (267 specimens)

d) Aphidius (Diaeretiella) species

Only one undetermined female specimen of Aphidius (Diaeretiella) was reared from a mummified M. persicae collected from Lasswade on 22:8:69. It took eleven days to emerge from the aphid mummy.

e) Aphidius picipes (Nees)

This parasite attacked both M. persicae and M. euphorbiae at all sites during the study period. It was scarce during 1968 but was of about the same abundance as D. rapae in 1969 and half as numerous as D. rapae in 1970 (Figure 19).

The developmental period was determined under the same laboratory conditions as were used for D. rapae. The duration of oviposition to adult emergence from aphid mummy was 16.0 ± 0.7 days; oviposition to mummification, 9.5 ± 0.3 days, and mummification to emergence 6.5 ± 0.6 days. These periods were comparable to those of D. rapae.

The adult parasite was the first of the primary parasites to emerge out from hibernation in April during spring (Figure 25 and Appendix 43). In the experimental plots mummies of Aphidius species and/or Diaeretiella rapae were encountered a week or two earlier before that of Praon species (Tables 39, 40 and 41).

Plate VIII. Mummified Myzus persicae with emergence holes of Diaeretiella rapae.

Results in Tables 26 and 27 show that M. persicae was parasitised to a greater extent by A. picipes and other parasites than was M. euphorbiae. The results might have been influenced by the host abundance and parasitic competition. After August, M. euphorbiae disappeared and M. persicae was generally still in abundance (Figures 10c and 11c).

The sex ratio showed a preponderance of females during the study period.

Female : male 1.8 : 1 (139 specimens).

(f) Aphidius ervi Haliday

Only two specimens of this species were recorded. The first emerged from M. euphorbiae mummy collected in 1968. The other of uncertain identification was reared from a M. persicae mummy collected from Lasswade in 1969.

(g) Aphidius urticae group

This species was found at both Lasswade and Newington in 1969 and 1970 as a parasite of M. persicae and M. euphorbiae but was not reared from any aphid mummy collected in 1968. A. urticae group was not common. In 1969 only twelve and thirteen adults, respectively, emerged from M. persicae and M. euphorbiae. The only two adults found in 1970 were also reared from M. persicae and M. euphorbiae. Aphid mummies from which they emerged during the study period were collected mainly in August and September. It was determined as a group because related species are yet to be separated taxonomically (Mackauer & Stary, 1967, Ferguson per. comm. 1971).

(h) Aphidius rosae group

Only three adults were reared from M. euphorbiae during the present study. The aphid mummies were collected from Lasswade on 8:8:69, 29:8:69 and 12:9:69, and the parasites emerged on 22:8:69, 4:9:69 and 23:9:69, as two females and one male.

(i) Ephedrus plagiator Nees

Both M. persicae and M. euphorbiae were attacked by E. plagiator. Only one adult was reared in 1968. In the following year, at both Lasswade and Newington, twelve adults emerged from each of the two hosts. In 1970, twenty-four adults were reared from M. euphorbiae and only one from M. persicae. The numbers are too small for any definite conclusion, but it shows an indication of host preference.

Under the same laboratory condition in which the developmental periods of D. rapae and A. picipes were determined, E. plagiator was found to take a period of 20.4 $\pm$ 0.9 days to develop from oviposition to adult in M. persicae. The duration is significantly longer ($P < 0.01$) than those for D. rapae and A. picipes. The periods of oviposition to mummification, and mummification to adult emergence from the mummy, respectively, took 11.5 $\pm$ 0.9 and 9.2 $\pm$ 0.02 days. At the mature larval instar stage, as the parasite fastens the aphid host on the substratum, the host distends and completely turns black. The emerging adult cuts a large exit hole at the posterior portion, sometimes both cornicles form part of the emergence lid. The emergence hole is often larger than those for the D. rapae and Aphidius species which are also situated at the posterior dorsal side of the aphid host.

Sex ratio showed abundance of males during the study period.

Male : female 2 : 1 (45 adults).

The probable cause of the preponderance of males might be the low density of the parasites. As indicated in Table 25 E. plagiator formed less than 1% of the primary parasite complex. At such a low density the chances of both sexes meeting were low and the unmated females would reproduce only males as it was observed during the study.

(j) Toxares deltiger Haliday

This parasite occurred on only two occasions with M. persicae as the host. Both were reared from live aphids collected from Newington on 11:8:69 and 18:8:69.

(k) Monoctonus pseudoplatani Marshall

This species emerged only once as a parasite of M. euphorbiae. The female emerged from an aphid mummy collected from Lasswade on 22:8:69.

Stary (1966) referred to this parasite as Monoctonus (Falciconus) pseudoplatani but Mackauer & Stary (1967) catalogued it as Falciconus pseudoplatani.

(l) Dyscritulus planiceps Marshall

Three mummified M. euphorbiae containing D. planiceps were collected on 29:8:69, 5:9:69 and 12:9:69 from Lasswade and only the first mummy yielded a parasite thirteen days after the collection. The mummy of this species is constructed in a similar way to that of Praon species

described on Page106 but the main distinction is the thicker and well defined circular edge.

(m) Aphelinus asychis Walker

This species appeared only once as a parasite of M. euphorbiae. The mummified aphid was collected from Lasswade on 31:7:70 and the parasite emerged twenty-one days later.

(n) Aphelinus flavipes Kurdjumov

Three adults were reared, two of which emerged from mummified M. euphorbiae collected from the field and the other from a M. persicae which was initially brought to the laboratory alive. All were obtained from Lasswade in August 1969.

(o) Aphelinus sp. nr. tibialis Nees

There seems to be some uncertainty about the taxonomy of A. tibialis. The specimen found during the present study was determined by Mr. J. C. Hall, University of California, Riverside, U.S.A. Peck (1963) synonymised A. tibialis with A. chaonia Walker, while Ferriere (1965) considered it to be the same as A. varipes Foerster. However, he catalogued as a separate specific group.

Aphelinus sp. nr. tibialis parasitised Macrosiphum euphorbiae and two adults emerged from mummies collected in August 1969 at Lasswade.

(p) Aphelinus sp. nr. davicola Foerster

This species occurred on only one occasion as a parasite of M. euphorbiae. The aphid mummy was collected from Lasswade on 8:8:69 and the parasite emerged six days later.

(q) Aphelinus sp. ?mali (Haldeman)

Like Aphelinus sp. nr. davicola, only one specimen of this parasite emerged out of a M. euphorbiae mummy collected at Lasswade. The mummy was collected on 15:8:69 and the parasite emerged ten days later.

3. The hyperparasites

(a) Cynipids

All the hyperparasites belonging to the family Cynipidae, subfamily Charipinae are discussed together because of the difficulties of their taxonomy (Hellen, 1963; Evenhuis, 1964; Quinlan, per. comm. 1970).

Of more than 100 specimens sent to the British Museum in 1970 from 1969 collections, the majority of them belonged to the genus Phaenoglyphis Foerster, only five were of the genus Alloxysta Foerster (Quinlan, per. comm.). This indicated that Phaenoglyphis species are probably the most common of the cynipids around Edinburgh. Only one adult of the brachypterous species of Alloxysta was found during the present study. It emerged from M. persicae through Aphidius species and/or D. rapae.

Cynipids were the most numerous hyperparasites (49.8%) found in the present study. The earliest record of emergence from overwintering was on April 20th, 1970, through D. rapae and/or Aphidius species. They could overwinter for longer durations than Asaphes vulgaris, the next common hyperparasite (43.8%), as indicated on Figures 30 and 31. The maximum period of the time between collection of the mummies in the field and the emergence of the adult was 368 days (at least the hibernation period could be longer than this period in the field).

To obtain some indication of the adult longevity, a newly emerged cynipid was kept in a glass tube (7.5 cm. x 2.5 cm.) provided with cotton wool soaked in honey solution as food. The top of the tube was covered with nylon organdie held in position with a rubber band. Ten of the tubes were placed into each of the various constant temperature conditions as described on Page 39 . The maximum longevity of the adult cynipids at the various constant temperatures were as follows: 5^{o}, 107 days; 10^{o}, 133 days; 17^{o}, 102 days; 25^{o}C, 47 days.

With a decrease in temperature, the adult longevity tended to increase but at 5^{o}C the harmful effects of the low temperature started to be evident.

The cynipids were reared from Myzus persicae and Macrosiphum euphorbiae through Praon volucre, D. rapae and/or Aphidius species and Ephedrus plagiator.

The results shown in Tables 30, 31, and 32 indicate that cynipids seem to exhibit preference in the selection of the host. In 1969, at Lasswade, D. rapae and/or Aphidius species were parasitised by cynipids through M. persicae to the extent of 21.9% and by Asaphes vulgaris, 13.2% (X^2 = 9.6, d.f = 1, $P < 0.01$). At the same site, cynipids parasitised D. rapae and/or Aphidius species to the extent of 53.1% and A. vulgaris, 30.8% (X^2 = 8.54 d.f = 1, $P < 0.01$). Through M. euphorbiae at Newington, it was further confirmed that cynipids parasitised more of D. rapae and/or Aphidius species than did A. vulgaris (X^2 = 13.8 d.f = 1, $P < 0.001$). In 1970, at Lasswade a similar relationship of statistically non-significant results were observed (X^2 = 3.0 d.f = 1, $P < 0.05$). One of the important factors

TABLE 30

Percentage infection of the primary parasites by the hyperparasites - Newington 1969

Aphid host	Primary parasites		Hyperparasites				% parasitism by hyperparasites				
	Species	No.	Dend. spp.	Cyns	A.vul.	C.clav.	Dend. spp.	Cyns	A.vul.	C.clav.	TOTAL
M. per. & M. euph.	P.volucre	320	3	20	10	3	0.69	4.6	19.0	2.3	26.6
	D.rapae/ or Aphidius spp	84	1	62	2	1	0.57	35.2	15.3	1.4	52.5

M. per. = Myzus persicae
M. euph. = Macrosiphum euphorbiae
/ or = and/or

Dend. spp. = Dendrocerus species;
A. vul. = Asaphes vulgaris;
C. clav. = Coruna clavata:

TABLE 31

Percentage infection of the primary parasites by the hyperparasites - Newington 1969

Aphid host	Primary parasites		Hyperparasites				% Hyperparasitism				
	Species	No.	Dend. spp.	Cyns	A.vul.	C.clav.	Dend. spp.	Cyns	A.vul.	C.clav.	Total
M. per.	P.volucre	326	4	35	66	2	0.92	8.1	15.2	0.46	24.7
	D.rapae/or Aphidius spp	95	3	33	20	0	2.00	21.9	13.2	0	37.1
M. euph.	P.volucre	54	0	41	52	0	0	27.9	35.4	0	63.3
	D.rapae/or Aphidius spp	22	0	76	44	1	0	53.1	30.8	0.70	84.6

M. per. = Myzus persicae; Dend. spp. = Dendrocerus species;

M. euph. = Macrosiphum euphorbiae; A. vul. = Asaphes vulgaris;

/ or = and/or C. clav. = Coruna clavata;

TABLE 32

Percentage infestation of the primary parasites by the hyperparasites - Lasswade 1970

Aphid host	Primary parasite		Hyperparasites		% Hyperparasitism		
	Species	No.	Cynipids	Asaphes	Cynipids	A. vul.	Total
Myzus persicae and Macrosiphum euphorbiae	Praon volucre	123	28	22	16.2	12.7	28.9
	D. rapae and/or Aphidius spp.	117	92	70	33.0	25.1	58.1

A. vul. = A. vulgaris

/ or = and/or

in the above comparison was that cynipids and A. vulgaris were almost of the same numbers at the various sites during 1969 and 1970 (Table 25).

Fielding (1953), Evenhuis (1964) and Gutierrez & van den Bosch (1970) found some Cynipids to exhibit preferences in the primary parasites they attacked. The reasons and mechanism for the host preferences of hyperparasites were not known, but factors such as different densities and different times of appearances of the aphid hosts, primary parasites and hyperparasites might all play a part.

Although the cynipids are external parasites on aphidiid within the aphid hosts, they could be parasitised by A. vulgaris which could act as a tertiary parasite. It is most likely that the numbers of cynipids were reduced as a result of such attack.

(b) Asaphes vulgaris Walker

This hyperparasite was slightly less common than the cynipids. It constituted 43.8% of the hyperparasite complex. It was much more abundant within the mummies during September and October (Tables 26 & 27). Although this species undergoes overwintering, there could be sporadic adult emergences during the winter period (Figures 24 and 26). Such adults particularly the females could probably survive mild winters, as under a constant temperature of 5°C adult females could live, when fed on honey solution, to a maximum period of 248 days.

Adult longevity at various constant temperatures was determined using the same materials and methods as that for cynipids (Page141).

The results shown in Table 33 indicate that, as in other insects, the increase in temperature reduced the longevity of the adult

A. vulgaris and that the female significantly lived longer than the male. However, the adverse effect of the cold temperature became evident at 5°C, as it did with cynipids.

A. vulgaris parasitised Praon volucre, D. rapae and/or Aphidius species and E. plagiator through M. persicae and the same primary parasites through M. euphorbiae. In contrast with cynipids, A. vulgaris seems to be a more effective parasite of Praon volucre than D. rapae and/or Aphidius species through both M. persicae and M. euphorbiae. Data in Table 31 shows that in 1969, at Lasswade, A. vulgaris parasitised P. volucre to the extent of 15.2%, cynipids, 8.1% (X^2 = 9.6 d.f = 1, $P < 0.01$) through M. persicae and again, A. vulgaris, 35.4%; cynipids, 27.9% non-significantly (X^2 = 1.3, d.f = 1 $P > 0.05$) through M. euphorbiae.

(c) Coruna clavata Walker

This hyperparasite attacked M. persicae through P. volucre, and D. rapae and/or Aphidius species, and M. euphorbiae through D. rapae and/or Aphidius species and E. plagiator. C. clavata was a less common hyperparasite (3.9%). In 1968 only three individuals hyperparasitised M. persicae through P. volucre and D. rapae and/or Aphidius species. At both Lasswade and Newington, in 1969, fourteen were reared from M. persicae through P. volucre and D. rapae and/or Aphidius species, and three from M. euphorbiae through D. rapae and/or Aphidius species and E. plagiator.

A diapausing mummy containing C. clavata collected in the field on 5:9:69 emerged after 278 days, the longest hibernation period recorded in the open insectary (the hibernation period in the field might be

TABLE 33

Effect of temperature on adult longevity of Asaphes vulgaris

Temp C	Number & sex	Longevity in days		Stat'l sig'ce P
		Range	Mean	
5	11 ♂	33 - 157	101.8 ± 12.8	0.05
	5 ♀	59 - 248	139.4 ± 36.6	0.05
10	7 ♂	67 - 145	111.7 ± 10.4	0.05
	6 ♀	103 - 239	174.7 ± 20.0	0.05
17	4 ♂	16 - 90	50.0 ± 17.1	0.05
	5 ♀	83 - 198	148.3 ± 28.1	0.05
25	7 ♂	15 - 48	31.7 ± 3.9	0.01
	4 ♀	45 - 88	70.5 ± 9.3	0.01

longer than this). The earliest time of adult emergence from diapausing mummy was May 30th, 1970.

(d) Dendrocerus (Macrostigma)aphidum (Rondani) and Dendrocerus (Macrostigma) bicolor (Kieffer)

In a recent study, now in press, Dessart (per. comm. 1970) has revised the genus, Dendrocerus (=Lygocerus), and the names used in this work are those which appear in this revision. The female D. bicolor has yellow legs while the D. aphidum has dark legs except the fore tibiae. The males may be separated only by genitalia characters. The mounted slides of the genitalia in the Department of Agricultural Zoology, Edinburgh School of Agriculture, are enough to verify minute important characters, but insufficient for an accurate study of the genitalia.

Both species hyperparasitised M. persicae through P. volucre and D. rapae and/or Aphidius species and M. euphorbiae through the same primary parasites.

Like C. clavata, they were scarce hyperparasites (2.7%) during the study. None of the species was found in 1968, but in 1969, at Lasswade and Newington three females and three males of D. bicolor and six females and four males of D. aphidum were reared from M. persicae and M. euphorbiae through D. rapae and/or Aphidius species and P. volucre. In 1970, nine specimens of both species were recorded as hyperparasites of the same aphid hosts through the same primary parasites as in the previous year (Appendix 39). The early appearance of both species from overwintering was in late June and the maximum period they stayed in hibernation after collection of mummies from the field was 260 days.

Like all the other hyperparasites, they emerged from the mummies usually by biting through the dorsal side. The edge of the emergence holes are irregularly cut and their positions on the mummies are not definite - they varied from mummy to mummy - as compared to that of the primary parasites (Plates VIII; IX). Such characteristics could probably be used to distinguish between empty mummies, which previously contained primary parasites, and hyperparasites during sampling in the field.

4. The trend of primary parasite and hyperparasite emergence from the aphid mummies

During the summer and autumn, the emergence of the primary parasites from the non-diapausing mummies preceded that of the hyperparasites, as illustrated in Figures 21 and 22.

In 1969 the time lag between the peak of emergence of the primary parasites and that of the hyperparasites was 25 days and in the following year it was about 35 days. This emergence time difference between the primary parasites and the hyperparasites was to be expected. In nature, for the hyperparasites to thrive, the primary parasites should appear first to attack the aphid host and then the hyperparasites follow to parasitise the larvae or the pupae of the primary parasites.

Among the primary parasites, A. picipes was the first to emerge over the shortest period after the aphid mummies were collected from the field. They appeared between 1 - 20 days with a peak time of emergence after about 10 days. E. plagiator had an emergence range of 3 - 21 days. D. rapae and A. picipes also emerged, respectively, within the range of

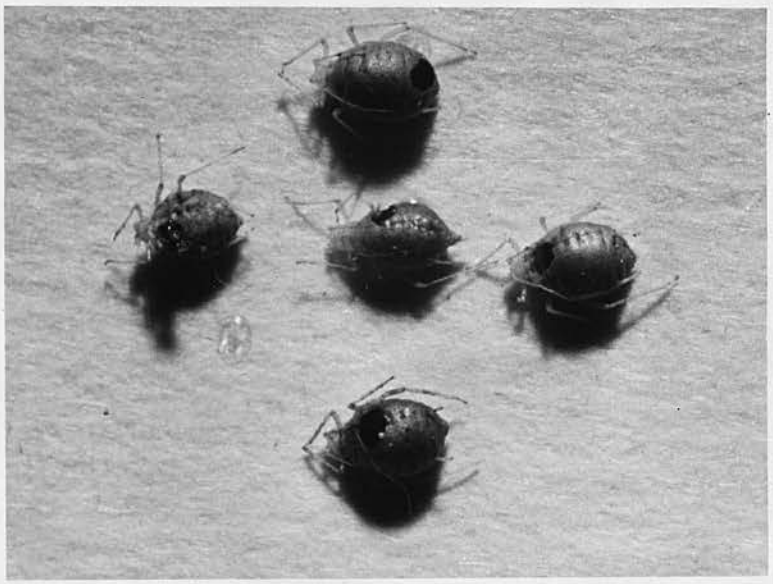

Plate IX . Mummified Myzus persicae and Macrosiphum euphorbiae with emergence holes of cynipids.

1 - 28 and 1 - 65 days.

The hyperparasites have longer time ranges for emergence. The cynipids, like A. vulgaris, emerged at infrequent intervals over a period of 1 -103 days with the main emergence peak at about 35 days after the aphid mummies were collected from the field. A. vulgaris appeared to have no definite peak during the summer and autumn emergence, but most of the adults emerged between 30th and 45th day after being kept in the open insectary. A. vulgaris emerged over the longest period of 6 - 121 days.

In 1970, the succession and length of the emergence periods for the primary parasites and hyperparasites were of the same trend as those for 1969. However, the actual durations and the peak ranges appeared varied, mainly because of the differences between the environmental conditions of the two years. The emergence ranges and peak periods of 1970 were as follows:

Primary parasites	Emergence range in days	Approximate peak period
Aphidius picipes	1 - 11	5
Ephedrus plagiator	1 - 17	10
Diaeretiella rapae	1 - 21	5
Praon volucre	1 - 39	15
Hyperparasites		
Asaphes vulgaris	15 - 57	35
Cynipids	5 - 54	15 - 35

After summer and autumn emergence the parasites emerged from the diapausing mummies later in spring. In 1969, as shown in Figure 23

there was sporadic emergence of D. rapae from the overwintering mummies in Jamuary. Although M. persicae overwinter in the apterous form on dock weeds, such emerging parasites might not be able to parasitise any aphid host due to the cold weather which might inhibit activity. Even if they were able to attack the hosts, development might not be completed (Page 121).

During the last week of May a small emergence occurred but the major one appeared at about the third week of June. P. volucre started to emerge from the mummies in late May reached the peak which was lower than the small peak of D. rapae. A. vulgaris emerged from the mummies in small numbers from January to March and stopped. Emergence started again in early June and rose to a peak by the middle of the month and then suddenly declined to zero inside two weeks. Cynipids first appeared in May and continued to occur in irregular low numbers till the end of July (Figure 24).

In 1970, as shown in Figure 25, A. picipes was the first of the primary parasites to emerge from the overwintering mummies in March, and low numbers continued to emerge until June. D. rapae started to appear in the third week of April and like A. picipes the emergence numbers were low until the last one emerged in mid-July. P. volucre was the last of the primary parasites to emerge from overwintering during the second week of May and rose rapidly to reach a peak by the end of the month and then sharply declined to zero by mid-June. As in the previous year, A. vulgaris was the first of the hyperparasites to emerge in January, and like the cynipids the main emergence from the overwintering mummies started in May and numbers reached their peak in early June with that for A. vulgaris greater than for the cynipids (Figure 26). From the peaks, the rate of decline

of A. vulgaris was faster than that of the cynipids, which tailed off later in early August.

In 1971, only a few of the P. volucre and a single specimen of A. picipes emerged from the aphid hosts in spring (Appendix 44). The hyperparasites appeared later in April than in the previous years and the time lag of the peak emergence was a week earlier than in 1970. The hyperparasite numbers decreased to zero during late June and in early July (Figure 27).

It has been shown that the summer and autumn emergence of the primary parasites from the non-diapausing mummies preceded that of the hyperparasites and the appearances of the different parasites seemed to be in a definite order.

The successive emergences of the primary parasites and hyperparasites might be partially due to the differences in the lengths of the biologies of the different parasites under the same condition. Under the laboratory condition of 18° - 23°C and 50 - 60% relative humidity, the developmental period of the pupal stages of A. picipes, E. plagiator, and D. rapae were found to be 6.5, 9.2 and 5.7 days respectively. The pupal period of P. volucre took 9.6 days under constant temperature of 20°C and 75% relative humidity in a Gallenkamp cooled incubator. Haviland (1921) reared Charips species, a cynipid, in "an open air insectary" and reported a pupal period of 22 - 26 days. At 23°C Sekhar (1958) found the developmental time of egg to adult of the related Asaphes fletcheri to be 27 days.

Aphid mummies collected in the field contained various stages of development of the mature larvae or pupae of the primary parasites and the cynipids. But since A. vulgaris deposited its egg only through mummified aphids alongside the mature larva or pupa of the primary parasite, those

mummies collected in the field contained different growth stages of egg, larva and pupa of the hyperparasite, hence, possibly, the long emergence range period.

By the end of each of the three autumn seasons, a proportion of the mummies collected during the summer and autumn consisted of overwintering types (Tables 42 and 43). Parasite emergences from the overwintering mummies started from spring to summer with peaks in June.

