STUDIES OF PARASITISM BY A PRIMARY AND SECONDARY PARASITOID OF THE CABBAGE APHID.

A thesis submitted in fulfilment of the requirements for the degree of Ph.D. of the University of London and the Diploma of Imperial College

E.D.L. Berkeley

November 1989

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Acknowledgements.

I would like to thank Mike Hassell and Jeff Waage for their advice and encouragement during this project. I am also grateful to Mick Crawley for his assistance with the GLIM analysis. I was fortunate to share a laboratory with Charles Cheng, Hefin Jones, Carlos Garcia-Saez, Phil Hulme and Muhammed Ahkteruzzaman.

Finally, I am indebted to James Brooks for his help during this project and to my parents for the interest they have shown throughout my education.

This project was funded by the Department of Agriculture, Northern Ireland.

INTRODUCTION.

The first recorded observation of an insect parasitoid dates from 1602 when Aldrovanchi noted the parasitic larvae of Apanteles glomeratus (L.) emerging from the caterpillars of Pieris brassicae (he mistakenly believed the parasitoid's cocoons to be the eggs of the butterfly) (De Bach 1974). Since then it has been shown that there are probably over a quarter of a million species of parasitoids, developing as larvae feeding on host arthropods, but differing greatly in behaviour and ecology (van Alphen and Vet 1986). Parasitoids have been the focus of numerous laboratory and field experiments which have examined various aspects of their biology. Their popularity as experimental systems has been partly due to their importance as biological control agents of several agricultural pests and also because their small size and relatively short generation times facilitate their manipulation in the laboratory.

Hyperparasitism, or the development of the larvae of one parasitoid species in or on another, is of common occurrence in insect communities as almost all species of the parasitic Hymenoptera and many of the Tachinidae and other parasitic Diptera are attacked by hyperparasitoids (or secondary parasitoids) (Smith 1916, Muesebeck and Dohanian 1927, Hammond 1979). Frequently, such an insect community includes many hyperparasitic species attacking only one or a few species.

For example, Muesebeck and Dohanian (1927) recorded 35 hyperparasitoids attacking A. melanoscelus, a parasitoid of the gypsy moth, Lymantria dispar L.

Hyperparasitoids may be divided into obligate and facultative species; the latter act as primary, secondary and, in some cases, tertiary or even quarternary parasitoids. Obligate hyperparasitoids develop only on or in primary parasitoids; there is no record of an obligate tertiary parasitoid. It has been suggested that facultative hyperparasitism provides a transitional evolutionary stage for obligatory hyperparasitoids (Telenga 1952).

Hyperparasitoids may also be categorised according to their mode of oviposition, as indirect or direct species. Smith (1916) defined an indirect hyperparasitoid as one 'which attacks a host insect upon which it cannot develop for the sake of the parasitoid which it may harbour'. Direct hyperparasitism occurs when the adult secondary parasitoid oviposits directly in or on the body of the primary. Flanders (1943) redefined indirect hyperparasitism as occurring when the primary's phytophagous host is attacked irrespective of whether or not it is parasitised. In this case the presence of unparasitised hosts greatly delays the finding of the primary parasitoid by the secondary. An extreme example of this type of oviposition behaviour is the ichneumonid, Euceros frigilus Cress., which attacks parasitoids of the sawfly, Neodiprion swainei Midd. The adult hyperparasitoid oviposits near colonies of sawfly larvae. Planidia hatch from these eggs and attach themselves to passing larvae. They remain on the larvae for at least 10 months and hibernate externally upon the prepupa within the

sawfly cocoon. Although they obtain nourishment from the body fluids of the intermediate host they cannot develop beyond the planidia stage until the sawfly is parasitised (Tripp 1961).

Direct hyperparasitism occurs when only the primary parasitoid's parasitised host or the primary itself are attacked (Flanders 1943). An extreme example of this type of behaviour is that of the chalcid, Brachymeria colorandensis (Cress), which attacks sarcophagid larvae within grasshoppers. The hyperparasitoids were observed to follow one grasshopper for a long period, attempting to oviposit. In every instance the grasshopper was shown to contain a sarcophagid larva (Spencer 1958).