In the first two years of this study, the peak emergences of the primary parasites from the overwintering mummies preceded that of the hyperparasites by 1 - 3 weeks, or in some cases they coincided with each other, especially in 1969. The difference in the population densities of the various parasites in the different years could be attributed to factors such as the different occurrence of the aphid host populations and the various parasites at different times of the seasons. Another consideration was the different effects of weather conditions particularly in autumn, winter and spring.

The hyperparasites, particularly cynipids, overwintered early in the season and exerted less influence on the parasitised aphids in September thereby causing the overwintering mummies of the primary parasite to be increased. By early September 1970 however, other mortality factors reduced the aphid population almost to zero at Lasswade, therefore the overwintering mummies of the primary parasites were scarce. There were thus very few primary parasites but numerous hyperparasites, especially cynipids, in spring of 1971.

A. picipes and D. rapae emerged sporadically from the overwintering mummies in March and April of the first two seasons. In nature it was possible for them to find aphid hosts to parasitise on weeds and to start

building the parasite population for the seasons. The important point was the occurrence of the peak emergence of the primary parasites during late May and early June which overlapped with the time of the rapid population increase of the overwintering M. persicae on dock weeds. In addition, other aphids had started to infest weed plants - Aphis fabae was found on nettle (Urtica urens) and thistle (Carduus arvensis) at the time. The earliest mummy was found on dock on April 29, 1970, at Gilmerton. During late May, 1971, Gerard (per. comm.) found aphid mummies of both Praon species and D. rapae and/or Aphidius species on strawberry at Dryden (Midlothian). The primary parasites being polyphagus, probably two or three generations could occur on weeds before they attacked aphids on brussels sprout crops in July.

EXTENT OF PARASITISM IN THE FIELD

In a previous section (Page 86) the population dynamics of aphids on brussels sprout crops and the mortality factors which influence these changes were discussed. In view of the importance of Myzus persicae as a pest even at low densities in Scotland, and a possible use of parasites as a controlling agent, field parasitism was carefully evaluated in relation to the changing host population.

ASSESSMENT BY REARING NYMPHS FROM THE FIELD

Method

It has been found in this work that M. persicae is parasitised by more than one primary parasite in south east Scotland. The different species of the primary parasites were not likely to be easily identified when the aphids were to be dissected. To have indications of the role played by various primary parasites in attacking M. persicae, the live aphids were reared for the parasitised ones to mummify. Parasitism was evaluated by weekly collection of the advanced apterous nymphs from the sprout plants during aphid sampling at Lasswade and Newington in 1969 and 1970. They were reared on brussels sprout leaves in plastic containers with lids (24 cm. x 12 cm. x 6 cm.) in Gallenkamp cooled incubators or in the laboratory under conditions of about 20°C and 75% relative humidity, for a duration of fourteen days. The aphids were checked daily for mummified ones. They were counted and cut out with a small leaf attached and each was put into a glass tube (7.5 cm. x 2.5 cm.) the tops of which were covered with nylon organdie held in position with rubber bands. The tubes were placed in the laboratory and parasites and hyperparasites which emerged from the mummies were sexed and recorded.

Generally, about 100 aphids were reared but when aphids were scarce, for instance, at Newington, in 1970, fewer were collected. Advanced apterous nymphs were selected for rearing because they were the group containing the immature stages of the parasites to a greater extent than any group of live aphids. The proportion of the mummified aphids was taken as the rate of parasitism. However, this could not be taken as the absolute rate of parasitism for the whole aphid population.

Results.

Year 1969

Figures 10b, 11b, and Table 34, 35, show the results of the rearing of nymphs collected at Lasswade and Newington. At Lasswade, the rate of parasitism increased steadily and slowly to the first peak in mid-August, which declined to a low level of 4.0% by early September. Again, parasitism increased sharply to 18.0% and was maintained at about this level until mid-October when there was gradual decline to zero by mid-November. At Newington the trend of the rate parasitism was very similar to that of Lasswade, although it was higher, particularly in July and August.

P. volucre was a much more effective parasite than D. rapae and A.picipes at both sites. Of the common primary parasites which emerged out of the mummies at Lasswade, P. volucre formed 88.2%, D. rapae, 2.0% and A. picipes, 9.8% (X^2 = 69.7, d.f. = 2, $P < 0.001$); at Newington, P. volucre formed 65.1%; D. rapae, 16.7%; A. picipes, 18.3% (X^2 = 59.1, d.f. = 2, $P < 0.001$). A total of only three E. plagiator appeared at both sites, and the only two specimens of Toxares deltiger found during the present investigations occurred at Newington on 11:8:69 and 18:8:69. Cynipids scarcely parasitised the larvae

TABLE 34

Percentage parasitism of Myzus persicae in the field (based on rearing of about 100 advanced nymphs)

Lasswade

Sampling date	No.of M. per. reared	Praon volucre		D.rapae/Aphidius sp.			% Parasitism
		Mums	Em'ce	Mums	Em'ce D.r.	Em'ce A.p.	
16/ 7/69	23	0	0	0	0	0	0
23/ 7/69	74	1	1	1	0	0	2.7
30/ 7/69	98	4	2	2	0	1	6.1
6/ 8/69	108	18	15	3	0	0	19.4
13/ 8/69	101	8	6	6	1	3	13.9
20/ 8/69	100	3	2	2	0	1	5.0
27/8/69	99	2	1	2	0	0	4.0
3/ 9/69	100	12	8	4	0	1	18.0
10/ 9/69	100	10	5	6	1	2	16.0
17/ 9/69	102	9	9	6	0	0	14.7
24/ 9/69	98	10	7	4	0	0	14.3
1/10/69	100	12	8	6	0	1	18.0
8/10/69	110	18	14	4	0	1	20.0
15/10/69	100	9	6	3	0	0	12.0
22/10/69		No sampling					
29/10/69	103	7	4	2	0	0	8.7
5/11/69	105	3	2	0	0	0	2.9
12/11/69	100	0	0	0	0	0	0
19/11/69	78	0	0	0	0	0	0
26/11/69	80	0	0	0	0	0	0

Also 1 Cynipid on 6/8/69 and 2 Ephedrus plagiator on 3/9/69

M. per. = Myzus persicae; D.r. = D. rapae; A.p. = A. picipes:

Mums = mummies

Em'ce = emergence

TABLE 35

Percentage parasitism of Myzus persicae in the field (based on rearing of about 100 advanced nymphs)

Newington

Sampling date	No. of M.per reared	Praon volucre		D.rapae/Aphidius sp.			% Parasitism
		Mums	Em'ce	Mums	Emergence D.r.	A.p.	
21/ 7/69	35	0	0	1	0	0	2.9
28/ 7/69	80	6	3	14	2	3	25.0
4/ 8/69	88	5	4	13	3	4	20.5
11/ 8/69	100	14	7	19	5	4	33.0
18/ 8/69	102	12	8	8	2	2	19.6
25/ 8/69	98	15	10	2	0	0	17.3
1/ 9/69	100	10	8	0	0	0	10.0
8/ 9/69	100	7	4	7	1	2	14.0
15/ 9/69	95	7	2	5	2	1	12.6
22/ 9/69	90	5	3	7	3	2	13.3
29/ 9/69	100	8	5	6	1	1	14.0
6/10/69	105	11	7	9	1	2	19.0
13/10/69	108	11	5	5	1	1	14.8
20/10/69			No	sampling			
27/10/69	100	11	6	0	0	0	12.0
3/11/69	100	7	4	0	0	0	7.0
10/11/69	103	8	4	0	0	0	7.8
17/11/69	100	4	2	0	0	0	4.0
24/11/69	97	1	0	1	0	0	2.1
1/12/69	49	0	0	0			0

Also 28/7/69 2 Cynipids
4/8/69 1 "
11/8/69 2 " 1 Toxares deltiger
18/8/69 1 " 1 "
1/9/69 1 "

M. per. = Myzus persicae; D.r. = D.rapae; A.p. = A.picipes:

Mums = mummies

Em'ce = emergence

TABLE 36

Percentage parasitism of Myzus persicae in the field (based on rearing of about 100 advanced nymphs)

Lasswade 1970

Sampling date	No. of M. per. reared	Praon volucre		D.rapae/Aphidius sp.			% parasitism
		Mums	Em'ce	Mums	Emergence D.r.	A.p.	
15/ 7/70	95	2	1	19	5	5	22.0
22/ 7/70	100	2	1	32	17	2	35.0
29/ 7/70	102	4	4	23	12	2	26.5
5/ 8/70	107	13	9	11	5	7	24.3
12/ 8/70	118	11	6	16	12	2	22.9
19/ 8/70	90	11	10	12	11	1	26.7
26/ 8/70	86	10	2	10	2	0	23.3
2/ 9/70	60	2	0	1	0	0	5.0
9/ 9/70	50	0	0	1	1	0	2.0
16/ 9/70	0	0	0	0	0	0	0

Also on 22/7/70 2 Cynipids; 1 Aphelinus species:
29/7/70 2 Cynipids:
5/8/70 1 Aphelinus species:
19/8/70 1 Ephedrus plagiator:

M. per. = Myzus persicae; D.r. = D. rapae; A.p. = A. picipes:
Mums = mummies;
Em'ce = emergence.

TABLE 37

Percentage parasitism of Myzus persicae in the field (based on rearing mostly less than 50 advanced nymphs

Newington 1970

Sampling date	No. of M. per. reared	Praon volucre		D.rapae/ Aphidius sp.			% parasitism
		Mums	Em'ce	Mums	Emergence D.r.	Emergence A.p.	
20/ 7/70	20	0	0	0	0	0	0
27/ 7/70	22	2	2	1	0	0	13.6
3/ 8/70	33	4	1	4	0	2	24.2
10/ 8/70	50	6	2	2	0	0	16.0
17/ 8/70	45	5	0	4	0	1	20.0
24/ 8/70	37	10	2	3	1	0	35.1
31/ 8/70	50	5	1	0	0	0	10.0
7/ 9/70	37	5	2	1	0	0	16.2
14/ 9/70	18	2	0	1	0	1	16.7
21/ 9/70	No sampling						
28/ 9/70	15	1	0	0	0	0	6.6
5/10/70	5	1	0	0	0	0	10.0

Also on 10/8/70 - 1 Cynipid

M. per. = Myzus persicae; D.r. = D. rapae; A.p. = A. picipes:

Em'ce = emergence:

TABLE 38

Percentage parasitism of both Myzus persicae and Macrosiphum euphorbiae in the field (based on the proportion of mummies to the total advanced nymphs + apterous adults + mummies.

Lasswade 1969

Sampling date	No. of Praon spp. per sprout plant	No. of D.rapae/ or Aphidius spp. per sprout plant	Total parasitism
2/ 7/69	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
9/ 7/69	0	0	0
16/ 7/69	0	0	0
23/ 7/69	0.2 ± 0.1	0	0.7 ± 0.4
30/ 7/69	0.9 ± 0.2	0.4 ± 0.2	3.8 ± 1.2
6/ 8/69	1.7 ± 0.5	1.4 ± 0.5	8.8 ± 2.8
13/ 8/69	2.1 ± 1.2	0.3 ± 0.2	3.2 ± 2.2
20/ 8/69	0.6 ± 0.3	0.2 ± 0.2	0.7 ± 0.3
27/ 8/69	0.2 ± 0.1	0.2 ± 0.1	0.6 ± 0.4
3/ 9/69	4.9 ± 4.3	0.4 ± 0.2	3.5 ± 2.6
10/ 9/69	5.5 ± 2.1	0.8 ± 0.3	2.6 ± 1.0
17/ 9/69	8.3 ± 3.0	0.9 ± 0.6	3.6 ± 2.1
24/ 9/69	2.6 ± 1.3	0.3 ± 0.2	0.8 ± 0.4
1/10/69	4.5 ± 1.5	0	1.9 ± 1.1
8/10/69	5.0 ± 2.4	0	2.5 ± 2.3
15/10/69	4.2 ± 1.1	0.3 ± 0.2	1.8 ± 0.9
22/10/69	No sampling		
29/10/69	0.8 ± 0.4	1.5 ± 0.6	1.0 ± 0.6
5/11/69	1.4 ± 0.5	0.3 ± 0.2	0.9 ± 0.3
12/11/69	0.8 ± 0.4	0.5 ± 0.3	0.8 ± 0.5
19/11/69	0	0	0
26/11/69	0	0	0

/ or = and/or

TABLE 39

Percentage parasitism of both Myzus persicae and Macrosiphum euphorbiae in the field (based on the proportion of mummies to total advanced nymphs + apterous adults + mummies)

Newington 1969

Sampling date	No. of Praon spp. per sprout plant	No. of D.rapae/ or Aphidius spp per sprout plant	Total parasitism
30/ 6/69	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
7/ 7/69	0	0.1 ± 0.1	3.7 ± 2.7
14/ 7/69	0	0	0.8 ± 0.8
21/ 7/69	0.1 ± 0.0	0	0.6 ± 0.4
28/ 7/69	0.3 ± 0.1	0.2 ± 0.1	12.8 ± 4.8
4/ 8/69	0.1 ± 0.1	0.2 ± 0.1	3.1 ± 1.6
11/ 8 /69	0.8 ± 0.4	1.5 ± 0.6	8.7 ± 2.8
18/ 8/69	1.1 ± 0.6	3.8 ± 1.7	9.0 ± 3.9
25/ 8/69	3.2 ± 1.9	1.8 ± 0.9	5.6 ± 2.6
1/ 9/69	17.3 ± 5.9	3.1 ± 1.2	6.8 ± 2.7
8/ 9/69	9.4 ± 2.6	1.3 ± 0.5	3.7 ± 1.0
15/ 9/69	25.3 ± 6.2	9.2 ± 2.8	5.5 ± 1.5
22/ 9/69	31.1 ± 8.7	12.3 ± 5.2	4.5 ± 1.2
29/ 9/69	22.6 ± 7.4	7.6 ± 2.4	4.5 ± 1.5
6/10/69	8.8 ± 2.9	4.6 ± 1.3	4.4 ± 1.0
13/10/69	10.2 ± 2.8	3.9 ± 1.1	2.7 ± 0.9
20/10/69		No sampling	
27/10/69	9.3 ± 2.5	2.4 ± 0.9	5.2 ± 2.9
3/11/69	16.4 ± 5.5	6.0 ± 1.8	1.2 ± 0.3
10/11/69	3.3 ± 1.2	7.3 ± 3.3	3.6 ± 1.7
17/11/69	4.6 ± 2.3	2.1 ± 1.0	0.7 ± 0.3
24/11/69	6.3 ± 2.4	5.0 ± 2.3	2.2 ± 0.6
1/12/69	1.9 ± 0.8	1.4 ± 0.3	4.0 ± 1.1

/ or = and/or

TABLE 40

Percentage parasitism of both Myzus persicae and Macrosiphum euphorbiae in the field (based on the proportion of mummies to total advanced nymphs + apterous adults + mummies)

Lasswade 1970

Sampling date	No. of Praon spp. per sprout plant	No. of D.rapae/ or Aphidius spp per sprout plant	Total parasitism
1/ 7/70	0.0 ±0.0	0.0 ±0.0	0.0 ±0.0
8/ 7/70	0	0	0
15/ 7/70	0	0.5 ±0.4	0.5 ±0.3
22/ 7/70	0.2 ±0.1	1.0 ±0.4	1.0 ±0.5
29/ 7/70	0.6 ±0.3	1.2±0.3	1.3 ±0.4
5/ 8/70	0.9 ±0.4	3.6 ±0.9	2.3 ±0.5
12/ 8/70	3.3 ±1.3	4.0 ±1.2	2.8 ±1.2
19/ 8/70	5.1 ±1.5	4.9 ±1.7	8.3 ±3.3
26/ 8/70	5.6 ±1.0	6.1 ±1.3	5.3 ±0.9
2/ 9/70	4.5 ±1.4	4.5 ±2.3	8.7 ±4.3
9/ 9/70	2.0 ±1.2	0.5 ±0.5	3.5 ±2.2
16/ 9/70	0.4 ±0.3	0.1 ±0.1	0.7 ±0.3
23/ 9/70		No sampling	
30/ 9/70	0.1 ±0.1	0	0.1 ±0.1
7/10/70	0.5 ±0.3	0	0.4 ±0.3

/ or = and/or

TABLE 41

Percentage parasitism of both Myzus persicae and Macrosiphum euphorbiae in the field (based on the proportion of mummies to total advanced nymphs + apterous adults + mummies)

Newington 1970

Sampling date	No. of Praon spp. per sprout plant	No. of D.rapae/ or Aphidius spp. per sprout plant	Total parasitism
29/ 6/70	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
6/ 7/70	0	0	0
13/ 7/70	0	0.1 ± 0.1	0.3 ± 0.3
20/ 7/70	0	0	0
27/ 7/70	0.2 ± 0.1	0.2 ± 0.1	0.8 ± 0.5
3/ 8/70	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2
10/ 8 /70	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.2
17/ 8/70	0.3 ± 0.2	0.2 ± 0.1	0.4 ± 0.2
24/ 8/70	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
31/ 8 /70	2.0 ± 1.8	0.1 ± 0.1	0.8 ± 0.4
7/ 9/70	0.2 ± 0.1	0.2 ± 0.2	0.3 ± 0.2
14/ 9/70	0.3 ± 0.2	0.0 ± 0.0	0.3 ± 0.2
21/ 9/70		No sampling	
28/ 9/70	0	0	0
5/10/70	0.4 ± 0.3	0.2 ± 0.1	0.6 ± 0.3
12/10/70		No sampling	
19/10/70	0	0	0

/ or = and/or

TABLE 42

Relative numbers of primary parasites and hyperparasites of Myzus persicae and Macrosiphum euphorbiae emerged from Praon species mummies collected from 1968 to 1970

		Summer emergence	% of total mummies	Spring emergence	% of total mummies	Total %
P.volucre	1968	7	9.9	14	19.7	29.6
	1969	499	36.4	198	14.5	50.9
	1970	111	41.0	25	9.2	50.2
A.vulgaris	1968	2	2.8	12	16.9	19.7
	1969	57	4.2	146	IO.6	14.8
	1970	24	8.9	3	1.1	IO.0
C.clavata	1968	0	0	1	1.4	1.4
	1969	2	0.2	11	0.8	1.0
	1970	0	0	3	1.1	1.1
Cynipids	1968	0	0	1	1.4	1.4
	1969	34	2.9	77	5.6	8.5
	1970	12	4.4	19	7.0	11.4
Dend. spp.	1969	2	0.2	9	0.7	0.9
	1970	1	0.4	0	0	0.4
Non-emergence	1968			34	47.9	47.9
	1969			334	24.4	24.4
	1970			73	27.0	27.0
Total emerg'ce	1968	9	12.7	28	39.4	52.1
	1969	594	43.4	441	32.2	75.6
	1970	148	54.6	50	18.5	73.1

Species abbreviations (or genera) - P. = Praon; A. = Asaphes; C. = Coruna; Dend. = Dendrocerus

TABLE 43

Relative numbers of primary parasites and hyperparasites of Myzus persicae and Macrosiphum euphorbiae emerged from Diaertiella rapae/or Aphidius species mummies collected from 1968 to 1970

		Summer emergence	% of total mummies	Spring emergence	% of total mummies	Total %
D. rapae/or Aphidius sp.	1968	148	35.7	99	23.9	59.6
	1969	166	23.2	46	6.4	29.6
	1970	119	32.0	1	0.3	32.3
A. vulgaris	1968	16	3.9	53	12.8	16.7
	1969	51	7.1	43	6.0	13.1
	1970	50	13.4	20	5.4	18.8
C. clavata	1968	0	0	2	0.5	0.5
	1969	3	0.4	3	0.4	0.8
	1970	1	0.3	I0	2.7	3.0
Cynipids	1968	3	0.7	23	5.6	6.3
	1969	I04	14.5	II0	15.4	29.9
	1970	25	6.7	67	18.0	24.7
Dend. spp.	1969	5	0.7	0	0	0.7
	1970	6	1.6	0	0	1.6
Non-emergence	1968			70	16.9	16.9
	1969			185	25.8	25.8
	1970			73	19.6	19.6
Total emergence	1968	167	40.3	177	42.8	83.1
	1969	329	45.9	202	28.2	74.1
	1970	20I	54.0	98	26.3	80.3

Species abbreviations – A. = Asaphes; C. = Coruna;
(or genera) Dend. = Dendrocerus

/ or = and/or

TABLE 44

The maximum number of days parasites stayed in collected overwintering aphid mummies

	Date of collecting mummy	Date of emergence	Days para. stayed in mummy
Primary parasites			
Praon volucre	19/ 9/69	25/ 7/70	309
	28/ 8/70	24/ 6/71	307
Aphidius picipes	5/ 9/69	29/ 5/70	266
Diaeretiella rapae	19/ 9/69	22/ 6/70	276
Hyperparasites			
Cynipids	1/ 8/69	4/ 8/70	368
	14/ 8/70	29/ 6/71	319
Asaphes vulgaris	8/ 8/69	25/ 5/70	290
	4/ 9/70	18/ 6/71	286

of P. volucre and D. rapae and/or Aphidius species at Lasswade and Newington.

Year 1970

The results of the aphid reared from both sites as shown in Figures 12b, 13b, and Tables 36, 37, indicate that parasitism at Lasswade was consistently at about 20% till about the end of August and that it then suddenly fell to zero by mid-September as the aphid host population dropped. The rate of parasitism at Newington did not show any seasonal trend, presumably because of the low densities of the aphid host and the parasites. However, like the previous year at Newington, the most common of the primary parasites was P. volucre, 66.7%, followed by A. picipes, 26.7%, and D. rapae, 6.7% ($X^2 = 8.4$, d.f. = 2, $P<0.05$). At Lasswade, D. rapae appeared to be the effective parasite, 55.6%, while P. volucre formed 28.8% and A. picipes, 16.3% of the primary parasites ($X^2 = 28.5$, d.f. = 2, $P<0.001$). Both mummies of Aphelinus species and E. plagiator were found only at Lasswade, in low numbers. Cynipids again scarcely hyperparasitised M. persicae at Lasswade and Newington through D. rapae and/or A.picipes.

Discussion

The correlation of the degree of parasitism and the population changes of M. persicae during the two seasons on the two different plots indicate that apart from the parasites other mortality factors controlled the aphid host densities. For the parasites to be the only agents of mortality, the changes in parasitism and the aphid host populations should be in 'reciprocal' oscillation, that is, the interactions between the two would have delayed influence of one upon the other. Such relationship was not shown in Figures 10b, 11b, 12b and 13b.

Some of the possible factors which obscured the dominance of the parasites as a mortality agent were:-

1. Total population densities of different aphid species. It was observed that Aphis fabae appeared in July on some of the weeds, particularly fat hen (Chenopodium album), nettle (Urtica urens) and thistle (Carduus arvensis) in the brussels sprout crops, and the numbers declined to zero by late October. A.fabae was parasitised by P. volucre, the most common parasite, D. rapae, A.picipes and E. plagiator. Since A. fabae is not a pest of brussels sprouts, its presence on the weeds helped to augment the population of the primary parasites of M. persicae. This increase in parasite numbers probably caused a change in the density dependence.

2. Other natural enemies. Different natural enemies responded differently to the same environmental conditions and appeared at different times, for instance, the syrphids made their first appearance in the experimental plots before the parasites, and the syrphids were more dominant in late August and September (Appendices 21, 23, and 25). Although the action of natural enemies could be complementary, competition and displacement could occur.

3. Hyper parasites. Hyperparasitism could limit the effectiveness of the primary parasites as has been pointed out earlier on Page 141 .

In November, the decline of the aphid population and hibernation of the primary parasites and hyperparasites caused the trend of the parasitism to fall to zero by the end of the month.

ASSESSMENT BY COUNTING OF THE APHID MUMMIES

Method

The unemerged mummies of M. persicae and M. euphorbiae were counted together during the aphid sampling at Lasswade and Newington for the two seasons of 1969 and 1970 as described on Page 53. In the field the mummies of the aphid species could not be distinguished from each other. Parasitism was calculated on the basis of the proportion of the mummies to the sum of apterous adults, advanced nymphs and mummies for both M. persicae and M. euphorbiae per plant per week. The weekly assessments gave an indication of the trend of parasitism for each site at each season.

Results

Tables 38,39, 40, and 41 show the results of the rates of parasitism obtained by the counting method for the two sites during the two seasons. Although the numbers of both M. persicae and M. euphorbiae were used in the estimation of the parasitism, the results were mainly influenced by the higher numbers of the former. The trends of parasitism at the various sites during the seasons were similar to those obtained with the rearing method at the corresponding sites and seasons.

Discussion

The difference between the two methods was the sizes of the results. The counting method tended to give lower values, and the following points may have influenced the results:-

1. The varying periods during which the parasites remained in the mummies before emergence could give incorrect indication of the rate of parasitism. About mid-August, for instance, the parasites started to

hibernate at the last instar stage within the mummy. This increasingly accumulated the number of the mummies.

2. During sampling the aphids were found on the under surface of the most bottom leaves. Aphid infested senescent leaves often carried mummified aphids and reductions in numbers of the mummies were caused during defoliation.

3. Only unemerged mummies were counted but since dead parasites within mummies could not be separated from live ones on external examination they might have been counted again some time later.

4. Parasitised alate adults and alate fourth instar nymphs might not mummify before they flew off or moulted into adults. However, since their numbers per plant were generally low and mummified aphids formed less than 1% of the total mummies collected during the study period, their exclusion from the calculation would have a negligible effect on the results.

The degrees of parasitisation at the two different sites during the two seasons as obtained by the above two methods indicated that parasitism as a mortality factor of the total aphid populations, especially of M. persicae, was solely ineffective. Although it was not the dominant mortality factor, it was, however, important in complementing the action of the other mortality factors in stabilizing the aphid population on the sprout crops, particularly during late July - August and October (Figures 10, 11, 12, and 13).

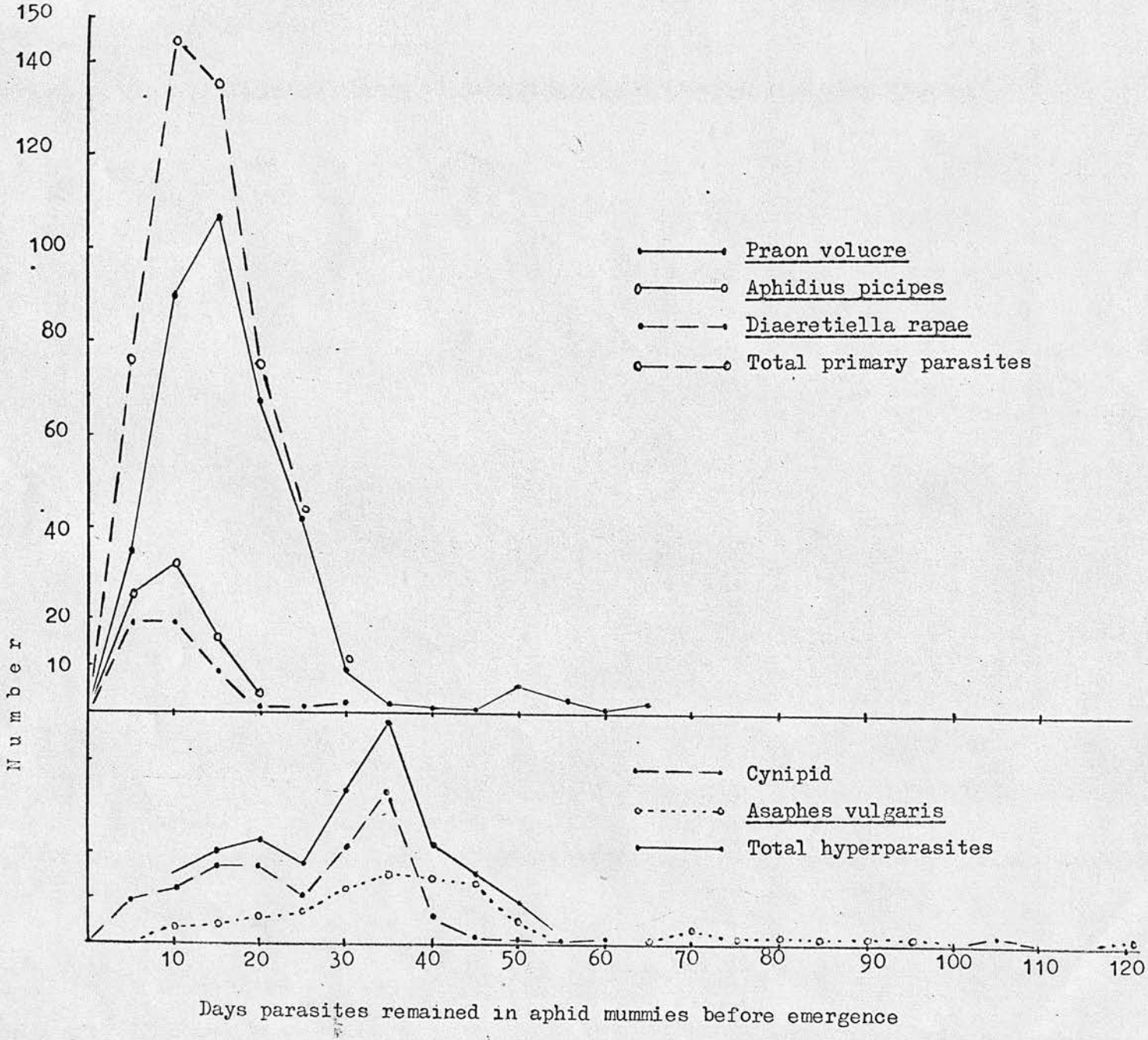

Fig.21. Summer/autumn emergence of primary parasites and hyperparasites - 1969.

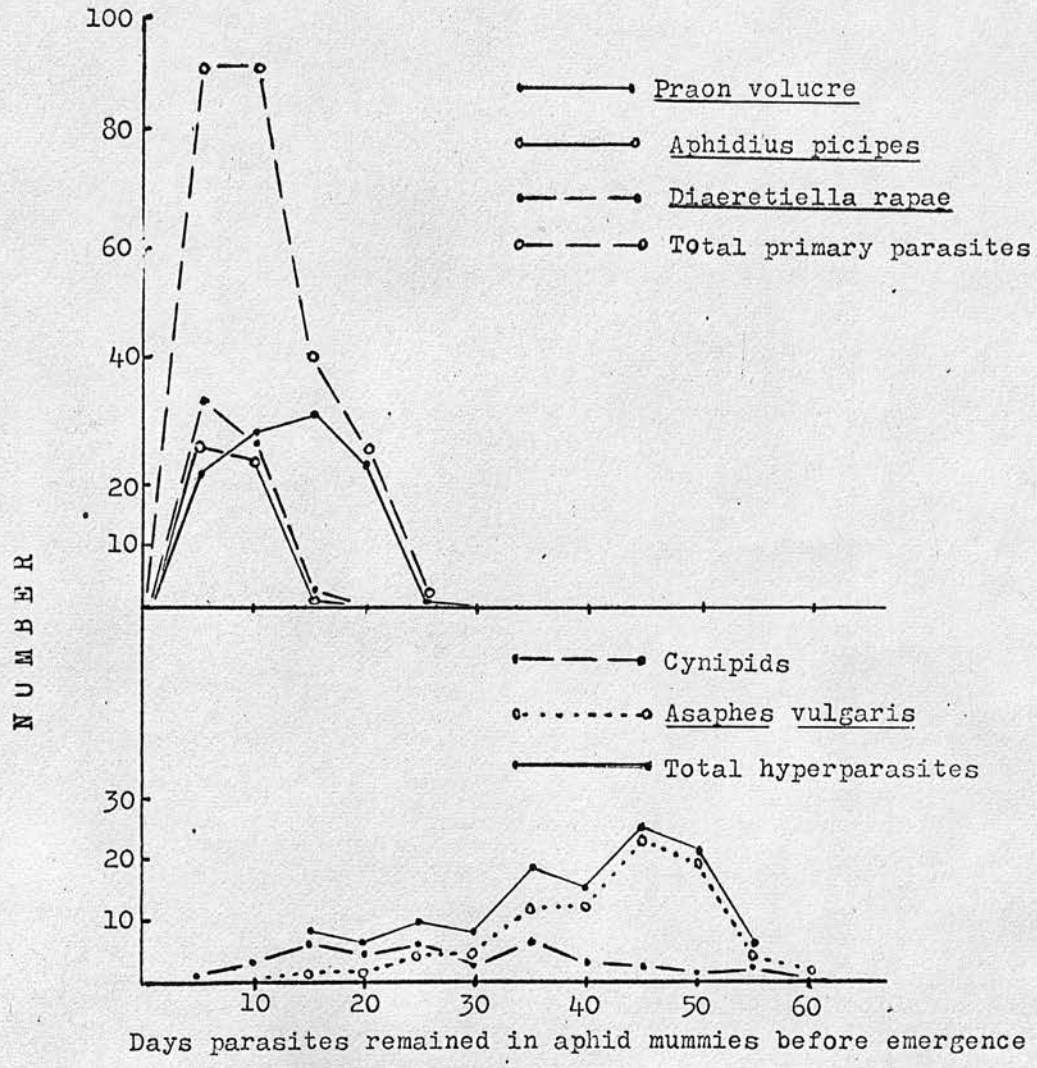

Fig. 22. Summer/autumn emergence of primary parasites and hyperparasites - 1970.

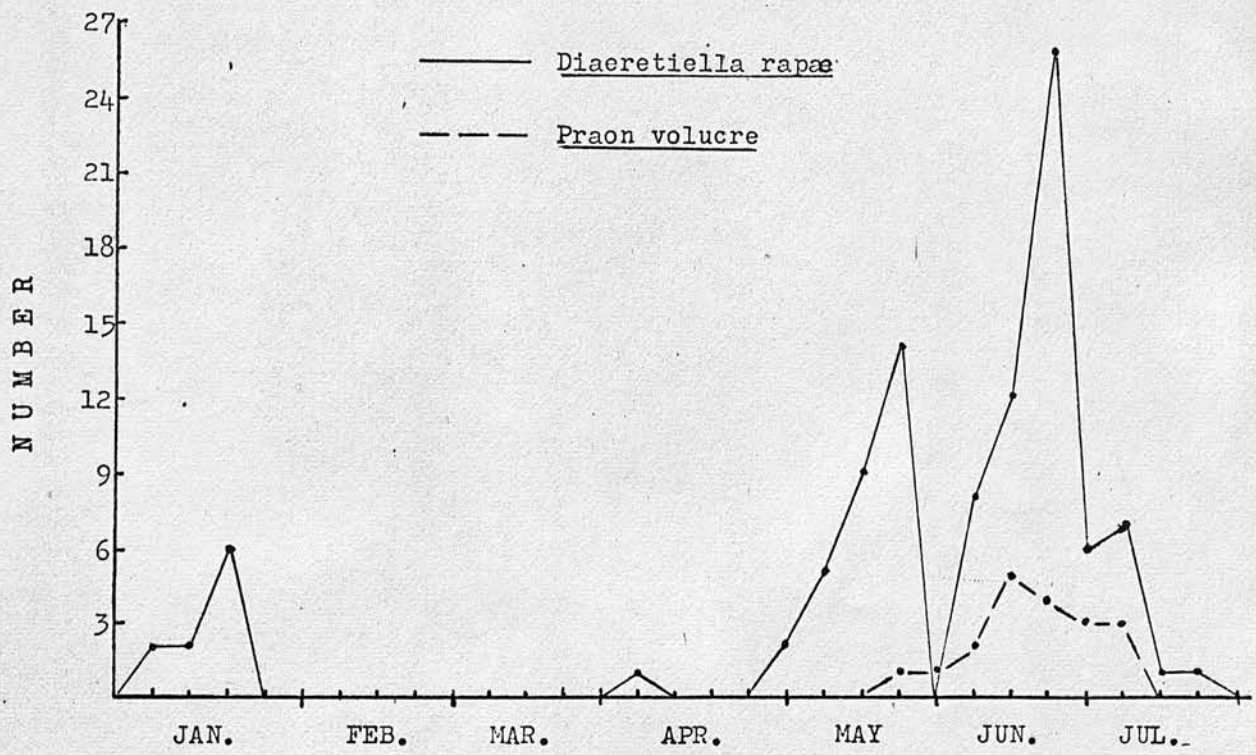

Fig. 23. Emergence of D. rapae & P. volucre in spring/summer 1969 from mummies collected during summer/autumn 1968.

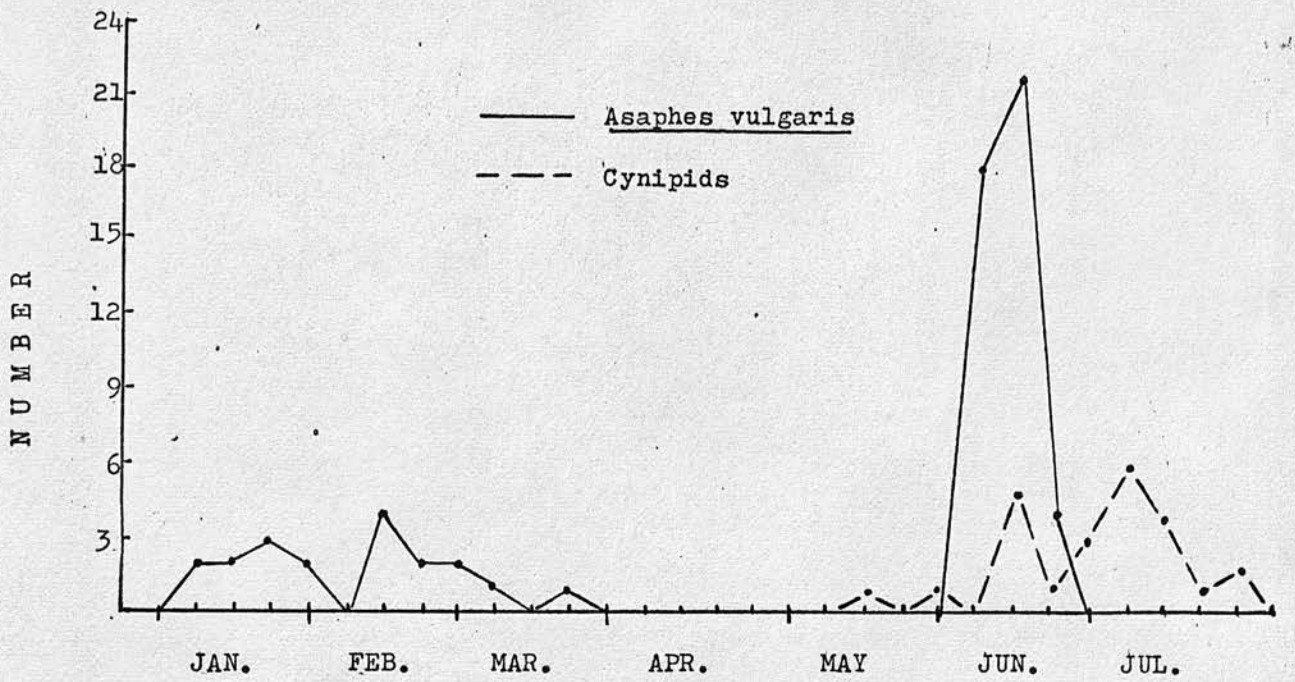

Fig. 24. Emergence of A. vulgaris and cynipids in spring/summer 1969 from mummies collected during summer/autumn 1968.

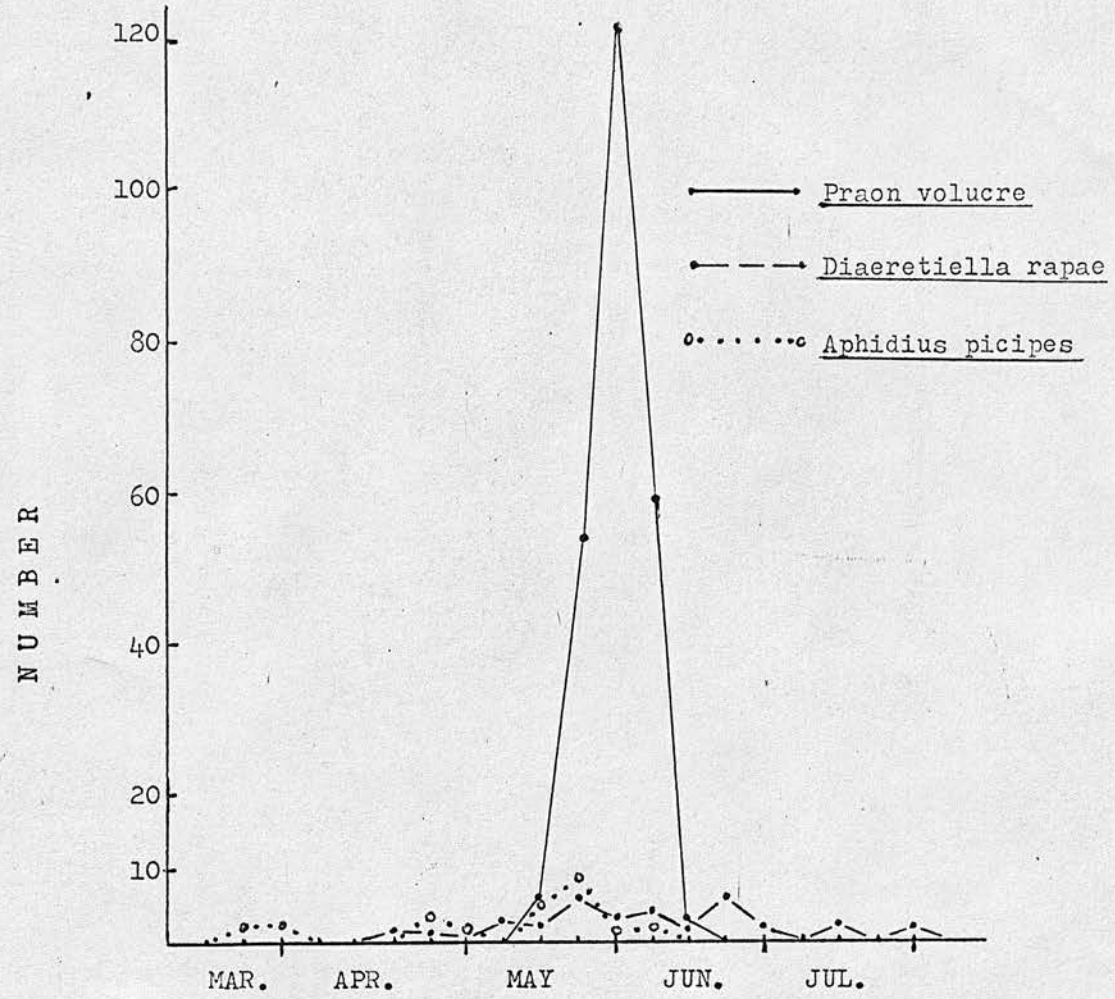

Fig. 25. Emergence of D. rapae, P. volucre and A. picipes in spring/summer 1970 from mummies collected during summer/autumn 1969.

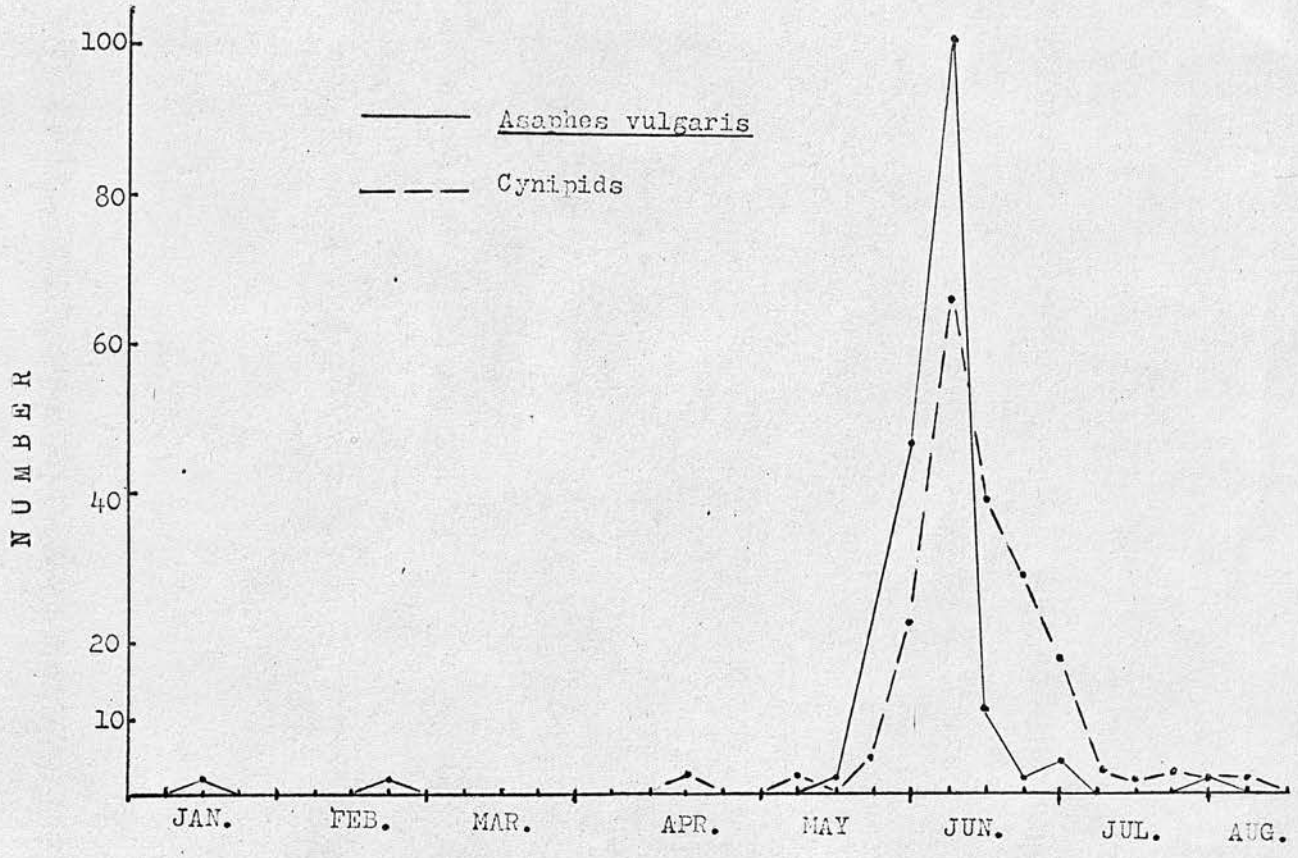

Fig. 26. Emergence of A. vulgaris and cynipids in spring/summer 1970 from mummies collected during summer/autumn 1969.