Despite their ubiquity, the interactions between insect hyperparasitoids and their parasitoid hosts have been neglected by ecologists in comparison to those between parasitoids and phytophagous insects. In many cases hyperparasitoids receive only passing reference in studies of parasitoid systems (major exceptions include the studies by Muesebeck and Dohanian (1927) on the hyperparasitoids of A. melanoscelus, Gutierrez on the host specificity of an aphid hyperparasitoid, Charips (=Alloxysta) victrix, (Gutierrez and van den Bosch 1970 a and b, Gutierrez 1970 a, b, c and d) and various studies by Sullivan also on aphid hyperparasitoids (Sullivan and van den Bosch 1971, Sullivan 1972, Bennet and Sullivan 1978, Keller et al 1976, Levine and Sullivan 1983, Matejko and Sullivan 1979, 1984)).

Hyperparasitoids are likely to have an important impact on the population dynamics of many parasitoid - phytophagous

insect systems and are, therefore, of consequence to the implementation of biological control programmes. It is surprising, therefore, that hyperparasitism has remained one of the most neglected areas of insect biology (Rosen 1981).

The patterns of parasitism resulting from the activities of a primary and a secondary parasitoid within the same insect community are compared in this thesis, in an attempt to discover adaptations which may be of particular importance or peculiar to, the hyperparasitic mode of life. The hosts attacked by an obligate hyperparasitoid (i.e. parasitised phytophagous insects) must be more difficult to locate than those of a primary parasitoid because the hyperparasitoid must detect parasitised individuals within an otherwise healthy population so adding a further level of 'patchiness' to the environment. Also, because the hosts attacked are at the trophic level above those of a primary parasitoid, they must be of lower energetic value, so reducing the energy available to developing hyperparasitoid larvae. Differences in host distribution and quality may be reflected in differences in basic aspects of primary and secondary parasitoid biology such as daily fecundity, number of ovarioles per ovary and developmental rates. Behavioural characteristics such as the ability to avoid superparasitism and the process used to detect and exploit host patches may also be affected. A comparative approach was, therefore, adopted to contrast the interactions between a parasitoid and its phytophagous host and a hyperparasitoid and its parasitoid host, within one insect community.

The system chosen for this study was that of the cabbage aphid, Brevicoryne brassicae (L), its primary parasitoid Diaeretiella rapae M'Intosh and the obligate hyperparasitoid Alloxysta fuscicornis. All three species occur commonly in the field at Silwood Park, Berkshire, and are easy to manipulate in the laboratory. The interaction between B. brassicae and D. rapae has been the subject of several studies (see Hafez 1961, Akinlosotu 1973, Raworth et al 1984 and Cheng 1985) and as a result, the ecology of both the aphid and parasitoid is fairly well known, providing a basis for this study.

A review of the biologies of B. brassicae, D. rapae and A. fuscicornis follows the review of the literature relating to hyperparasitism in Chapter 2. The reproductive strategies adopted by A. fuscicornis and D. rapae, will, in part, influence their foraging strategies, and their longevity and fecundity schedules are considered in Chapter 3. The ability to develop in several host instars will increase the proportion of the host population which is available to a parasitoid female. The rates of successful parasitism and of development in different host instars were considered for both parasitoid species. To provide a further comparison of developmental rates, their thermal constants were also determined in Chapter 3. The functional responses of the D. rapae - B. brassicae and A. fuscicornis - D. rapae interactions are described in Chapter 4. These provided a method of comparing certain parameters which relate to the exploitation of both host species by their respective parasitoids. This was extended by considering the changes in

searching activity in the presence and absence of light over a range of temperatures. The ability to search for hosts under a wide range of environmental conditions will increase the total time available for searching and thus, the searching efficiency. Even though a parasitoid may have a high searching efficiency this may be negated by an inability to recognise and avoid hosts which have already been parasitised. The advantages and disadvantages of avoiding superparasitism and the ability of D. rapae and A. fuscicornis to do so are discussed in Chapter 5.

To understand the foraging behaviour of D. rapae and A. fuscicornis it is necessary first to have detailed knowledge of the distribution of their host populations in space and time, as this distribution defines the context in which they forage. A sampling programme was therefore carried out to examine the field distributions of unparasitised and parasitised aphids (i.e. hosts of D. rapae and A. fuscicornis, respectively). The distribution of colonies of parasitised and unparasitised aphids on plants in Brussels plot over a period of 2 months are described in Chapter 6. The overall spatial pattern of parasitism resulting from the parasitoid's foraging behaviour will depend on both the aggregative response over all patches and on the factors limiting the rate of parasitism within each patch. As A. fuscicornis forages for parasitised aphids within aphid colonies and has been shown to waste time handling both healthy and parasitised aphids, the aggregative response to aphid colonies of different sizes and also to groups of parasitised aphids within a fixed overall colony size was examined in the field.