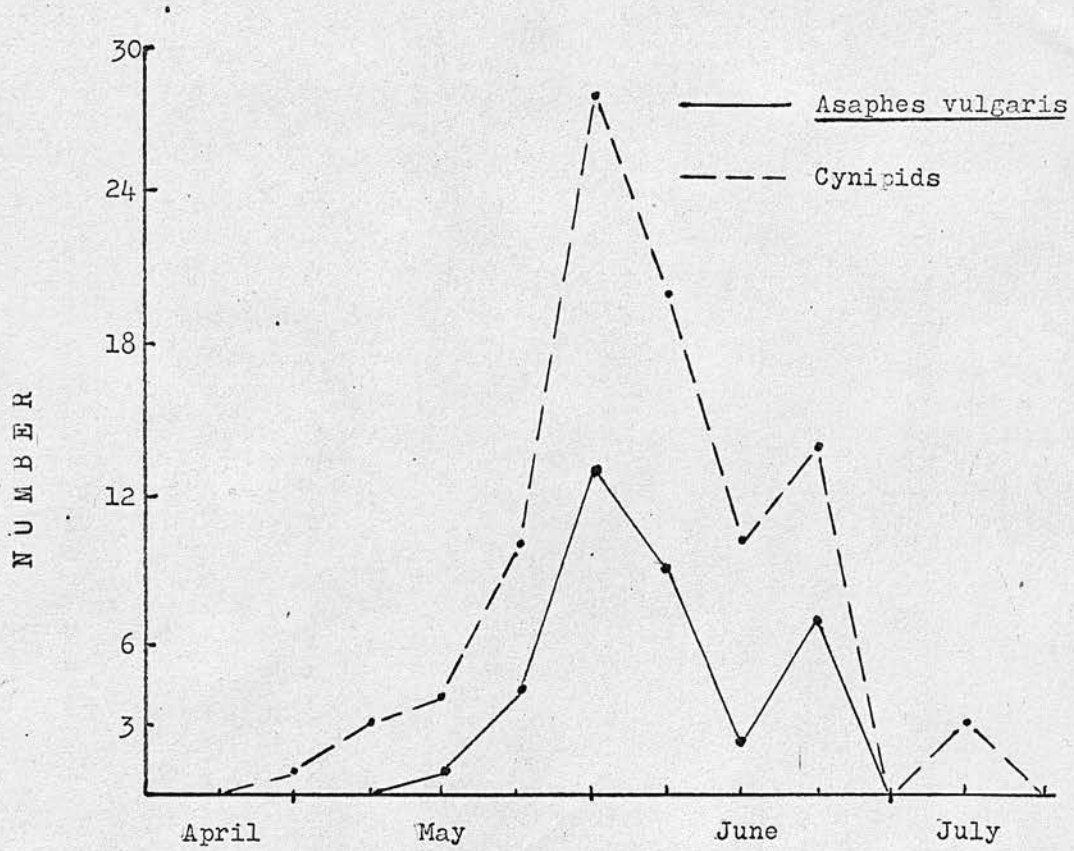

Fig. 27. Emergence of A. vulgaris and cynipids in spring/summer 1971 from mummies collected during summer/autumn 1970.

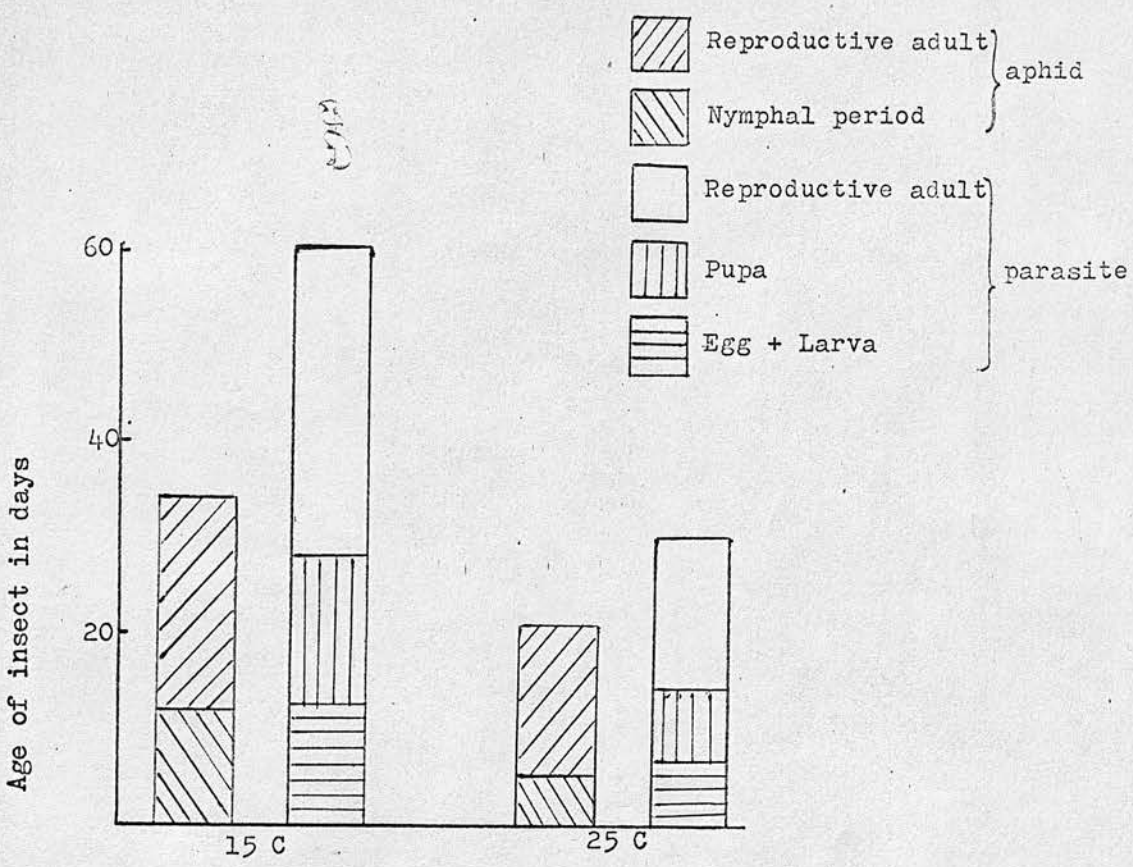

Fig. 28. Relative durations of development and reproduction for Myzus persicae and Praon volucre.

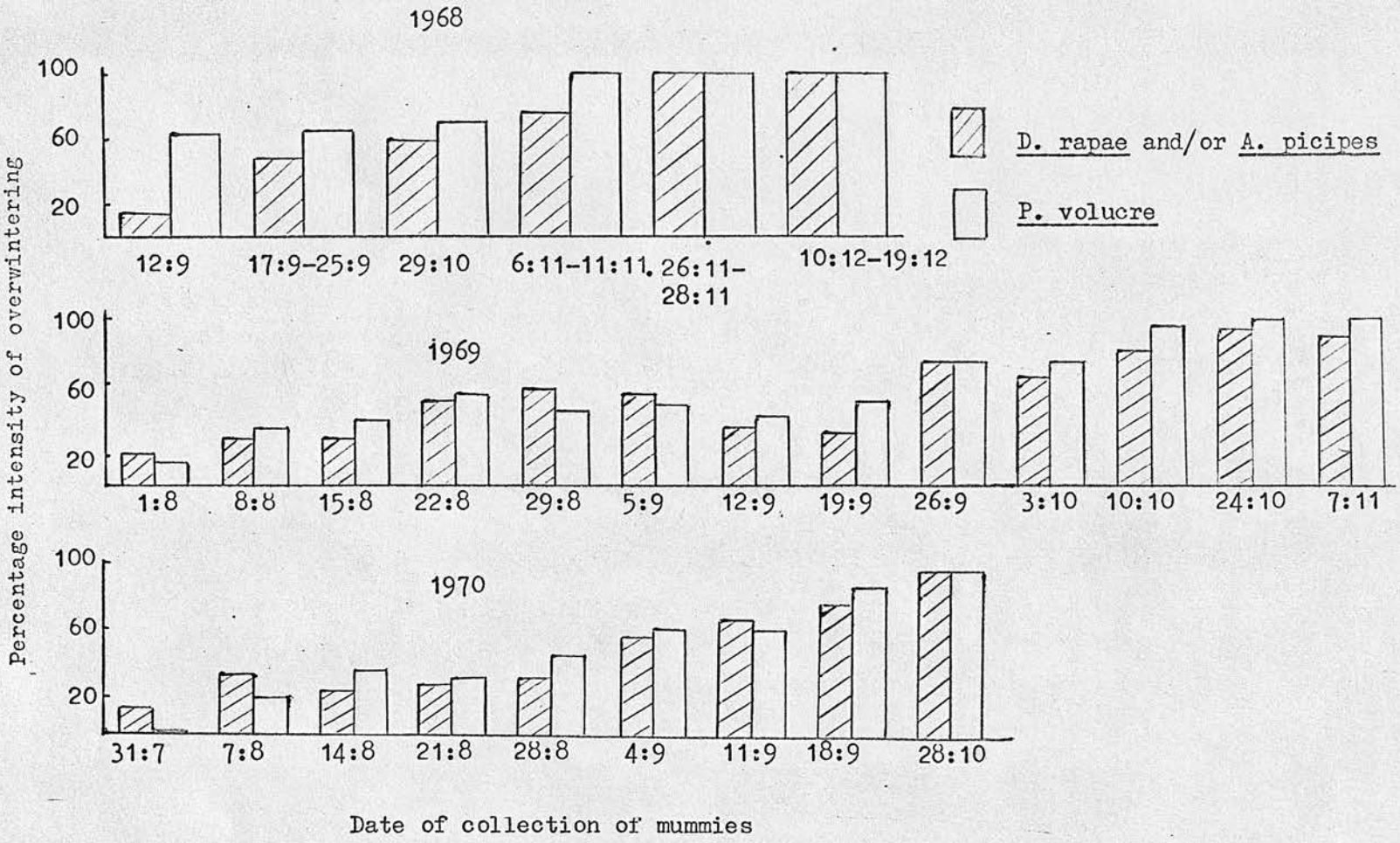

Fig.29. Intensity of overwintering aphid mummies collected from brassicas around Edinburgh 1968-1970.

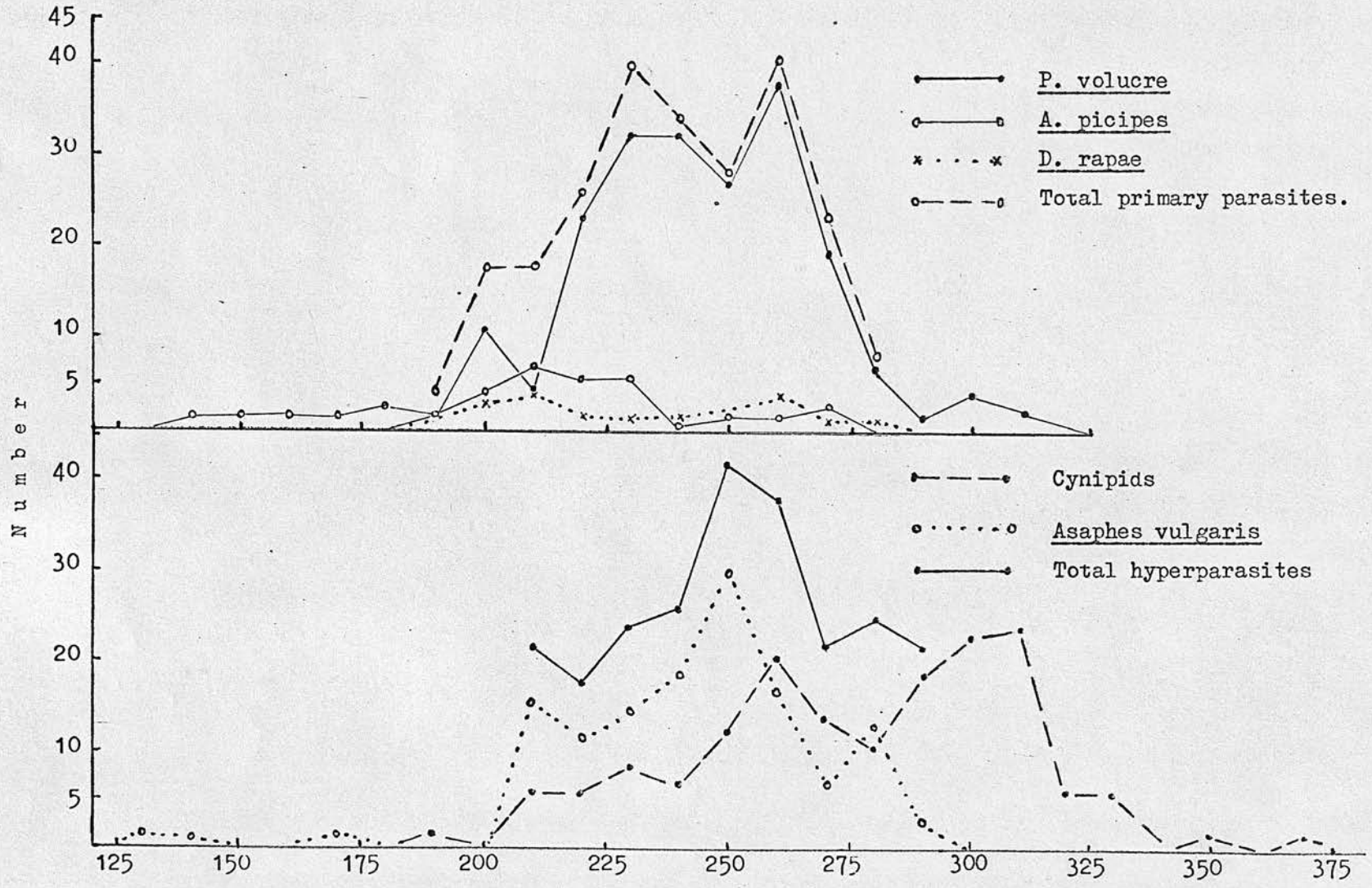

Fig. 30 Overwintering emergence of primary parasites and hyperparasites during spring/summer - 1970.

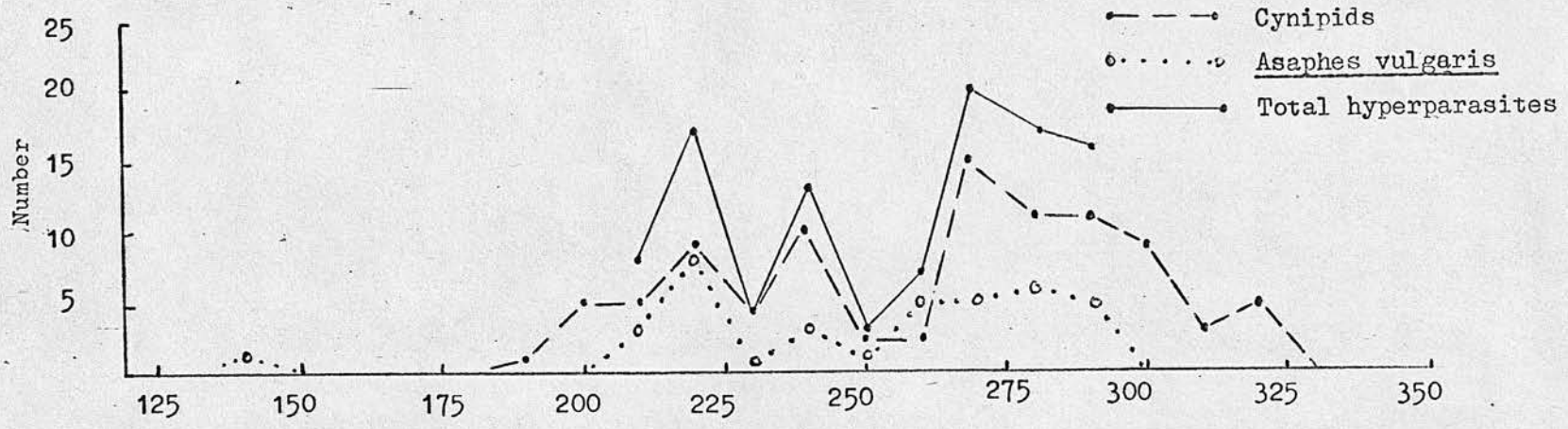

Fig. 31. Overwintering emergence of primary parasites and hyperparasites during spring/summer - 1971.

CONCLUDING DISCUSSION

Seasonal histories of the primary parasites and the hyperparasites

During the present study, ten species of primary parasites were reared from M. persicae. In 1968 P. volucre, D. rapae, A. picipes and E. plagiator were recorded from M. persicae and the following year six additional species were reared from the aphid, including Toxares deltiger, which was not recorded from the other host. The maximum number of the primary parasites in the M. persicae mummies usually occurred during September, and in 1968 D. rapae was the most numerous of the primary parasites but was replaced the following year by P. volucre.

Cynipids and Asaphes vulgaris were the most important hyperparasites with Coruna clavata as a less common one which infested Praon volucre through M. persicae. The hyperparasites parasitised D. rapae and/or Aphidius species through M. persicae. In contrast to A. vulgaris, Cynipids were found to be the dominant parasites of D. rapae and/or Aphidius species through both M. persicae and M. euphorbiae and A. vulgaris the most effective parasite of P. volucre through the same aphid hosts.

In this work, the number of primary parasites which emerged from M. euphorbiae was higher (15) than that of M. persicae (11). The parasites which attacked the former but not the latter were Aphidius rosae, Dyscritulus planiceps, Monoctonus pseudoplantani, Aphelinus sp. nr. tibialis and Aphelinus sp. nr. davicola. Strikingly, M. euphorbiae was less common than M. persicae and appeared for a shorter period in the field than M. persicae. Although M. persicae had fewer parasites, it was more heavily parasitised than M. euphorbiae, particularly by P. volucre. The greater parasitization of M. persicae might have been due to its abundance.

Inside M. euphorbiae mummies the main primary parasites, P. volucre and A. picipes, showed no definite seasonal fluctuation but in the mummies of M. persicae the maximum occurred in September.

Through P. volucre and D. rapae and/or Aphidius species, M. euphorbiae was attacked by A. vulgaris, cynipids, Dendrocerus species and Coruna clavata only through the former primary parasite. The seasonal variations of the hyperparasites in the mummies of M. euphorbiae, like that of M. persicae, were erratic.

Except for Dendrocerus species which was not recorded as a parasite of Ephedrus plagiator, the remaining hyperparasites attacked the primary parasite less commonly, probably due to the scarcity of E. plagiator.

It appeared that host selection by the main hyperparasites, A. vulgaris and cynipids, was influenced by the primary parasites more than aphid host. A. vulgaris was found to be an effective parasite of P. volucre and cynipids of D. rapae and/or Aphidius species irrespective of the aphid host. The explanation of the mechanism for host preference is unknown. However, possible influences might have been the differences in the density and population trends of the aphid hosts, and seasonal fluctuation differences among the aphid hosts, primary parasites and the hyperparasites.

The primary parasites and hyperparasites considered in this study, like some other insects, overwinter to survive through the unfavourable period of the year. This period tides them over to the time of the year when biological development is speeded up. In addition to the influence of the external ecological conditions, physiological preparation in the parasites enables them to survive the long period of the adverse conditions (Danilevskii, 1965).

During the decline in temperature and photoperiod in late August the aphid mummies of the overwintering parasites appeared and the mummies of D. rapae, A. picipes and particularly P. volucre deepened in colour and became tough to dissect. But the aphid mummies containing the overwintering hyperparasites showed no apparent external signs. Generally as the season progressed there was less emergence of the parasites from the aphid mummies collected from the field. This is exemplified in Figure 29, showing the degree of intensity of diapausing exhibited by mummies of P. volucre and D. rapae and/or Aphidius species as the season progressed in each of the three years. The occurrence of diapausing mummies early in August could be attributed mainly to the hyperparasites which appeared to overwinter earlier than the primary parasites. In 1969, the first overwintering aphid mummies containing cynipids were collected on August 1 and that with A. vulgaris on August 8, while the first overwintering aphid mummies which gave rise to the primary parasites, P. volucre, E. plagiator, A. picipes and D. rapae, were collected on August 15, September 12, September 19 and October 3, respectively. In the following year hyperparasites were again noted to be overwintering earlier (July 31, cynipids; August 14, A.vulgaris) than the primary parasite, (August 21, P. volucre).

As stated above, the hyperparasites overwintered earlier than the primary parasites and they again appeared to show greater intensity of overwintering, particularly cynipids, (Table 44. Figures 30 and 31). P. volucre also seemed to undergo hibernation with greater intensity than the rest of the primary parasites, but as a common parasite around Edinburgh during this work, the hibernation could affect its efficiency in controlling the aphid hosts particularly in spring and autumn when the host may be reproducing.

Interaction of mortality factors of the aphid populations on the sprout crops and the importance of parasites as mortality factors.

The analysis of the mortality factors of the aphid population on the sprout crops was separately discussed (Page 88) and the interactions of the factors on the aphid population changes at the two sites in 1969 and 1970 may be considered as follows:-

Year 1969

At Lasswade, during early July the initially low-density Myzus persicae populations increased rapidly as there were no mortality factors effectively in operation at that time. A rapid increase in the aphid density then occurred up to early August. The prevailing climatic conditions at that time caused the brussels sprout leaves to be less turgid and also water droplets condensed on the aphids and drowned some of them; probably entomophagous fungus invaded the aphids later. In addition, parasitism and syrphid larvae number increased during early August and consequently these factors caused a sharp decline in aphid abundance. Macrosiphum euphorbiae were scarce but the population trend was similar to that of M. persicae with the same mortality factors affecting it. M. euphorbiae completely disappeared from the experimental plot by mid-August.

In September another high peak of M. persicae was reached due mainly to the favourable weather and the scarcity of syrphid larvae. Then there was a drop in the aphid abundance although it was not as considerable as the first one; caused mainly by the persistant parasitism.

The last peak of the season appeared late in October due to reduced activity by the natural enemies. The fall in the abundance of the aphids late in the season could be attributed to the cold weather which reduced

the rate of reproduction and caused the abscission of the lower leaves carrying the aphid population.

At Newington, there was an early build up of the population as at Lasswade, but parasitism in late July and to a lesser extent predation stabilized the population of M. persicae. However, parasitism was low in late August and early September and the weather conditions were ideal, so the first high peak was reached late in September. With increases in predation and parasitism early in October, there was a sharp decline in the M. persicae population followed by a rise again reaching a peak in early November when the activities of the natural enemies decreased. The end of the season decline was due to the low rate of reproduction and the defoliation of the leaves as at Lasswade.

M. euphorbiae appeared at the same time as M. persicae and the population numbers were low until the species disappeared early in September; the species was influenced by the same mortality factors.

Year 1970

At Lasswade, as in the previous year at the two sites, there was a small initial population of M. persicae which speedily built up to a peak in early August. Parasitism started early in mid-July and was followed by syrphid predation in early August but these mortality factors were not effective enough to control the aphid populations. However, climatic conditions during the peak period of aphid population in mid-August facilitated formation of water droplets on the aphids which killed many, probably with the additional effect of fungus disease. The M. persicae population therefore finally disappeared with that of M. euphorbiae. The latter aphid first appeared on the sprout crop at the same time as

M. persicae and the numbers reached their peak a week later than in the case of M. persicae.

At Newington, both M. persicae and M. euphorbiae were too scarce to have any indication of the causes for the population changes. However, a small population peak of M. persicae which occurred at the end of August might have been due to the good weather. The final decline of the aphid numbers to zero during the autumn was mainly due to the cold weather and the defoliation of the lower sprout leaves.

To find out how factors in the field, particularly temperature, influence the relationship between the aphid host and its parasites, experiments were carried out with M. persicae and P. volucre in the laboratory. It was shown experimentally that temperature was important in determining the rates of development and reproduction of both the aphid host and the parasite, but to a different extent in each case. As shown in Figure 2, the developmental periods of both the host and the parasite increased with a decrease in temperature, but the durations of the parasite for the same temperatures were longer.

At 5°C the development of the parasite was not completed but the host, M. persicae thrived and reproduced at this temperature. The threshold of development of both M. persicae and P. volucre was estimated (Figure 3) and it was shown that the host, M. persicae developed at a temperature of about 3.5°C and that of the parasite at 5.0°C. This indicated that in the field, particularly during the autumn and spring, the host could reproduce and develop at lower temperatures which might be lethal to the parasite.

M. persicae was able to develop from birth to adulthood faster than P. volucre at different temperatures (Figure 28). At 15°C the rate of

development of the aphid host was about twice as fast as that of the parasite, and so the reproductive period of the aphid life cycle began earlier. Although the parasite has a higher reproductive capacity than the host ($P < 0.001$) the aphid does not search for an appropriate place to deposit its progeny as the parasite does. It was therefore not likely that the parasite deposited its full complement of eggs during the greater part of the season since the host populations were generally low on the sprout plants. In addition, it was observed in the laboratory that both adult and advanced nymph even if parasitised could reproduce some of their progeny to increase the aphid population, before mummification.

The effectiveness of the primary parasites was further reduced by the activities of the hyperparasites. In 1969 and 1970, hyperparasitism of the aphids on sprout crops were respectively 39.4% and 46.9%. Another possible limiting factor of parasitism was the harvesting of the brassicas during the autumn and this destroyed some of the aphid mummies; and secondly the harvesting suddenly reduced the host populations which could be parasitised to increase the numbers of the overwintering mummies.

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APPENDIX 1

Number of Myzus persicae counted on 50 plants per crop during 1968-69 winter

Site & sampling date	Spring cabbage			Summer cabbage			Brussels sprout			Broccoli		
	ALA	APT	N	ALA	APT	N	ALA	APT	N	ALA	APT	N
Newington												
7/11/68	2	15	60	3	23	201	8	467	4292	3	59	902
20/11/68	1	11	33	1	12	98	1	100	1792	0	19	489
27/11/68	0	6	18	0	9	72	0	9	433	0	10	143
4/12/68	0	6	4	0	4	12	0	19	364	0	7	99
12/12/68	0	3	2	0	2	4	0	17	125	0	2	10
3 / 1/69	0	1	0	0	1	1	0	0	3	0	1	0
21/ 1/69	0	0	2	0	1	0	0	0	0	0	0	0
28/ 1/69	0	1	0	0	0	0	0	0	0	0	0	0
4/ 2/69	0	0	0	0	0	0	0	0	0	0	0	0
Liberton												
14/11/68				2	23	105	0	360	5040	3	121	821
20/11/68				1	9	79	0	163	2575	1	84	534
27/11/68				2	2	12	4	84	1434	0	40	201
4/12/68					1	3	0	38	1023	0	19	93
18/12/68					1	0	0	4	92	0	2	8
2/ 1/69					0	0	0	0	0	0	1	2
7/ 1/69					0	0	0	0	0	0	0	0
14/ 1/69					0	0	0	0	0	0	0	0
22/ 1/69					0	0	0	0	0	0	0	0
*Musselburgh												
22/11/68	0	9	13	0	51	103	2	100	985	5	46	257
29/11/68	0	4	10	0	21	85	1	81	651	2	30	188
13/13/68	0	3	3	0	6	40	3	56	471	1	15	63
27/12/68	0	2	4	0	4	18	0	16	81	0	11	30
9/ 1/69	0	1	6	0	0	0	0	5	42	0	34	26
6/ 2/69	0	0	0	0	0	0	harvested			0	0	0

ALA = Alate; APT = Apterous; N = Nymphs

* = 40 plants sampled during each sampling date.

APPENDIX 2

Number of Myzus persicae counted on 30 plants per crop during the 1969-70 winter

Site & sampling date	Spring cabbage			Summer cabbage			Brussels sprout			Broccoli		
	ALA	APT	N	ALA	APT	N	ALA	APT	N	ALA	APT	N
Newington												
8/12/69	1	7	9	0	10	19	3	14	15	1	10	20
22/12/68	0	3	10	0	3	9	0	10	21	0	8	23
7/ 1/70	0	4	7	0	2	0	0	4	12	0	5	10
21/ 1/70	0	2	3	0	0	0	0	3	9	0	2	7
3/ 2/70	0	2	0	0	0	0	0	0	1	0	0	0
17/ 3/70	0	0	0	0	0	0	0	0	0	0	0	0

ALA = Alate; APT = Apterous; N = Nymphs

APPENDIX 3

Numbers of Myzus persicae counted on dock plants on the headlands during the 1968-69 winter

Site and counting date	No. of plants	Alate	Alate nymphs	Apterae	Apterous nymphs	Middle nymphs	Young nymphs
Newington							
27/ 1/69	IO	0	0	4	3	4	3
3/ 3/69	8	0	0	2	6	15	16
26/ 3/69	4	0	0	1	2	2	3
1/ 4/69	4	0	0	6	6	3	13
23/ 4/69	2	0	0	1	1	1	0
29/ 4/69	2	1	3	IO	42	42	20
Musselburgh							
6/ 2/69	IO	0	0	5	2	5	11
18/ 4/69	6	0	0	4	9	5	3
2/ 5/69	5	0	0	8	14	23	9
16/ 5/69	5	0	0	11	IO	41	72
24/ 5/69	5	1	18	7	8	47	20
30/ 5/69	5	2	22	2	7	27	7
6/ 6/69	5	2	6	3	3	14	9
13/ 6/69	4	0	5	4	5	24	17
20/ 6/69	4	0	0	0	0	0	0

APPENDIX 4

Numbers of Myzus persicae counted on dock plants on the headlands during the 1969-70 winter

Site and counting date	No. of plants	Alate	Alate nymphs	Apterae	Apterous nymphs	Middle nymphs	Young nymphs
Newington							
27/11/69	6	3	4	13	9	8	5
22/12/69	6	0	0	8	4	2	1
21/ 1/70	5	0	0	7	2	2	3
30/ 1/70	5	0	0	2	1	2	1
24/ 2/70	5	0	0	1	0	2	2
17/ 3/70	5	0	0	9	0	7	23
8/ 4/70	5	0	0	1	1	27	3
5/ 5/70	4	0	0	6	0	2	10
19/ 5/70	2	0	2	1	4	7	0
1/ 6/70	2	0	2	1	3	1	1
8/ 6/70	2	2	5	8	11	11	20
15/ 6/70	2	2	7	8	12	8	5
22/ 6/70	0	0	0	0	0	0	0

APPENDIX 5

Numbers of Myzus persicae counted on dock plants on the headlands during the 1970-71 winter

Site and counting date	No. of plants	Alate	Alate nymphs	Apterae	Apterous nymphs	Middle nymphs	Young nymphs
Newington & Lasswade							
27/11/70	7	2	1	7	IO	8	5
18/12/70	7	0	0	5	7	4	4
7/ 1/71	7	0	0	5	5	3	2
22/ 1/71	7	0	0	6	5	1	0
5/ 2/71	7	0	0	4	6	1	0
26/ 2/71	7	0	0	7	4	2	2
12/ 3/71	7	0	0	6	3	2	6
26/ 3/71	7	0	0	8	6	9	4
15/ 4/71	7	0	0	8	7	7	5
30/ 4/71	7	0	0	7	IO	14	8
14/ 5/71	7	2	12	11	9	23	17
28/ 5/71	7	1	18	9	8	11	9
11/ 6/71	7	3	7	5	6	13	15
25/ 6/71	7	0	0	0	0	0	0

APPENDIX 6

Duration of developmental stages of Myzus persicae at various constant temperatures

Temp C	Duration of 1st instar			Duration of 2nd instar			Duration of 3rd instar			Duration of 4th instar			Duration of nymphal stage			Pre-Reproductive period			Birth to 1st nymphal reprod'n			A	B
	No. aphids	Range	Mean	No. aphids	Range	Mean	No. aphids	Range	Mean	No. aphids	Range	Mean	No. aphids	Range	Mean	No. aphids	Range	Mean	No. aphids	Range	Mean		
5	69	8.5 - 15.0	10.9±0.44	56	8.5 - 12.0	10.1±0.27	52	8.0 - 14.5	10.9±0.24	50	10.0 - 14.5	11.9±0.25	50	36.0 - 53.5	43.9±0.72	50	7.0 - 13.0	9.2±0.31	50	44.5 - 65.5	53.1±0.95	9	13
10	71	3.5 - 6.5	4.6±0.13	63	4.0 - 6.5	5.3±0.14	58	4.5 - 7.5	5.6±0.14	50	5.5 - 6.5	5.9±0.08	50	19.5 - 24.5	21.3±0.33	50	1.5 - 3.0	2.0±0.09	50	21.5 - 26.0	23.3±0.33	6	11
*10		4.0 - 4.5	4.3±0.12		5.0 - 6.5	5.7±0.25		6.0 - 10.0	7.2± 0.72	5	8.0 - 10.5	8.9±0.43	5	24.0 - 30.0	26.1±1.10	5	3.5 - 4.0	3.9±0.13	5	28.0 - 34.0	29.8±1.44		
15	67	2.5 - 3.5	2.8±0.07	60	2.0 - 3.5	2.6±0.07	54	2.0 - 3.5	2.8±0.09	34	2.5 - 4.0	3.4±0.10	34	10.5 - 13.5	11.6±0.22	34	0.5 - 2.0	1.2±0.11	34	11.5 - 14.5	12.7±0.26	4	14
*15		2.5 - 4.0	3.0±0.80		2.5 - 3.5	2.8±0.07		2.5 - 5.5	3.2±0.12	20	5.0 - 6.5	5.6±0.09	20	13.5 - 17.5	14.7±0.19	20	1.5 - 4.0	2.2±0.14	20	15.0 - 19.5	16.9±0.26		
20	65	1.0 - 2.5	1.7±0.06	62	1.0 - 2.0	1.6±0.04	57	1.5 - 3.0	1.8±0.07	49	2.0 - 2.5	2.2±0.04	49	6.5 - 9.0	7.5±0.14	49	0.5 - 1.5	0.83±0.08	49	7.0 - 10.0	8.3±0.17	5	14
*20		1.5 - 2.0	1.8±0.13		1.5 - 2.0	1.7±0.19		1.5 - 3.0	1.8±0.82	4	2.5 - 3.0	2.8±0.24	4	8.5 - 10.0	9.2±0.25	4	1.0 - 1.5	1.3±0.12	4	10.0 - 13.0	10.5±1.12		
25	64	1.0 - 2.0	1.3±0.05	61	1.0 - 1.5	1.2±0.05	50	1.0 - 2.0	1.4±0.05	45	1.0 - 2.5	1.6±0.05	45	4.5 - 6.5	5.4±0.13	45	0.5 - 1.0	0.63±0.39	45	5.0 - 8.5	6.2±0.15	15	12
30	60	1.0 - 1.5	1.2±0.04	40	1.0 - 2.0	1.2±0.05	31	1.0 - 1.5	1.5±0.08	15	1.0 - 2.5	2.2±0.18	15	4.5 - 7.0	5.6±0.13	15	1.5 - 3.5	2.2±0.60	15	6.5 - 10.5	7.9±0.31	40	17

* = alatae

A = number of aphids died before maturity;

B = number of nymphs killed and accidentally lost:

APPENDIX 7

Age-specific life and fecundity tables for Myzus persicae reared on brussels sprouts at constant temperatures of 5° C, 10° C, and 15° C

	5° C		10° C		15° C	
Age (days) x	Survival rate % lx	Nymphs / aphid mx	Survival rate lx	Nymphs / aphid mx	Survival rate lx	Nymphs / aphid mx
0	100		100		100	
5	98		97		97	
10	97		93		94	
15	96		91		80	8.6
20	95		90		59	14.0
25	92		85	2.8	44	20.2
30	91		78	7.2	28	17.8
35	90		74	7.7	12	9.7
40	87		74	8.0	8	2.5
45	84	0.2	65	6.8	8	0.5
50	83	1.0	41	5.8	4	
55	79	1.4	33	8.4	4	
60	79	2.0	21	7.2		
65	79	2.5	16	6.3		
70	77	2.7	12	2.9		
75	77	2.8	4	4.0		
80	73	2.9	4			
85	68	2.9	0			
90	63	2.8				
95	63	2.4				
100	54	1.6				
105	43	0.9				
110	37	0.8				
115	28	0.5				
120	14	0.2				
125	8	0.1				
130	6					
135	3					
140	0					

APPENDIX 7a

Age-specific life and fecundity tables for Myzus persicae reared on brussels sprouts at constant temperatures of 20°C, 25°C and 30°C

	20°C		25°C		30°C	
Age (days) x	Survival rate % lx	Nymphs / aphid mx	Survival rate % lx	Nymphs / aphid mx	Survival rate % lx	Nymphs / aphid mx
0	100		100		100	
5	93		75		28	
10	86	8.8	66	15.9	20	7.9
15	71	16.9	27	18.6	7	4.2
20	35	15.2	15	14.4		
25	25	14.2	5	7.7		
30	16	7.2				
35	5	0.8				
40						

APPENDIX 8

Reproduction and longevity of Myzus persicae (in days)

T. °C	No. of aphids	Reproductive period		Nymphs reproduced daily			Total nymphs reproduced/female		Adult longevity		Total longevity	
		Range	Mean	Range	Based on reprod. per'd	Based on adult long'y	Range	Mean	Range	Mean	Range	Mean
5	49	42-67	53.2 ± 1.8	0-3	0.52 ± 0.02	0.41 ± 0.01	19-38	27.8 ± 1.0	52.0-87.0	67.2 ± 2.5	97-133	II0.6 ± 2.2
I0	50	21-57	32.4 ± 2.7	0-5	1.50 ± 0.05	1.30 ± 0.05	30-80	48.4 ± 3.7	22.5-59.0	35.8 ± 2.7	45-81	58.0 ± 2.9
I0*	5	9-51	27.3 ± 8.9	0-3	0.8 ± 0.65	0.53 ± 0.47	15-29	18.8 ± 4.6	16.0-66.5	36.9 ± I0.7	41-91	62.8 ± I0.4
15	31	8-28	18.8 ± 2.0	0-7	3.5 ± 0.26	2.80 ± 0.33	28-85	57.7 ± 7.2	9.5-42.5	28.1 ± 4.4	20-45	30.2 ± 4.2
15*	18	5-27	13.3 ± 1.8	0-6	1.6 ± 0.13	1.40 ± 0.13	8-42	21.0 ± 2.8	11.5-33.5	21.2 ± 2.3	21-47	32.8 ± 2.2
20	48	9-27	16.7 ± 1.4	0-9	3.3 ± 1.88	3.20 ± 0.20	31-86	55.0 ± 4.9	8.5-28.0	17.0 ± 1.4	17-35	25.0 ± 1.5
20*	4	14-23	18.0 ± 4.2	0-7	2.8 ± 0.56	2.40 ± 0.62	39-60	50.3 ± 5.4	15.5-27.0	20.7 ± 6.3	25-37	31.0 ± 4.2
25	43	9-22	14.7 ± 1.1	0-I0	3.8 ± 0.23	3.50 ± 0.25	25-74	53.9 ± 3.6	8.5-24.0	15.6 ± 1.6	14-29	21.2 ± 1.4
30	15	2-8	4.4 ± 0.6	0-4	1.7 ± 0.19	0.90 ± 0.13	4-I0	7.5 ± 0.6	5.0-12.5	8.2 ± 0.2	11-18	13.9 ± 1.1

* = Alate

APPENDIX 9

Alate aphids in yellow water traps; - weekly totals per two traps at Lasswade 1969

Week No.	Week ending	M.persicae	M.euphorbiae	Others	Total
1	4/ 6	0	0	3	3
2	11/ 6	0	0	7	7
3	18/ 6	0	0	15	15
4	25/ 6	0	0	7	7
5	2/ 7	0	0	73	73
6	9/ 7	0	1	109	110
7	16/ 7	0	5	43	48
8	23/ 7	0	4	12	16
9	30/ 7	1	19	36	56
10	6/ 8	45	29	82	156
11	13/ 8	76	52	155	283
12	20/ 8	9	9	90	108
13	27/ 8	8	3	36	47
14	3/ 9	18	15	115	148
15	10/ 9	22	12	256	290
16	17/ 9	6	2	81	89
17	24/ 9	3	0	37	40
18	1/10	0	0	12	12
19	8/10	5	0	86	91
20	15/10	12	0	135	147
21	22/10	24	3	84	111
22	29/10				
23	5/11	0	0	1	1
24	12/11	0	0	0	0
25	19/11	0	0	0	0
Total		229	154	1475	1858

APPENDIX IO

Alate aphids caught in yellow water traps; - weekly totals per two traps at Newington 1969

Week No.	Week ending	M.persicae	M.euphorbiae	Others	Total
1	9/ 6	0	0	6	6
2	16/ 6	1	0	25	26
3	23/ 6	0	0	21	21
4	30/ 6	0	2	148	150
5	7/ 7	2	6	52	60
6	14/ 7	2	6	47	55
7	21/ 7	4	IO	I09	123
8	28/ 7	40	53	388	481
9	4/ 8	79	66	718	863
IO	11/ 8	125	95	I056	1276
11	18/ 8	I05	31	640	776
12	25/ 8	15	15	306	336
13	1/ 9	39	3	240	282
14	8/ 9	74	IO	358	442
15	15/ 9	40	0	422	462
16	22/ 9	26	5	496	527
17	29/ 9	24	2	206	232
18	6/IO	3	0	202	205
19	13/IO	112	0	894	I006
20	20/IO	260	2	860	1122
21	27/IO				
22	3/11	IO	0	15	25
23	IO/11	0	1	0	1
	Totals	961	307	7209	8477

APPENDIX 11

Alate aphids caught in yellow water traps; - weekly totals per two water traps at Lasswade 1970

Week No.	Week ending	M.persicae	M.euphorbiae	Others	Total
1	10/ 6	1	0	24	25
2	17/ 6	1	0	50	51
3	24/ 6	0	3	62	64
4	1/ 7	1	1	50	52
5	8/ 7	1	0	25	26
6	15/ 7	0	6	7	13
7	22/ 7	2	33	29	64
8	29/ 7	10	55	85	150
9	5/ 8	18	70	196	284
10	12/ 8	16	56	165	237
11	19/ 8	17	13	141	171
12	26/ 8	4	2	46	52
13	2/ 9	4	1	34	39
14	9/ 9	1	0	10	11
15	16/ 9	0	0	3	3
16	23/ 9	0	0	244	244
17	30/ 9				
18	7/10	0	0	9	9
19	14/10	0	0	15	15
20	21/10				
21	28/10	1	0	5	6
22	4/11	0	0	4	4
23	11/11	0	0	0	0
24	18/11	0	0	0	0
	Total	77	239	1104	1520

APPENDIX 12

Alate aphids caught in yellow water traps; - weekly total per two traps at Newington 1970

Week No. –	Week ending	M.persicae	M.euphorbiae	Others	Total
1	8/ 6	0	1	197	198
2	15/ 6	0	0	157	157
3	22/ 6	0	4	186	190
4	29/ 6	0	6	888	894
5	6/ 7	0	0	820	820
6	13/ 7	1	7	357	367
7	20/ 7	8	25	I095	1128
8	27/ 7	4	30	416	450
9	3/ 8	20	41	I037	I098
I0	I0/ 8	12	27	579	618
11	17/ 8	11	13	890	914
12	24/ 8	4	I0	838	852
13	31/ 8	16	3	517	546
14	7/ 8	4	0	182	186
15	14/ 9	3	0	144	147
16	21/ 9	3	0	319	322
17	28/ 9	13	0	2551	2564
18	5/I0	1	0	189	190
19	12/I0	1	0	125	126
20	19/I0	8	0	I02	II0
21	26/I0	1	0	40	41
22	2/11	0	0	3	3
23	9/11	0	0	1	1
24	15/11	0	0	0	0
25	22/11	0	0	0	0
	Total	II0	167	11645	11922

APPENDIX 13

The mean numbers (± standard error) of Myzus persicae per brussels sprout plant at Lasswade 1969

Week No.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. nymphs + adults
1	2/7	0.0 ± 0.0	0.4 ± 0.2	0.1 ± 0.1	1.0 ± 0.5	2.0 ± 0.8	0.8 ± 0.5	4.3 ± 1.8
2	9/2	0	0.2 ± 0.1	0	0.8 ± 0.2	1.5 ± 0.6	0.8 ± 0.7	3.2 ± 1.4
3	16/7	0.1 ± 0	1.2 ± 0.3	0.2 ± 0.2	1.3 ± 0.4	8.8 ± 3.8	8.3 ± 3.8	19.8 ± 6.4
4	23/7	0.1 ± 0	4.5 ± 1.0	1.0 ± 0.4	7.8 ± 2.4	25.7 ± 5.5	29.5 ± 5.8	68.5 ± 14.2
5	30/7	0.5 ± 0.3	9.6 ± 1.4	5.7 ± 1.8	9.9 ± 1.5	52.9 ± 8.8	62.7 ± 10.7	141.4 ± 21.4
6	6/8	2.0 ± 0.6	9.7 ± 2.6	28.1 ± 9.7	12.3 ± 2.7	102.1 ± 22.4	61.6 ± 16.9	215.8 ± 48.9
7	13/8	2.6 ± 1.7	2.0 ± 0.9	3.9 ± 1.5	5.6 ± 2.8	41.0 ± 14.3	32.8 ± 11.1	87.8 ± 25.5
8	20/8	0.2 ± 0.2	4.9 ± 1.8	1.7 ± 1.0	6.0 ± 3.5	17.5 ± 5.6	28.6 ± 12.2	58.9 ± 19.5
9	27/8	0.3 ± 0.2	4.4 ± 2.7	0.2 ± 0.1	0.9 ± 0.4	8.4 ± 3.4	15.5 ± 8.2	29.6 ± 13.6
10	3/9	0.9 ± 0.6	15.9 ± 4.7	4.6 ± 1.8	11.7 ± 4.0	58.2 ± 16.3	52.2 ± 14.5	143.4 ± 36.4
11	10/9	1.0 ± 0.5	20.5 ± 5.1	10.3 ± 2.3	15.8 ± 4.2	69.8 ± 18.2	62.9 ± 18.4	180.3 ± 39.5
12	17/9	1.5 ± 0.7	22.3 ± 4.3	15.7 ± 4.2	21.9 ± 6.4	85.3 ± 21.3	71.7 ± 22.5	218.4 ± 51.3
13	24/9	0.9 ± 0.4	5.6 ± 1.8	16.7 ± 7.5	10.0 ± 3.0	30.5 ± 11.1	23.8 ± 8.0	87.4 ± 26.0
14	1/10	2.1 ± 0.6	10.9 ± 2.6	18.5 ± 3.6	14.5 ± 3.3	41.2 ± 6.5	40.6 ± 11.4	127.8 ± 21.2
15	8/10	1.1 ± 0.4	5.3 ± 1.4	25.9 ± 10.1	17.3 ± 5.9	46.6 ± 17.1	23.4 ± 5.8	119.5 ± 37.3
16	15/10	2.0 ± 0.8	6.5 ± 1.5	21.5 ± 3.1	18.7 ± 5.4	59.3 ± 16.2	29.8 ± 7.5	137.8 ± 25.2
17	22/10	No sampling	-	-	-	-	-	-
18	29/10	3.9 ± 1.7	8.0 ± 2.6	28.8 ± 13.0	12.2 ± 3.2	98.0 ± 41.9	35.5 ± 11.3	186.2 ± 70.1
19	5/11	2.1 ± 1.2	11.2 ± 4.2	18.5 ± 5.8	10.1 ± 2.7	53.5 ± 15.2	35.7 ± 14.3	130.9 ± 37.1
20	12/11	0.3 ± 0.2	2.5 ± 1.5	3.5 ± 1.1	7.5 ± 2.3	22.5 ± 7.1	15.3 ± 8.1	51.6 ± 19.0
21	19/11	0.3 ± 0.2	2.1 ± 1.1	3.6 ± 1.3	5.7 ± 2.1	25.1 ± 8.8	11.2 ± 6.9	48.0 ± 20.3
22	26/11	0.2 ± 0.2	3.0 ± 2.1	3.8 ± 2.0	12.9 ± 7.9	30.9 ± 21.8	6.8 ± 4.1	57.6 ± 37.0

APPENDIX 14

The mean numbers (+ standard error) of Myzus persicae per brussels sprout plant at Newington 1969

Week No.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. nymphs & adults
1	30/6	0.1 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	0.4 ± 0.1	1.1 ± 0.4	0.6 ± 0.3	2.3 ± 0.6
2	7/7	0	0.5 ± 0.3	0	0.6 ± 0.2	1.7 ± 0.6	1.4 ± 0.5	4.1 ± 1.4
3	14/7	0.2 ± 0.1	0.7 ± 0.2	0.3 ± 0.2	1.5 ± 0.4	5.3 ± 1.6	3.0 ± 0.9	11.1 ± 2.9
4	21/7	0.9 ± 0.2	2.8 ± 0.6	3.1 ± 1.3	7.0 ± 1.6	15.2 ± 2.0	19.7 ± 4.2	48.7 ± 7.6
5	28/7	1.1 ± 0.3	3.2 ± 0.7	8.8 ± 2.5	8.5 ± 1.6	40.3 ± 8.3	33.5 ± 5.7	95.4 ± 16.1
6	4/8	2.2 ± 0.4	2.2 ± 0.8	3.1 ± 0.9	I0.1 ± 2.2	46.7 ± 7.1	24.0 ± 6.1	88.4 ± 12.4
7	11/8	7.6 ± 3.3	8.5 ± 1.5	3.1 ±1.0	14.5 ± 2.6	I00.5 ± 14.6	70.4 ± 7.0	204.1 ± 20.1
8	18/8	2.4 ± 1.0	11.7 ± 3.5	7.2 ± 2.0	26.4 ± 8.6	163.4 ± 31.4	70.9 ± 15.6	281.9 ± 54.8
9	25/8	0.5 ± 0.2	12.7 ± 5.3	12.5 ± 4.1	22.5 ± 6.8	116.1 ± 27.6	I04.5 ± 34.7	268.6 ± 56.2
I0	1/9	2.3 ± 1.2	37.0 ± 11.7	52.4 ± 19.0	53.1 ± 12.1	343.8 ± 129.9	222.6 ± 66.1	711.2 ± 223.6
11	8/9	3.1 ± 1.4	49.6 ± 8.2	47.1 ± 11.0	49.8 ± 5.4	430.2 ± 72.6	312.1 ± 60.9	891.8 ± 141.2
12	15/9	4.1 ± 1.2	63.5 ± 12.1	184.1 ± 31.5	67.9 ± 9.1	341.4 ± 61.9	311.8 ± 70.1	972.8 ± 165.0
13	22/9	6.2 ± 1.5	72.4 ± 20.4	191.3 ± 40.1	76.5 ± 20.2	350.1 ± 52.8	352.7 ± 90.2	I049.2 ± 232.1
14	29/9	4.0 ± 1.5	68.4 ± 25.2	190.8 ± 48.1	56.7 ± 17.7	266.0 ± 51.1	371.8 ± II0.8	957.8 ± 239.6
15	6/I0	2.5 ± 1.0	22.8 ± I0.1	40.8 ± 12.0	24.4 ± 4.3	136.4 ± 41.5	121.9 ± 44.2	348.8 ± I00.2
16	13/I0	3.4 ± 1.1	29.4 ± 8.5	49.2 ± 15.4	35.2 ± 9.1	163.9 ± 20.7	141.2 ± 39.5	422.3 ± 44.2
17	20/I0	No sampling	-	-	-	-	-	-
18	27/I0	7.2 ± 1.4	43.3 ± 7.9	78.0 ± 11.5	68.2± I0.2	387.9 ± 39.3	195.1 ± 21.7	779.6 ± 78.0
19	3/11	8.8 ± 3.3	60.3 ± 14.0	180.6 ± 70.8	94.5± 23.8	373.0 ± 88.6	263.9 ± 63.4	954.0 ± 250.9
20	I0/11	3.3 ± 1.1	32.1 ± 7.4	24.2 ± 6.0	39.5± I0.7	195.8 ± 44.5	116.5 ± 25.3	411.4 ± 90.0
21	17/11	8.4 ± 3.0	22.0 ± 7.2	46.9 ± 22.3	47.2 ± I0.9	302.7 ± II0.1	64.9 ± 17.0	492.0 ± 164.5
22	24/11	4.7 ± 2½2	26.0 ± 8.4	46.7 ± 17.5	50.5 ± 13.8	212.5 ± 63.6	140.9 ± 41.7	481.4 ± 143.8
23	1/12	0.2 ± o.1	3.2 ± 1.4	2.0 ± 0.5	13.3 ± 3.1	67.5 ± 14.6	17.5 ± 7.2	I03.6 ± 22.6

APPENDIX 15

The mean numbers (± standard error) of Macrosiphum euphorbiae per brussels sprout plant at Lasswade 1969

Week No.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. of nymphs & adults
1	2/7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0,0	0.0 ± 0.0	0.0 ± 0.0
2	9/7	0.03 ± 0.03	0.03 ± 0.03	0	0.2 ± 0.1	0.2 ± 0.2	0.1 ± 0.1	0.6± 0.4
3	16/7	0.1 ± 0.04	0	0	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.6 ± 0.4
4	23/7	0.04 ± 0.03	0.1 ± 0.1	0.02 ± 0.02	0.2 ± 0.1	0.4 ± 0.2	0.2 ± 0.2	0.9 ± 0.4
5	30/7	0.5 ± 0.2	0.2 ± 0.1	0	0.3 ± 0.2	0.8 ± 0.4	0.5 ± 0.3	2.2 ± 0.9
6	6/8	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0.7 ± 0.3	3.0 ± 1.3	0.8 ± 0.6	4.8 ± 1.8
7	13/8	0.2 ± 0.1	0	0	0.2 ± 0.2	0.4 ± 0.3	0.2 ± 0.2	0.9 ± 0.7
8	20/8	0	0	0	0	0.2 ± 0.2	0	0.2 ± 0.2
9	27/8	0	0	0	0	0	0	0
IO	3/9	0	0	0	0	0	0	0
11	IO/9	0	0	0	0	0	0	0
12	17/9	0	0	0	0	0	0	0
13	24/9	0	0	0	0	0	0	0
14	1/IO	0	0	0	0	0	0	0
15	8/IO	0	0	0	0	0	0	0
16	15/IO	0	0	0	0	0	0	0
17	22/IO	No sampling	-	-	-	-	-	-
18	29/IO	0	0	0	0	0	0	0
19	5/11	0	0	0	0	0	0	0
20	12/11	0	0	0	0	0	0	0
21	19/11	0	0	0	0	0	0	0
22	26/11	0	0	0	0	0	0	0

APPENDIX 16

The mean numbers (± standard error) of Macrosiphum euphorbiae per brussels sprout plant at Newington 1969

Week no.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. of nymphs & adults
1	30/6	0.0 ± 0.0	0.01 ± 0.01	0.03 ± 0.03	0	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.1
2	7/7	0	0	0	0.1 ± 0.1	0	0	0.1 ± 0.1
3	14/7	0.1 ± 0.1	0.3 ± 0.1	0.5 ± 0.1	1.6 ± 0.3	2.3 ± 0.4	1.1 ± 0.2	5.7 ± 1.5
4	21/7	0.3 ± 0.1	0.1 ± 0.1	0.03 ± 0.2	0.3 ± 0.1	0.3 ± 0.1	0.03 ± 0.03	1.0 ± 0.3
5	28/7	0.2 ± 0.1	0	0	0.2 ± 0.1	0;4 ± 0.1	0.2 ± 0.1	0.9 ± 0.3
6	4/8	0.8 ± 0.3	0.2 ± 0.2	0	0.2 ± 0.1	1.2 ± 0.6	0.8 ± 0.4	3.2 ± 1.2
7	11/8	1.5 ± 0.7	0	0.2 ± 0.2	0.1 ± 0.1	0.4 ± 0.2	0.3 ± 0.1	2.3 ± 0.9
8	18/8	0	0	0	0.3 ± 0.2	0.7 ± 0.5	0	1.0 ± 0.6
9	25/8	0	0	0	0	0	0	0
IO	1/9	0	0	0	0	0	0	0
11	8/9	0	0	0.2 ± 0.2	0	0	0	0.2 ± 0.2
12	15/9	0	0	0	0	0	0	0
13	22/9	0	0	0	0	0	0	0
14	29/9	0	0	0	0	0	0	0
15	6/IO	0	0	0	0	0	0	0
16	13/IO	0	0	0	0	0	0	0
17	20/IO	No sampling	-	-	-	-	-	-
18	27/IO	0	0	0	0	0	0	0
19	3/11	0	0	0	0	0	0	0
20	IO/11	0	0	0	0	0	0	0
21	17/11	0	0	0	0	0	0	0
22	24/11	0	0	0	0	0	0	0
23	1/12	0	0	0	0	0	0	0

APPENDIX 17

The mean numbers (± standard error) of Myzus persicae per brussels sprout plant at Lasswade 1970

Week no.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. of nymphs & adults
1	1/7	0.1 ± 0.1	0.5 ± 0.3	0.0 ± 0.0	1.0 ± 0.5	4.2 ± 2.0	0.5 ± 0.4	6.3 ± 2.6
2	8/7	0	1.7 ± 0.6	1.0 ± 0.6	1.3 ± 0.4	6.9 ± 1.7	6.2 ± 2.8	17.2 ± 4.8
3	15/7	0.5 ± 0.2	3.4 ± 0.6	6.6 ± 2.4	3.5 ± 0.8	20.1 ± 5.6	14.4 ± 3.1	48.4 ± 11.0
4	22/7	0.9 ± 0.2	5.5 ± 1.2	13.7 ± 3.6	11.5 ± 3.5	40.1 ± 10.2	33.9 ± 7.1	105.6 ± 23.4
5	29/7	2.3 ± 0.7	5.3 ± 1.2	8.0 ± 1.9	8.4 ± 2.0	20.6 ± 4.4	26.5 ± 6.9	71.2 ± 15.1
6	5/8	2.8 ± 0.6	4.4 ± 1.1	6.7 ± 1.9	8.1 ± 2.0	31.8 ± 8.8	34.8 ± 8.8	88.4 ± 20.6
7	12/8	5.3 ± 1.8	15.6 ± 5.0	16.3 ± 6.6	18.0 ± 8.0	42.0 ± 16.1	70.2 ± 23.7	167.3 ± 54.9
8	19/8	1.9 ± 0.8	5.1 ± 1.2	6.8 ± 2.0	9.8 ± 2.5	19.1 ± 5.4	30.2 ± 7.4	72.9 ± 16.9
9	26/8	0.2 ± 0.1	2.1 ± 0.6	3.1 ± 1.3	5.2 ± 1.1	12.8 ± 3.8	9.2 ± 2.7	32.4 ± 8.1
10	2/9	0	0.3 ± 0.2	0.5 ± 0.3	2.3 ± 1.3	2.0 ± 1.1	1.0 ± 0.8	6.0 ± 2.5
11	9/9	0	0	0.3 ± 0.2	0.8 ± 0.4	0	0	1.0 ± 0.4
12	16/9	0	0	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0	0.4 ± 0.2
13	23/9	No sampling	-	-	-	-	-	-
14	30/9	0	0	0.2 ± 0.1	0.3 ± 0.2	0	0	0
15	7/10	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.5 ± 0.2	0	0	1.1 ± 0.4

APPENDIX 18

The Mean numbers (± standard error) of Myzus persicae per brussels sprout plant at Newington 1970

Week no.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. of nymphs & adults
1	29/6	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	2.0 ± 1.1	2.3 ± 1.0	1.0 ± 0.5	5.7 ± 2.1
2	6/7	0	0.7 ± 0.5	0.2 ± 0.1	1.3 ± 0.5	1.5 ± 0.7	2.0 ± 1.4	5.6 ± 3.0
3	13/7	0	0.2 ± 0.1	0.2 ± 0.2	1.1 ± 0.3	2.7 ± 1.3	0.4 ± 0.3	4.5 ± 1.8
4	20/7	0.1 ± 0.1	0.1 ± 0.1	0.6 ± 0.4	1.7 ± 0.6	4.1 ± 1.8	1.0 ± 0.8	7.6 ± 2.9
5	27/7	0.5 ± 0.3	0.6 ± 0.2	0.5 ± 0.2	1.8 ± 0.5	5.1 ± 1.6	4.4 ± 1.6	12.9 ± 3.5
6	3/8	0.5 ± 0.2	0.8 ± 0.3	0.5 ± 0.2	2.0 ± 0.5	1.4 ± 0.5	4.0 ± 1.2	9.2 ± 1.8
7	10/8	0.5 ± 0.3	1.4 ± 0.9	0.9 ± 0.2	3.5 ± 0.9	10.2 ± 4.1	9.2 ± 3.5	25.7 ± 8.3
8	17/8	0.6 ± 0.3	2.5 ± 1.0	3.8 ± 1.9	4.9 ± 1.5	15.9 ± 6.2	12.9 ± 3.8	40.6 ± 10.7
9	24/8	0.8 ± 0.5	3.1 ± 1.1	6.2 ± 3.1	7.2 ± 2.1	23.5 ± 8.9	18.9 ± 9.7	59.7 ± 20.5
10	31/8	0	4.2 ± 1.9	3.6 ± 1.5	12.5 ± 6.3	32.8 ± 21.3	28.2 ± 18.3	81.3 ± 46.7
11	7/9	0.1 ± 0.1	1.9 ± 0.9	3.8 ± 1.3	4.0 ± 1.6	7.9 ± 3.7	9.6 ± 5.7	27.3 ± 12.8
12	14/9	0.1 ± 0.1	1.5 ± 0.6	3.0 ± 1.6	5.8 ± 3.3	8.6 ± 6.4	4.5 ± 1.8	23.5 ± 12.8
13	21/9	No sampling	-	-	-	-	-	-
14	28/9	0.3 ± 0.2	2.3 ± 0.9	3.3 ± 1.7	4.3 ± 1.5	10.8 ± 3.5	8.6 ± 3.4	29.6 ± 8.5
15	5/10	0.4 ± 0.2	1.0 ± 0.4	3.7 ± 1.1	2.0 ± 0.6	3.6 ± 1.1	3.9 ± 1.8	14.6 ± 4.4
16	12/10	No sampling	-	-	-	-	-	-
17	19/10	0	0.3 ± 0.3	0.5 ± 0.4	0.9 ± 0.5	1.1 ± 1.1	0.9 ± 0.7	3.6 ± 2.8

APPENDIX 19

The mean numbers (± standard error) of Macrosiphum euphorbiae per brussels sprout plant at Lasswade 1970

Week no.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. of nymphs & adults
1	1/7	0.2 ± 0.1	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.1 ± 0.1	0.6 ± 0.3
2	8/7	0.1 ± 0.1	0.2 ± 0.1	0	0.2 ± 0.1	0.6 ± 0.3	0.5 ± 0.3	1.5 ± 0.8
3	15/7	0.5 ± 0.2	0.3 ± 0.1	0	0.2 ± 0.1	1.5 ± 0.6	1.7 ± 0.7	4.0 ± 1.7
4	22/7	0.8 ± 0.4	0.4 ± 0.2	0	0.8 ± 0.4	0.6 ± 0.3	0.9 ± 0.4	3.5 ± 1.4
5	29/7	0.8 ± 0.3	0.9 ± 0.4	0	1.6 ± 0.6	1.8 ± 0.7	0.3 ± 0.1	5.5 ± 2.0
6	5/8	0.8 ± 0.3	0.9 ± 0.4	0	1.3 ± 0.7	1.9 ± 0.8	2.3 ± 1.1	7.3 ± 2.8
7	12/8	0.8 ± 0.5	0.3 ± 0.2	0.3 ± 0.2	2.7 ± 1.2	3.7 ± 1.7	0.3 ± 0.3	8.2 ± 3.1
8	19/8	0.9 ± 0.4	1.6 ± 0.7	0	4.9 ± 2.0	3.9 ± 1.4	1.7 ± 1.1	13.0 ± 3.8
9	26/8	0	0	0	0.3 ± 0.2	0.4 ± 0.2	0	0.7 ± 0.3
10	2/9	0	0	0	0	0	0	0
11	9/9	0	0	0	0	0	0	0
12	16/9	0	0	0	0	0	0	0
13	23/9	No sampling	-	-	-	-	-	-
14	30/9	0	0	0	0	0	0	0
15	7/10	0	0	0	0	0	0	0

APPENDIX 20

The mean numbers (± standard error) of Macrosiphum euphorbiae per brussels sprout plant at Newington 1970

Week no.	Week ending	Alate adults	Apterous adults	Alate 4th instar nymphs	Advanced nymphs	Medium nymphs	Young nymphs	Total no. of nymphs & adults
1	29/6	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.3	1.4 ± 0.6	0.0 ± 0.0	2.0 ± 0.8
2	6/7	0	0.1 ± 0.1	0	0.4 ± 0.3	0.1 ± 0.1	0.2 ± 0.2	0.8 ± 0.5
3	13/7	0	0.1 ± 0.1	0	0	0.1 ± 0.1	0.4 ± 0.3	0.5 ± 0.4
4	20/7	0.2 ± 0.2	0	0	0.1 ± 0.1	0.9 ± 0.6	0.9 ± 0.6	2.0 ± 1.2
5	27/7	0.3 ± 0.2	0	0	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.8 ± 0.5
6	3/8	0.6 ± 0.2	0	0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.8 ± 0.3
7	10/8	0	0	0	0	0	0	0
8	17/8	0	0	0	0	0	0	0
9	24/8	0	0	0	0	0	0	0
10	31/8	0	0	0	0	0	0	0
11	7/9	0	0	0	0	0	0	0
12	14/9	0	0	0	0	0	0	0
13	21/9	No sampling	-	-	-	-	-	-
14	28/9	0	0	0	0	0	0	0
15	5/10	0	0	0	0	0	0	0
16	12/10	No sampling	-	-	-	-	-	-
17	19/10	0	0	0	0	0	0	0

APPENDIX 21

Aphidophagous syrphids in yellow water traps; - weekly totals per two traps at Lasswade 1969

		Sy. ribesii	Sy.balteatus	Sy. corollae	Sy. vitripennis	Sy. luniger	Sy. auricollis	P.manicatus	P.albimanus	P.scutatus	P.tarsalis	P.clypeatus	P.pelatus	P.strictícus	M.mellinum	M.scalare	Py.granditarsi	Sp.menthastri	Total
1	4/6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	2
2	11/6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
3	18/6	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
4	25/6	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	6
5	2/7	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	5
6	9/7	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	4
7	16/7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
8	23/7	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2
9	30/7	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	3
10/	6/8	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3
11	13/8	1	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	5
12	20/8	0	1	1	0	0	0	1	0	0	0	0	0	0	3	0	0	0	6
13	27/8	5	6	6	0	1	0	0	0	0	0	2	0	0	2	1	0	0	23
14	3/9	12	10	7	2	0	0	0	0	0	0	0	0	0	1	2	7	0	41
15	10/9	21	5	1	3	1	0	0	1	0	1	0	1	0	0	0	11	0	45
16	17/9	11	9	2	1	0	0	4	0	2	0	0	0	0	1	0	5	0	35
17	24/9	20	6	2	4	1	0	8	2	0	0	0	0	0	0	0	3	0	46
18	1/10	23	3	0	2	0	0	2	1	0	0	0	0	0	0	0	0	0	31
19	8/10	22	3	2	1	1	0	4	1	0	0	0	0	0	0	0	0	0	34
20	15/10	14	1	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	20
21	22/10	6	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	10
22	29/10																		
23	5/11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	12/11	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2
25	19/11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total Y		135	46	26	18	6	1	45	7	3	3	2	1	0	7	4	26	0	330

Sy. = Syrphus; P. = Platychaerus; M. = Melanostoma; Py. = Pyrophaena; Sp. = Sphaerophora:

APPENDIX 22

Aphidophagous syrphids in yellow water traps; - weekly totals per two traps at Newington 1970

Week No.	Week ending	Sy. ribesii	Sy. baleatus	Sy. vitripennis	Sy. luniger	Sy. corollae	P. albimanus	P. manicatus	P. scambus	P. scutatus	P. clypeatus	M. mellinum	M. scalare	Total
1	9/6	0	0	0	0	0	0	0	0	0	0	0	0	0
2	16/6	0	0	0	0	0	0	0	0	0	0	0	0	0
3	23/6	0	0	0	0	0	0	0	0	0	0	0	0	0
4	30/6	0	0	0	0	0	0	2	0	0	0	0	0	2
5	7/7	0	0	0	0	0	0	0	0	1	0	0	0	1
6	14/7	1	0	0	0	0	0	0	0	0	0	0	0	1
7	21/7	0	0	0	0	0	0	0	0	0	0	0	0	0
8	28/7	0	0	0	0	1	0	0	0	0	0	0	0	1
9	4/8	1	1	0	0	1	0	0	0	0	0	0	0	3
IO	11/8	0	0	0	0	0	0	0	0	0	0	0	0	0
11	18/8	2	0	0	0	0	0	0	1	0	0	0	0	3
12	25/8	8	13	0	1	0	0	0	0	0	0	5	0	27
13	1/9	9	1	1	0	0	4	0	0	0	0	1	1	17
14	8/9	IO	2	0	2	0	1	1	0	0	0	0	1	17
15	15/9	8	1	2	1	1	0	0	0	0	0	0	0	13
16	22/9	6	0	1	1	0	1	0	0	0	0	1	1	11
17	29/9	12	5	0	2	0	0	0	0	0	1	0	0	20
18	6/IO	1	0	5	0	0	0	0	0	0	0	0	0	6
19	13/IO	3	2	1	1	0	0	0	0	0	0	0	0	7
20	20/IO	3	0	2	0	0	0	0	0	0	0	0	0	5
21	27/IO													
22	3/11	0	0	0	0	0	0	0	0	0	0	0	0	0
23	IO/11	0	0	0	0	0	0	0	0	0	0	0	0	0
Total		64	25	12	8	3	6	3	1	1	1	3	3	134

Sy. = Syrphis; P. = Platycheirus; M. = Melanostoma:

APPENDIX 23

Non-aphidophagous syrphids in yellow water traps ;- weekly totals per two traps at Lasswade 1969

Week no.	Week ending	Er. arbustorum	Er. tenax	Er. intricarius	Er. pertinax	Sy. pipiens	N. podagrica	C. variablis	Chilosa spp.	X. segnis	Xylota spp.	H. pendulus	Total
1	4/6	0	0	0	0	0	3	0	0	0	0	0	3
2	11/6	0	0	0	0	0	0	0	0	0	0	0	0
3	18/6	0	0	0	0	2	0	1	0	0	0	0	3
4	25/6	0	0	0	0	0	0	0	0	0	0	0	0
5	2/7	0	1	2	0	1	0	0	0	0	0	0	4
6	9/7	0	2	0	0	1	1	0	0	0	0	0	4
7	16/7	0	0	1	0	0	0	0	0	0	0	0	1
8	23/7	0	0	0	0	0	0	0	0	0	0	0	0
9	30/7	1	1	0	0	0	0	0	0	0	0	0	2
10	6/8	1	1	0	0	0	0	0	0	0	0	0	2
11	13/8	1	0	1	0	1	0	0	0	0	0	0	3
12	20/8	5	0	0	0	0	0	0	0	0	0	0	5
13	27/8	12	1	0	0	0	0	0	0	0	0	1	14
14	3/9	6	2	0	0	0	0	0	0	0	0	0	8
15	10/9	1	0	0	0	0	1	0	0	0	1	0	3
16	17/9	12	0	0	0	1	0	0	2	0	0	1	16
17	24/9	2	0	0	1	0	0	0	0	0	0	1	15
18	1/10	7	1	0	0	0	0	0	0	0	0	0	8
19	8/10	6	3	0	0	0	0	0	0	0	0	2	11
20	15/10	6	2	0	0	0	0	0	0	3	0	1	12
21	22/10	2	7	0	1	0	0	0	0	0	0	1	11
22	29/10												
23	5/11	0	0	0	0	0	0	0	0	0	0	0	0
24	12/11	0	2	0	0	0	0	0	0	0	0	0	2
25	19/11	0	0	0	0	0	0	0	0	0	0	0	0
	Total	71	25	4	1	7	5	1	2	3	1	7	127

Er. = Eristalis; Sy. = Syritta; N. = Neoascia; C. = Chilosia;
X. = Xylota; H. = Helophilus:

APPENDIX 24

Non-aphidophagous syrphids in yellow water traps ;- weekly totals per two traps at Haddington 1969

Week no.	Week ending	Er. tenax	Er. arbustorum	Er. intricarius	N. podogrica	Sy. pipiens	H. pendulus	Chilosia spp.	Xylotta spp.	Total
1	9/6	0	0	0	1.	0	0	0	0	1
2	16/6	0	0	0	0	0	0	0	0	0
3	23/6	0	0	0	0	0	0	0	0	0
4	30/6	0	0	0	0	0	0	0	0	0
5	7/7	0	0	0	0	0	0	0	0	0
6	14/7	0	1	0	0	0	0	0	0	1
7	21/7	0	0	0	0	0	0	0	0	0
8	28/7	0	0	0	0	0	0	0	0	0
9	4/8	0	0	0	0	0	0	0	0	0
IO	11/8	0	0	0	0	0	0	0	0	0
11	18/8	0	0	0	1	2	0	0	0	3
12	25/8	0	0	0	3	0	0	0	0	3
13	1/9	0	0	0	1	0	0	0	1	2
14	8/9	1	0	0	5	0	0	1	0	7
15	15/9	0	2	1	0	0	0	0	0	3
16	22/9	0	0	0	0	0	0	0	0	0
17	29/9	3	0	0	0	0	1	0	0	4
18	6/IO	1	2	0	0	1	0	0	0	4
19	13/IO	1	1	0	0	1	0	0	1	4
20	20/IO	6	0	0	0	0	0	0	0	6
21	27/IO									
22	3/11	4	0	0	0	0	0	0	0	4
23	IO/11	0	0	0	0	0	0	0	0	0
	Total	16	6	1	11	4	1	1	2	42

Er. = Eristalis; N. = Neoascia; Sy. = Syritta; H. = Helophilus; X. = Xylota

APPENDIX 25

Aphidophagous syrphids in yellow water traps; - weekly totals per two traps as Lasswade 1970

Week no.	Week ending	Sy.ribesii	Sy.baleatus	Sy.corollae	Sy.vitri-pennis	Sy.luniger	Pl.peltatus	Pl.manicatus	Pl.albimanus	Pl.clypeatus	Pl.strictícus	Sp.menthastri var. picta	M.scalare	M.mellinum	Py.grandi-tarsa	X.citrofas-iatum	
1	10/6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
2	17/6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
3	24/6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
4	1/7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	8/7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	15/7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	22/7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
8	29/7	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
9	5/7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
10	12/8	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2
11	19/8	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	3
12	26/8	0	0	3	0	0	0	1	0	0	0	1	3	0	2	0	10
13	2/9	1	0	1	0	0	1	0	0	0	0	0	1	1	1	0	6
14	9/9	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	4
15	16/9	7	6	12	1	0	0	0	1	0	0	0	2	1	0	0	30
16	23/9	31	10	34	6	2	0	0	0	0	0	0	0	1	0	1	85
17	30/9																
18	7/10	10	0	1	0	1	0	0	0	0	0	0	0	0	0	0	12
19	14/10	6	0	1	0	1	0	0	0	0	0	0	0	0	0	0	8
20	21/10																
21	28/10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	4/11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	11/11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Total	56	16	52	7	5	5	5	1	2	0	1	7	5	3	1	166

Sy. = Syrphid; Pl. = Platycheirus; Sp. = Sphaerophora; M. = Melanostoma; Py. = Pyrophaena;

X. = Xanthogramma:

APPENDIX 26

Aphidophagous syrphids in yellow water traps;- weekly totals per two traps at Newington 1970

Week no.	Week ending	Sy.ribesii	Sy.vitri-pennis	Sy.corollae	Sy.balteatus	Sy.luniger	Sy.auricoll-is	X.citro-fasciatum	Pl.albimanus	Pl.scutatus	Pl.manicatus	M.scalare	Total
1	8/6	0	0	0	0	0	0	0	0	0	0	0	0
2	15/6	0	0	0	0	0	0	0	0	0	0	0	0
3	22/6	0	0	0	0	0	0	0	0	0	0	0	0
4	29/6	0	0	1	0	0	0	0	0	0	0	0	1
5	6/7	0	0	0	0	0	0	0	0	0	0	0	0
6	13/7	0	0	0	0	0	0	0	0	0	0	0	0
7	20/7	0	0	0	0	0	0	0	0	0	0	0	0
8	27/7	0	0	0	0	0	0	0	0	0	0	0	0
9	3/8	2	0	0	0	0	0	0	0	0	0	0	2
IO	IO/8	0	0	0	0	0	0	0	0	0	0	0	0
11	17/8	0	0	0	0	0	0	0	1	0	1	0	2
12	24/8	2	2	2	0	0	0	0	0	0	0	1	7
13	31/8	7	0	0	2	0	0	2	1	0	0	0	12
14	7/9	8	0	0	0	1	0	0	3	0	0	1	13
15	14/9	1	2	2	2	1	1	0	2	0	0	0	11
16	21/9	3	0	2	0	0	0	1	4	0	0	2	12
17	28/9	3	1	0	0	0	0	0	0	0	0	1	5
18	5/IO	7	2	0	2	0	0	1	2	2	0	2	18
19	12/IO	2	0	0	0	0	0	0	0	0	0	2	4
20	19/IO	1	3	0	0	0	0	0	0	0	0	1	5
21	26/IO	1	2	0	0	1	0	0	0	0	0	1	5
22	2/11	0	0	0	0	0	0	0	0	0	0	0	0
23	9/11	0	0	0	0	0	0	0	0	0	0	0	0
	Total	37	12	7	6	3	1	4	13	2	1	11	97

Sy. = Syrphus; X. = Xanthogramma; Pl. = Platycheirus; M. = Melanostoma:

APPENDIX 27

Non-aphidophagous syrphids in yellow water traps; - weekly totals per two traps at Lasswade 1970

Week no.	Week ending	Er.tenax	Er.arbustorum	Er.pertinax	Er.nemorum	H.granditarsa	X.segnis	Total
1	10/6	0	0	0	0	0	0	0
2	17/6	0	0	0	0	0	0	0
3	24/6	0	0	0	0	0	0	0
4	1/7	0	0	0	0	0	0	0
5	8/7	0	0	0	0	0	0	0
6	15/7	0	0	0	0	0	0	0
7	22/7	0	0	0	0	0	0	0
8	29/7	0	0	0	0	0	0	0
9	5/8	0	0	0	0	0	0	0
10	12/8	0	3	0	1	0	0	4
11	19/8	0	4	0	0	0	0	4
12	26/8	0	2	0	0	0	0	2
13	2/9	0	3	1	1	0	2	7
14	9/9	0	0	0	0	0	0	0
15	16/9	1	1	0	0	0	0	2
16	23/9	3	4	4	0	1	1	13
17	30/9	3	2	0	0	0	0	5
18	7/10							
19	14/10	2	1	0	0	1	2	6
20	21/10							
21	28/10	2	0	0	0	0	0	2
22	4/11	0	0	0	0	0	0	0
23	11/11	0	0	0	0	0	0	0
	Total	11	20	5	2	2	5	45

Er. = Eristalis; H. = Helophilus; X. = Xylota:

APPENDIX 28

Non-aphidophagous syrphids in yellow water traps; - weekly totals per two traps at Newington 1970

Week no.	Week ending	Er.tenax	Er.arbustorum	Er.pertinax	Sy.pipiens	N.podagrica	H.pendulus	Total
1	8/6	0	0	0	0	0	0	0
2	15/6	0	0	0	0	0	0	0
3	22/6	0	0	0	0	0	0	0
4	25/6	0	0	0	0	0	0	0
5	6/7	0	0	0	0	0	0	0
6	13/7	0	0	0	0	0	0	0
7	20/7	0	0	0	0	0	0	0
8	27/7	0	0	0	0	0	0	0
9	3/8	0	0	0	0	0	0	0
10	10/8	0	0	0	1	0	0	1
11	17/8	0	1	0	1	0	0	2
12	24/8	0	0	0	0	6	0	6
13	31/8	0	0	0	1	19	1	21
14	7/9	0	0	0	2	5	0	7
15	14/9	0	0	0	0	4	0	4
16	21/9	0	0	0	0	3	1	4
17	28/9	0	0	0	0	1	0	1
18	5/10	0	0	0	0	2	1	3
19	12/10	0	0	0	0	0	0	0
20	19/10	0	0	0	0	0	0	0
21	26/10	1	0	0	0	0	0	1
22	2/11	0	0	0	0	0	0	0
23	9/11	0	0	0	0	0	0	0
	Total	1	1	0	5	40	3	50

Er. = Eristalis; Sy. = Syritta; N. = Neoascia;
H. = Helophilus:

APPENDIX 29

Maximum and minimum daily temperatures and daily relative humidities at Lasswade during August/September 1969

Date	Max. °C	Min. °C	R.H. % (10.0 am)
August			
1	18.9	10.0	60
2	17.8	13.9	95
3	15.6	13.3	92
4	20.0	11.7	85
5	20.6	13.3	68
6	19.4	11.1	69
7	24.4	11.7	79
8	25.6	15.0	60
9	20.6	16.1	95
10	22.2	15.0	79
11	23.9	14.4	83
12	20.0	14.4	90
13	19.4	13.3	92
14	17.2	11.7	90
15	18.3	13.3	68
16	21.7	12.2	80
17	21.1	12.2	71
18	21.7	14.4	72
19	18.3	12.2	65
20	16.1	11.7	77
21	18.3	10.6	90
22	16.1	8.3	61
23	16.7	10.0	92
24	17.2	6.1	85
25	17.2	6.1	78
26	15.6	10.0	81
27	17.2	9.4	75
28	19.4	10.6	80
29	20.0	8.9	73
30	22.8	11.7	64
31	19.4	11.1	80
Sept. 1	18.3	9.4	70
2	22.2	9.4	65
3	21.7	13.3	80
4	18.9	12.2	68
5	22.2	13.3	70
6	15.6	11.7	95
7	19.4	11.7	73
8	21.7	11.7	58
9	18.9	12.8	69
10	12.8	12.2	85
11	12.8	9.4	97
12	16.1	9.4	80
13	12.2	10.0	85
14	13.3	10.6	80
15	12.8	8.3	81

APPENDIX 30

Maximum and minimum daily temperatures and daily relative humidities at Lasswade during August/September 1970

Date	Max. °C	Min. °C	R.H. % (10.0 am)
August 1	22.2	11.1	90
2	20.0	13.9	82
3	16.7	11.7	92
4	18.9	12.8	94
5	23.9	11.7	80
6	16.7	11.7	81
7	21.1	13.1	89
8	18.3	12.8	79
9	18.9	11.1	75
10	19.4	12.8	74
11	20.0	7.8	72
12	18.9	7.8	65
13	18.9	14.4	79
14	17.8	8.9	62
15	18.9	8.9	60
16	15.6	9.4	90
17	15.0	10.6	62
18	18.9	8.9	78
19	17.8	11.7	80
20	12.8	11.7	82
21	13.3	11.7	90
22	13.9	11.7	92
23	16.1	12.2	94
24	12.2	10.0	95
25	14.4	10.6	74
26	19.4	10.6	76
27	20.0	9.4	94
28	22.8	10.6	69
29	20.6	13.3	80
30	19.4	14.4	70
31	17.2	15.0	71
Sept. 1	16.1	9.4	69
2	15.0	10.0	90
3	14.4	9.4	63
4	16.1	9.4	84
5	16.7	10.6	59
6	16.1	10.0	80
7	19.4	11.7	70
8	16.7	13.3	94
9	14.4	9.4	75
10	15.0	10.0	64
11	13.3	10.0	72
12	13.3	8.3	65
13	15.0	6.1	70
14	14.4	5.0	71
15	13.9	5.0	70

APPENDIX 31

The mean numbers (± standard error) of syrphid eggs and larvae per brussels sprout plant at Lasswade 1969

Week no.	Week ending	Syrphid eggs	Syrphid larvae	Total no. of Syrphid eggs & larvae
1	2/7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
2	9/7	0.1 ± 0.0	0	0.1 ± 0.0
3	16/7	0	0	0
4	23/7	0.3 ± 0.2	0.1 ± 0.1	0.4 ± 0.2
5	30/7	0.4 ± 0.2	0.6 ± 0.2	1.0 ± 0.3
6	6/8	1.9 ± 0.8	1.1 ± 0.5	3.0 ± 1.1
7	13/8	2.3 ± 1.2	0.5 ± 0.2	2.8 ± 1.3
8	20/8	7.7 ± 5.1	1.8 ± 1.2	9.6 ± 5.8
9	27/8	0.6 ± 0.4	0.2 ± 0.1	0.8 ± 0.4
10	3/9	0.5 ± 0.5	0.4 ± 0.2	0.9 ± 0.6
11	10/9	0.5 ± 0.4	0.2 ± 0.1	0.7 ± 0.4
12	17/9	0.6 ± 0.3	0.4 ± 0.2	1.0 ± 0.4
13	24/9	0	0.1 ± 0.1	0.1 ± 0.1
14	1/10	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.2
15	8/10	0	0	0
16	15/10	0	0	0
17	22/10	No sampling		
18	29/10	0	0	0
19	5/11	0	0	0
20	12/11	0	0	0
21	19/11	0	0	0
22	26/11	0	0.2 ± 0.2	0.2 ± 0.2

APPENDIX 32

The mean numbers (± standard error) of syrphid eggs and larvae per brussels sprout plant at Newington 1969

Week no.	Week ending	Syrphid eggs	Syrphid larvae	Total no. of Syrphid eggs & larvae
1	30/6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
2	7/7	0	0	0
3	14/7	0	0	0
4	21/7	0.2 ± 0.1	0.2 ± 0.1	0.4 ± 0.1
5	28/7	1.8 ± 0.6	0.1 ± 0.1	1.9 ± 0.4
6	4/8	0.6 ± 0.2	0.3 ± 0.2	0.9 ± 0.3
7	11/8	1.5 ± 0.7	0.6 ± 0.2	2.1 ± 0.8
8	18/8	6.5 ± 3.9	0.8 ± 0.4	7.3 ± 3.1
9	25/8	0.5 ± 0.4	0.6 ± 0.3	1.1 ± 0.5
IO	1/9	9.6 ± 3.6	1.3 ± 0.8	IO.9 ± 3.9
11	8/9	4.7 ± 1.2	0.8 ± 0.3	5.5 ± 1.3
12	15/9	2.5 ± 0.8	4.5 ± 1.3	7.0 ± 1.4
13	22/9	3.8 ± 1.6	6.8 ± 1.9	IO.6 ± 2.8
14	29/9	2.3 ± 1.2	4.2 ± 1.5	6.5 ± 2.7
15	6/IO	0.8 ± 0.4	3.2 ± 1.1	4.0 ± 1.2
16	13/IO	0.5 ± 0.2	0.9 ± 0.3	1.4 ± 0.6
17	20/IO	No sampling		
18	27/IO	0	0	0
19	3/11	0.9 ± 0.4	1.7 ± 1.2	2.6 ± 1.3
20	IO/11	0	0.6 ± 0.4	0.6 ± 0.4
21	17/11	0.2 ± 0.1	1.6 ± 0.6	1.8 ± 1.1
22	24/11	0	0	0
23	1/12	0	1.1 ± 0.7	1.1 ± 0.7

APPENDIX 33

The mean numbers (± standard error) of syrphid eggs and larvae per brussels sprout plant at Lasswade 1970

Week no.	Week ending	Syrphid eggs	Syrphid larvae	Total no. of Syrphid eggs & larvae
1	1/7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
2	8/7	0.1 ± 0.1	0	0.1 ± 0.1
3	15/7	0.1 ± 0.1	0	0.1 ± 0.1
4	22/7	0	0	0
5	29/7	0	0	0
6	5/8	0.7 ± 0.4	0.1 ± 0.1	0.8 ± 0.4
7	12/8	1.0 ± 1.0	0.3 ± 0.3	1.3 ± 1.2
8	19/8	0.4 ± 0.4	0.9 ± 0.3	1.3 ± 0.6
9	26/8	0	2.1 ± 0.8	2.1 ± 0.8
10	2/9	0	0.5 ± 0.3	0.5 ± 0.3
11	9/9	0	0.3 ± 0.2	0.3 ± 0.2
12	16/9	0	0.2 ± 0.2	0.2 ± 0.2
13	23/9	No sampling		
14	30/9	0	0	0
15	7/10	0	0	0

APPENDIX 34

The mean numbers (± standard error) of syrphid eggs and larvae per brussels sprout plant at Newington 1970

Week no.	Week ending	Syrphid eggs	Syrphid larvae	Total no. of Syrphid eggs & larvae
1	29/6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
2	6/7	0	0	0
3	13/7	0	0.1 ± 0.1	0.1 ± 0.1
4	20/7	0	0	0
5	27/7	0	0.2 ± 0.1	0.2 ± 0.1
6	3/8	0	0	0
7	10/8	0	0.1 ± 0.1	0.1 ± 0.1
8	17/8	0.1 ± 0.1	0	0.1 ± 0.1
9	24/8	0	0.1 ± 0.1	0.1 ± 0.1
10	31/8	0	0.3 ± 0.1	0.3 ± 0.1
11	7/9	0	0.1 ± 0.1	0.1 ± 0.1
12	14/9	0.2 ± 0.2	0	0.2 ± 0.2
13	21/9	No sampling		
14	28/9	0	0.2 ± 0.1	0.2 ± 0.1
15	5/10	0	0	0
16	12/10	No sampling		
17	19/10	0	0	0

APPENDIX 35

Determination of primary parasites and hyperparasites

Primary parasite	Determined by	Name used in main text
Praon volucre Haliday	T.H. 1970	As determined
Praon myzophagum Mackauer	M.M. 1970	As determined
Diaeretiella rapae(McIntosh)	T.H. 1968	
Aphidius (Diaeretiella) rapae McIntosh	T.H. 1970	Diaeretiella rapae
Aphidius (Diaeretiella) species	N.D.M.F. 1971	
Aphidius ervi Haliday ?	N.D.M.F. 1971	
Aphidius ervi Haliday	T.H. 1968	Aphidius ervi
Aphidius picipes (Nees) sensu	T.H. 1968	Aphidius picipes
Aphidius picipes group	N.D.M.F. 1971	
Aphidius urticae group ?	N.D.M.F. 1971	Aphidius urticae group
Aphidius urticae group	N.D.M.F. 1971	
Aphidius rosae group ?	N.D.M.F. 1971	As determined
Ephedrus plagiator Nees	T.H. 1970	"
Dyscritulus planiceps Marshall	T.H. 1970	"
Monoctonus pseudoplani (Marshall)	T.H. 1970	"
Aphelinus asychis Walker	L.R. 1971	"
Aphelinus flavipes Kurdjumov	J.C.H. 1971	"
Aphelinus sp. nr. davicola Foerst	J.C.H. 1971	"
Aphelinus sp. nr. tibialis Nees	J.C.H. 1971	"
Aphelinus sp. ? mali (Haldeman)	T.H. 1970	"
Aphelinus flavus Nees	T.H. 1970	"
Hyperparasites		
Asaphes vulgaris Walker	B.R.S-R 1968	"
Asaphes vulgaris Walker	T.H. 1970	"
Coruna clavata Walker	T.H. 1970	"
Dendrocerus (Macrostigma) bicolor (Kieffer)	P.D. 1970	"
Dendrocerus (Macrostigma) aphidum (Rondani)	P.D. 1970	"
Phaenoglyphis species	J.Q. 1970	"
Alloxysta species	J.Q. 1970	"
Alloxysta sp. ? curvicornis C.	J.Q. 1970	"
Alloxysta victrix Westwood	J.Q. 1970	"
Alloxysta species	G.J.K. 1971	"

T.H. = T. Huddleston; British Museum: M.M. = M. Mackauer; Simon Fraser Univ., Canada
N.D.M.F. = N.D.M. Ferguson; British Museum: J.C.H. = J.C. Hall; Univ. of California, U.S.A.
L.R. = L. Rogers; British Museum: B.R.S-R = B.R. Subra-Rao; British Museum:
P.D. = P. Dessart; Institut Royal des Sciences Naturelles, Belgium:
J.Q. = J. Quinlan; British Museum: G.J.K. = G.J. Kerrich; British Museum:

APPENDIX 36

Total numbers of primary parasites and hyperparasites of Myzus persicae and Macrosiphum euphorbiae which emerged from aphid mummies collected from August to December 1968 in the vicinity of Edinburgh

	Numbers of parasites emerged from M. persicae on brassica crops																	Numbers of parasites emerged from M. euphorbiae on brassica crops															
Date of collection of mummies	14-30/8	5/9	12/9	17/9	23/9	25/9	29/10	6/11	7/11	8/11	11/11	26/11	28/11	10/12	12/12	19/12	Total	14-30/8	5/9	12/9	17/9	23/9	25/9	29/10	6/11	7/11	8/11	11/11	26/11	28/11	10/12	12/12	19/12	Total
Praon volucre	0	0	7	0	1	6	5	1	1	1	0	1	3	0	0	1	27	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Diaeretiella rapae	35	3	26	5	22	32	24	4	16	19	9	24	15	0	3	4	241	0	0	2	0	0	4	0	0	1	0	1	0	0	0	0	0	8
Aphidius picipes	0	0	0	0	0	4	1	1	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2
Aphidius ervi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Ephedrus plagiator	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asaphes vulgaris																																		
ex Praon spp.	0	0	0	0	0	0	1	0	2	0	2	2	3	1	0	3	14	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
ex D. rapae &/or Aphidius spp.	0	0	0	0	2	1	6	4	3	7	3	6	16	0	3	8	59	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
ex Ephedrus plagiator	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coruna clavata																																		
ex Praon spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ex D. rapae &/or Aphidius spp.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cynipids																																		
ex Praon spp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ex D. rapae &/or Aphidius spp.	0	0	0	0	3	11	2	0	2	3	1	1	1	0	0	2	26	0	0	0	0	2	0	0	1	1	1	0	0	0	0	0	0	7

APPENDIX 37 Total numbers of primary parasites and hyperparasites of Myzus persicae which emerged from aphid mummies collected from August to November 1969

Date of collection of mummies	Lasswade (sprout field)													
	1/8	8/8	15/8	22/8	29/8	5/9	12/9	19/9	26/9	3/10	10/10	24/10	7/11	TOTAL
Praon volucre	6	3	1	4	6	22	45	57	31	34	37	14	8	268
P. myzophagum	0	0	0	0	0	0	0	0	0	0	1	0	0	1
D. rapae	0	4	0	1	0	4	1	0	1	0	2	2	4	19
Aphidius picipes	0	1	0	1	1	1	1	2	1	2	3	1	6	20
Aphidius ervi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphidius urticae group	0	0	0	1	0	0	2	0	0	0	0	0	0	3
Ephedrus plagiator	0	0	0	0	0	0	0	2	0	0	0	2	0	4
Aphelinus flavipes	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Asaphes vulgaris ex Praon spp.	0	0	2	0	1	1	0	2	6	14	7	5	2	40
ex D.rapae &/or Aphidius spp.	0	0	0	0	0	0	0	0	0	0	0	1	4	5
ex E.plagiator	0	0	0	0	0	0	0	0	0	0	0	2	2	4
Coruna clavata ex Praon spp.	0	0	0	0	0	1	0	0	0	0	1	0	0	2
ex D.rapae &/or Aphidius spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cynipids														
ex Praon spp.	2	3	1	2	1	0	6	0	4	2	3	1	0	25
ex D.rapae &/or Aphidius spp.	0	9	1	3	0	0	0	0	0	0	3	0	6	24
ex E.plagiator	0	0	0	0	0	0	0	0	0	2	0	0	0	2
Dendrocerus spp														
ex Praon spp.	0	0	0	0	0	0	1⊗	0	0	0	0	0	0	1
ex D.rapae &/or Aphidius spp.	1+,1⊗	0	0	0	0	0	0	0	0	0	0	0	0	2

Date of collection of mummies	Lasswade (cabbage field)													
	1/8	8/8	15/8	22/8	29/8	5/9	12/9	19/9	26/9	3/10	10/10	24/10	7/11	TOTAL
Praon volucre	1	2	6	2	6	1	14	21	6	6	8	1	0	74
P. myzophagum	0	0	0	0	1	0	0	0	0	2	0	0	0	3
D. rapae	0	0	1	2	6	0	1	9	1	4	0	0	2	27
Aphidius picipes	0	0	2	3	1	1	1	6	2	o	6	4	4	30
Aphidius ervi	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Aphidius urticae group	0	0	0	2	0	1	0	3	0	0	0	0	0	6
Ephedrus plagiator	0	0	0	0	0	0	0	0	0	1	1	0	0	2
Aphelinus flavipes	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asaphes vulgaris ex Praon spp.	0	0	4	0	1	3	1	0	3	2	4	4	4	26
ex D.rapae &/or Aphidius spp.	0	0	4	0	1	2	1	3	0	2	0	0	2	15
ex E.plagiator	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Coruna clavata ex Praon spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ex D.rapae &/or Aphidius spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cynipids														
ex Praon spp.	0	0	2	2	1	1	1	0	0	2	1	0	0	IO
ex D.rapae &/or Aphidius spp.	0	2	2	1	0	0	0	0	2	0	0	2	0	9
ex E.plagiator	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dendrocerus spp														
ex Praon spp.	0	0	0	0	0	0	0	0	0	2⊗	1+	0	0	3
ex D.rapae &/or Aphidius spp.	0	0	0	0	0	0	0	0	0	1+	0	0	0	1

Date of collection of mummies	Newington (sprout field)													
	1/8	8/8	15/8	22/8	29/8	5/9	12/9	19/9	26/9	3/10	10/10	24/10	7/11	TOTAL
Praon volucre	4	2	20	13	12	60	59	50	-	28	21	20	24	313
P. myzophagum	0	0		0	0	0	0	2	0	-	0	0	0	0	2
D. rapae	8	0	2	1	1	0	0	9	-	4	9	4	9	47
Aphidius picipes	4	0	4	4	1	4	0	0	-	8	8	1	0	34
Aphidius ervi	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Aphidius urticae group	00	0	1	0	2	0	0	0	-	0	0	0	0	3
Ephedrus plagiator	0	0	0	1	0	0	0	4	-	0	1	0	0	6
Aphelinus flavipes	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Asaphes vulgaris ex Praon spp.	0	1	1	2	4	19	10	4	-	8	9	2	10	70
ex D.rapae &/or Aphidius spp.	0	0	2	0	4	5	0	0	-	7	2	1	4	25
ex E.plagiator	0	0	0	2	0	0	0	0	-	0	0	0	0	2
Coruna clavata ex Praon spp.	0	0	0	0	0	5	2	2	-	1	0	0	0	10
ex D.rapae &/or Aphidius spp.	0	0	0	0	0	2	0	0	-	0	0	0	0	2
Cynipids														
ex Praon spp.	0	0	2	3	0	6	0	2	-	2	1	1	0	17
ex D.rapae &/or Aphidius spp.	0	0	9	8	7	0	0	2	-	7	2	9	0	43
ex E.plagiator	0	0	0	0	0	0	0	2	-	0	0	0	0	2
Dendrocerus spp														
ex Praon spp.	0	0	0	0	0	0	0	2	-	2	0	0	0	4
ex D.rapae &/or Aphidius spp.	0	1	0	0	0	0	0	0	-	0	0	0	0	1

+ = Dendrocerus bicolor; ⊗ = Dendrocerus aphidum:

P. = Praon; D. = Diaeretiella; E. = Ephedrus:

APPENDIX 38 Total numbers of primary parasites and hyperparasites of Macrosiphum euphorbiae which emerged from aphid mummies collected from August to November 1969

Date of collection of mummies	Lasswade (sprout field)													
	1/8	8/8	15/8	22/8	29/8	5/9	12/9	19/9	26/9	3/10	10/10	24/10	7/11	TOTAL
P. volucre	0	4	1	1	1	0	0	2	0	2	1	1	0	13
A. picipes	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Aphidius urticae group	0	2	0	2	0	0	0	0	0	0	0	0	0	4
Aphidius rosae group	0	0	0	0	0	0	1	0	0	0	0	0	0	1
E.plagiator	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dy. planiceps	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. pseudoplantani	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aph. sp.nr. tibialis	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Aph. flavipes	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Aph. sp.nr. davicola	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aph. sp. mali ?	0	0	1	0	0	0	0	0	0	0	0	0	0	1
As. vulgaris ex Praon spp	0	1	3	0	2	0	0	0	1	0	0	0	0	7
ex D.rapae &/or Aphelinus spp	0	4	0	2	0	0	0	0	0	2	0	0	0	8
ex E.plagiator	0	0	1	1	0	0	0	0	0	0	0	0	0	2
Coruna clavata														
ex D.rapae &/or Aphidius spp.	0	0	0	0	0	0	1	0	0	0	0	0	0	1
ex E.plagiator	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cynipids														
ex Praon spp	2	1	0	0	2	0	0	0	0	0	0	0	0	5
ex D.rapae &/or Aphidius spp	0	5	1	4	2	0	0	0	0	2	0	0	0	14
ex.E.plagiator	0	2	0	1	0	0	0	0	0	0	0	0	0	3
Dendrocerus spp														
ex.Praon spp	0	1	0	0	0	0	0	0	0	0	0	0	0	1
ex.Praon &/or Aphidius spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Date of collection of mummies	Lasswade (cabbage field)													
	1/8	8/8	15/8	22/8	29/8	5/9	12/9	19/9	26/9	3/10	10/10	24/10	7/11	TOTAL
P. volucre	1	3	4	2	9	6	3	6	2	2	1	2	0	41
A. picipes	0	1	1	2	1	4	4	7	0	0	1	0	0	21
Aphidius urticae group	0	2	1	2	2	1	2	0	0	0	0	0	0	IO
Aphidius rosae group	0	1	0	0	1	0	0	0	0	0	0	0	0	2
E.plagiator	0	0	0	2	1	2	2	0	0	4	1	0	0	12
Dy. planiceps	0	0	0	0	1	0	0	0	0	0	0	0	0	1
M. pseudoplantani	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Aph. sp.nr. tibialis	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Aph. flavipes	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Aph. sp.nr. davicola	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Aph. sp. mali ?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
As. vulgaris ex Praon spp	0	0	2	3	1	IO	0	3	3	8	0	7	8	45
ex D.rapae &/or Aphelinus spp	0	4	3	3	2	2	0	4	4	0	6	2	6	36
ex E.plagiator	0	1	0	0	0	2	1	0	3	8	1	2	0	18
Coruna clavata														
ex D.rapae &/or Aphidius spp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0
ex E.plagiator	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Cynipids														
ex Praon spp	0	0	1	6	5	3	2	0	6	6	2	1	4	36
ex D.rapae &/or Aphidius spp	3	12	2	7	12	7	3	2	7	2	1	0	4	62
ex.E.plagiator	0	1	0	1	1	2	1	1	2	0	1	0	6	16
Dendrocerus spp														
ex.Praon spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ex.Praon &/or Aphidius spp.	0	1	1	0	0	1	0	0	0	0	0	0	0	3

Date of collection of mummies	Newington (sprout field)													
	1/8	8/8	15/8	22/8	29/8	5/9	12/9	19/9	26/9	3/10	10/10	24/10	7/10	TOTAL
P. volucre	0	0	2	0	2	2	0	3	-	0	0	0	0	9
A. picipes	1	0	0	2	1	0	0	0	-	0	0	0	0	4
Aphidius urticae group	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Aphidius rosae group	0	0	0	0	0	0	0	0	-	0	0	0	0	0
E.plagiator	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Dy. planiceps	0	0	0	0	0	0	0	0	-	0	0	0	0	0
M. pseudoplantani	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Aph. sp.nr. tibialis	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Aph. flavipes	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Aph. sp.nr. davicola	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Aph. sp. mali ?	0	0	0	0	0	0	0	0	-	0	0	0	0	0
As. vulgaris ex Praon spp	0	0	0	0	2	1	0	0	-	0	0	0	0	3
ex D.rapae &/or Aphelinus spp	0	0	0	2	0	0	0	0	-	0	0	0	0	2
ex E.plagiator	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Coruna clavata														
ex D.rapae &/or Aphidius spp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0
ex E.plagiator	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Cynipids														
ex Praon spp	0	0	0	3	0	0	0	0	-	0	0	0	0	3
ex D.rapae &/or Aphidius spp	1	0	7	9	0	0	0	0	-	2	0	0	0	19
ex.E.plagiator	0	0	0	0	0	0	0	0	-	0	0	0	0	0
Dendrocerus spp														
ex.Praon spp	0	0	0	0	0	0	0	0	-	0	0	0	0	0
ex.Praon &/or Aphidius spp.	0	0	0	0	0	0	0	0	-	0	0	0	0	0

= Dendrocerus bicolor
= Dendrocerus aphidum
P. = Praon
A. = Aphidius
E. = Ephedrus
Dy = Dyscritulus
M. = Monoctonus
D. = Diaeretiella

APPENDIX 39

Total numbers of primary parasites and hyperparasites of Myzus persicae and Macrosiphum euphorbiae which emerged from aphid mummies collected from July to October 1970

Date of collection of mummies	Numbers of parasites emerged from M.persicae (Lasswade)										Numbers of parasites emerged from M.euphorbiae (Lasswade)											Nos. parasites emerged from M.p. + M.e (Newington)					
	31/7	7/8	14/8	21/8	28/8	4/9	11/9	18/9	2/10	Total	31/7	7/8	14/8	21/8	28/8	4/9	11/9	18/9	2/10	28/10*	Total	31/7	7/8	21/8	28/8	4/9	Total
Praon volucre	1	7	6	1	3	5	0	0	0	23	2	7	26	22	24	2	4	0	0	1	88	0	0	2	4	3	9
Praon myzophagum	0	0	1	0	2	1	0	0	0	4	0	0	1	2	3	2	1	0	0	0	9	0	0	0	0	0	0
Diaeretiella rapae	28	12	11	0	7	2	3	0	0	63	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aphidius picipes	11	1	3	1	1	0	0	0	0	17	2	8	8	16	3	1	0	0	0	0	38	1	1	0	1	0	3
Aphidius urticae group	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0
Ephedrus plagiator	0	0	0	1	0	0	0	0	0	1	1	4	0	6	9	3	1	0	0	0	24	0	0	0	0	0	0
Aphelinus asychis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Asaphes vulgaris																											
ex Praon species	0	1	3	0	1	0	0	0	0	5	0	2	4	3	2	3	5	1	0	0	20	0	1	0	0	0	1
ex D. rapae &/or Aphidius spp.	10	12	5	0	2	2	0	0	0	31	1	7	4	2	5	8	4	1	0	9	41	0	0	0	0	0	0
ex Ephedrus plagiator	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	6	5	0	5	20	0	0	0	0	0	0
Coruna clavata																											
ex Praon species	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	1	0
ex D. rapae &/or Aphidius spp.	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2	0	7	10	0	0	0	0	0	0
ex Ephedrus plagiator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	5	6	0	0	0	0	0	0
Cynipids																											
ex Praon species	1	0	2	0	3	0	1	0	1	8	0	2	9	2	1	1	2	1	0	4	22	0	2	0	1	0	3
ex D. rapae &/or Aphidius spp.	5	6	0	0	3	1	0	0	0	15	0	7	4	5	8	10	10	2	3	31	79	1	0	0	0	0	1
ex Ephedrus plagiator	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	2	6	0	0	0	0	0	0
Dendrocerus species																											
ex Praon species	0	0	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
ex D. rapae &/or Aphidius species	+2,⊗1	1	0	0	0	0	0	0	0	4	+1,⊗1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
ex Ephedrus plagiator	0	0	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	+1	0	0	0	2	0	0	0	0	0	0

+ = Dendrocerus bicolor; ⊗ Dendrocerus aphidum; * = Aphid mummies collected from adjacent cabbage plot

APPENDIX 40

Five days total numbers of summer and autumn emergence of primary parasites and hyperparasites from all aphid mummies collected in 1969

Days after mummy collection	Praon volucre	Diaer'a rapae	Aphidius picipes	Ephedrus plagiator	Cynipids	Asaphes vulgaris	Dend. spp.
5	32	19	24	1	7	0	0
10	86	19	31	4	12	3	0
15	107	9	16	3	17	4	1
20	67	1	4	3	17	6	1
25	42	0	0	1	10	7	3
30	0	2	0	0	21	12	0
35	2	0	0	0	33	15	0
40	1	0	0	0	6	14	0
45	1	0	0	0	2	13	1
50	6	0	0	0	5	4	0
55	3	0	0	0	1	2	0
60	0	0	0	0	1	0	0
65	2	0	0	0	0	0	0
70	0	0	0	0	0	3	0
75	0	0	0	0	0	0	0
80	0	0	0	0	0	1	0
85	0	0	0	0	0	1	0
90	0	0	0	0	0	0	0
95	0	0	0	0	0	1	0
100	0	0	0	0	0	0	0
105	0	0	0	0	1	0	0
110	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0
120	0	0	0	0	0	0	0
125	0	0	0	0	0	0	0
Total	349	50	75	12	133	88	6

APPENDIX 41

Five days total numbers of summer and autumn emergence of primary parasites and hyperparasites from all aphid mummies collected in 1970

Days after mummy collection	Praon vulgaris	Diaer'a rapae	Aphidius picipes	Ephedrus plagiator	Cynipids	Asaphes vulgaris	Dend. spp.
5	22	35	27	7	1	0	0
10	28	27	24	12	3	0	0
15	32	3	1	4	7	1	0
20	24	0	0	2	5	1	2
25	1	1	0	0	6	4	2
30	0	0	0	0	4	4	4
35	0	0	0	0	7	12	0
40	1	0	0	0	3	12	0
45	0	0	0	0	2	23	0
50	0	0	0	0	1	20	0
55	0	0	0	0	3	3	0
60	0	0	0	0	0	1	0
Total	108	66	52	25	42	81	8

APPENDIX 42

Total weekly emergence of the primary parasites and hyperparasites in spring/summer 1969, from overwintered mummies collected during summer / autumn 1968

Date of emergence	Praon volucre	Diaeretiella rapae	Aphidius picipes	Ephedrus plagiator	Aphidius ervi	Cynipids	Asaphes vulgaris	Coruna clavata
6/1	0	2	0	0	0	0	0	0
13/1	0	2	0	0	0	0	2	0
20/1	0	6	0	0	0	0	2	0
27/1	0	0	0	0	0	0	3	0
3/2	0	0	0	1	0	0	2	0
10/2	0	0	0	0	0	0	0	0
17/2	0	0	0	0	0	0	4	0
24/2	0	0	0	0	0	0	2	0
3/3	0	0	0	0	0	0	2	0
10/3	0	0	0	0	0	0	0	0
17/3	0	0	0	0	0	0	0	0
24/3	0	0	0	0	0	0	1	0
31/3	0	0	0	0	0	0	0	0
7/4	0	1	0	0	0	0	0	0
14/4	0	0	0	0	0	0	0	0
21/4	0	0	0	0	0	0	0	0
28/4	0	0	0	0	0	0	0	0
5/5	0	2	0	0	0	0	0	0
12/5	0	5	2	0	0	0	0	0
19/5	0	9	1	0	0	1	0	0
26/5	1	14	0	2	1	0	0	0
2/6	1	0	0	0	0	0	0	0
9/6	2	8	0	0	0	0	18	0
16/6	5	12	0	0	0	0	22	1
23/6	4	26	0	0	0	0	4	2
30/6	3	6	0	0	0	0	0	0
7/7	3	7	0	0	0	0	0	0
4/7	0	1	0	0	0	0	0	0
21/7	0	1	0	0	0	0	0	0
28/7	0	0	0	0	0	0	0	0
Total	19	102	3	3	1	1	63	3

APPENDIX 43

Total weekly emergence of the primary parasites and hyperparasites in spring/summer 1970, from overwintered mummies collected during summer /autumn 1969

Date of emergence	Praon volucre	Diaeretiella rapae	Aphidius Picipes	Ephedrus plagiator	Cynipids	Asaphes vulgaris	Coruna clavata	Dendrocerus species
20/1	0	0	0	0	0	1	0	0
24/2	0	0	0	0	0	1	0	0
24/3	0	0	1	0	0	0	0	0
30/3	0	0	1	0	0	0	0	0
7/4	0	0	0	0	0	0	0	0
14/4	0	0	1	0	0	0	0	0
21/4	0	1	1	0	1	0	0	0
28/4	0	1	4	0	0	0	0	0
5/5	0	1	1	0	0	0	0	0
12/5	0	3	1	0	1	0	0	0
19/5	6	2	5	2	0	1	0	0
26/5	47	6	9	7	5	3	0	1
2/6	122	2	1	3	23	46	2	4
9/6	59	4	1	0	66	101	7	0
16/6	3	2	0	0	39	11	7	2
23/6	0	6	0	0	29	1	0	0
30/6	0	2	0	0	18	4	0	0
7/7	0	0	0	0	3	0	0	0
14/7	2	0	0	0	1	0	0	2
21/7	0	0	0	0	2	0	0	0
28/7	1	0	0	0	1	1	0	0
4/8	0	0	0	0	1	0	0	0
Total	240	30	26	12	190	170	16	9

APPENDIX 44

Total weekly emergence of the primary parasites and hyperparasites in spring/summer 1971, from overwintered mummies collected during summer /autumn 1970

Date of emergence	Praon volucre	Aphidius picipes	Cynipids	Asaphes vulgaris	Coruna clavata	Dendrocerus species
17/3	-	-	-	1	-	-
21/4	0	0	0	0	0	0
28/4	0	0	0	0	0	0
5/5	0	0	1	0	0	0
12/5	0	1	3	0	0	0
19/5	2	0	4	1	0	0
26/5	3	0	IO	4	0	1
2/6	6	0	26	13	3	0
9/6	7	0	20	9	4	0
16/6	3	0	IO	2	2	0
23/6	4	0	14	7	3	0
30/6	1	0	0	0	5	0
7/7	0	0	3	1	1	0
Total	26	1	91	37	18	1

APPENDIX 45

Intensity of overwintering of the parasites - 1968

Date of collection of mummies	Total no. mummies		No. non-emerged		% non-emerged	
	D.rapae and/or A.picipes	Praon spp.	D.rapae and/or A.picipes	Praon spp.	D.rapae and/or A.picipes	Praon spp.
12/9	40	14	6	9	15.0	64.3
17/9 - 25/9	100	17	49	11	49.0	64.7
29/10	35	10	21	7	60.0	70.0
6/11- 11/11	91	14	70	14	76.9	100.0
26/11- 28/11	79	9	79	9	100.0	100.0
10/12- 19/12	21	7	21	7	100.0	100.0
Total	366	71	246	57	-	-

APPENDIX 46

Intensity of overwintering of the parasites - 1969

Date of collection of mummies	Total no. mummies		No. non-emerged		% non-emerged	
	D.rapae and/or	Praon spp.	D.rapae and/or	Praon spp.	D.rapae and/or	Praon spp.
1/8	41	30	8	5	19.5	16.6
8/8	73	44	22	16	30.1	36.4
15/8	40	72	12	30	30.0	41.6
22/8	77	60	37	30	48.1	50.0
29/8	69	90	37	38	55.2	42.2
5/9	36	129	19	57	52.8	44.2
12/9	16	133	5	51	31.3	38.3
19/9	31	113	9	53	29.0	46.9
26/9	22	88	17	68	77.3	77.3
3/10	32	80	21	60	65.6	75.0
10/10	45	109	37	106	82.2	97.2
24/11	17	68	16	68	94.1	100
Total	519	1084	258	650	-	-

APPENDIX 47

Intensity of overwintering of the parasites - 1970

Date of collection of mummies	Total no.mummies		No. non-emerged		% non-emerged	
	D.rapae and/or A.picipes	Praon spp.	D.rapae and/or A.picipes	Praon spp.	D.rapae and/or A.picipes	Praon spp.
31/7	72	3	12	0	16.7	0
7/8	65	32	21	7	32.3	21.9
14/8	46	62	12	25	26.1	40.3
21/8	29	43	9	14	31.0	32.6
28/8	34	63	11	31	32.4	49.2
4/9	28	19	17	12	60.7	63.2
11/9	20	23	15	16	75.0	69.6
18/9	15	22	12	20	80.0	90.9
Total	374	287	174	145	-	-