Generally, one aspect of primary parasitoid biology which has been studied in detail is the process by which host populations are detected and exploited. The majority of species whose foraging strategies have been studied have been shown to respond to a hierarchy of physical and/or chemical stimuli which lead them to their potential hosts (see Vinson 1976 and 1981 for a review). This aspect of parasitoid behaviour is especially interesting to ecologists because of the direct link between successful searching and the production of offspring which suggests that parasitoid searching behaviour must be strongly influenced by natural selection (van Alphen and Vet 1986). The series of chemical and physical stimuli on which the host selection processes of the parasitoid and hyperparasitoid are based was considered in the series of laboratory and field experiments described in Chapter 7. The mechanism of patch exploitation is also discussed in this chapter.

2. LITERATURE REVIEW

This chapter has two parts; in the first I review the occurrence of hyperparasitism within the Insecta and discuss the common biological characteristics of hyperparasitoids, their population dynamics and their importance to biological control programmes. In the second half of the chapter I consider the basic biology, host specificity and systematics of the cabbage aphid, Brevicoryne brassicae, its primary parasitoid, Diaeretiella rapae, and the obligate hyperparasitoid, Alloxysta fuscicornis, as these species form the basis of this study.

2.1 REVIEW OF HYPERPARASITISM.

2.11 Taxonomic Review

The majority of insect hyperparasitoids occur within the Hymenoptera, although a few species have been recorded from the Diptera and Coleoptera. This is in spite of the fact that the Diptera include large families, such as the Tachinidae, which are exclusively parasitic and yet from which hyperparasitism has not been recorded. Hyperparasitism occurs within the Hymenoptera, however, in five out of twenty superfamilies (i.e. the Ceraphanoidea, Chalcidoidea, Cynipoidea, Ichneumonoidea and Trigonaloidea). A few species belonging to the Proctotrupoidea are also hyperparasitic (Muesebeck and Dohanian 1927, Hammond 1979, Gordh 1981, Sullivan 1986, 1987). Surprisingly, hyperparasitism is unknown in several families which are largely parasitic, these include the Aphidiidae, Braconidae,

Trichogrammatidae, Mymaridae, Tetracampidae and Eucharitidae (Gordh 1981, Sullivan 1987).

The Ichneumonoidea is a large superfamily with many parasitoid species but hyperparasitism is restricted to a few genera within the Ichneumonidae. The Gelinae are ectoparasitoids of cocoon-forming insects (especially the Lepidoptera) and many species are hyperparasitic, attacking Ichneumonidae or Braconidae. Some Gelis species have apterous male forms (Muesebeck and Dohanian 1927, Puttler 1966), and thelytoky is another characteristic of some species in this genus (Caldwell and Wilson 1975). Mesochorines also attack ichneumonids and braconids and the subfamily Mesochorinae is solely hyperparasitic with most species developing endoparasitically. Mesochorus dimidiatus Holmgren is a highly specialised hyperparasitoid which attacks Olesicampe benefactor Hinz, a parasitoid of larch sawfly (Zwolfer 1970, Ives 1976).

The Trigonaloidea is a smaller superfamily with only one family, the Trigonalidae. Eggs are laid on foliage and the larvae do not hatch until they are eaten by the host. First instar larvae penetrate the haemocoel where they may encounter and attack a primary parasitoid larva. Their hosts are social vespoids (in which case they act as primary parasitoids) or ichneumonids and tachinids which parasitise Lepidoptera. One species, Lycogaster pullata Schuckard, appears transitional in its host association as it attacks both social vespoids and ichneumonids (Clausen 1940, Askew 1970, Gordh 1981).

The Ceraphronoidea has two families, the Ceraphronidae and the Megaspilidae, both of which include hyperparasitic species. Hyperparasitoids in the Megaspilidae have a smaller host range than those in the Ceraphronidae. Some Dendrocerus spp. are common hyperparasitoids of Aphididae in many different aphid species (Hagen and van den Bosch 1968) and in some systems they attack both primary and secondary parasitoids (Hafez 1961).

The superfamily Cynipoidea contains, in addition to many phytophagous species and several primary parasitoids, the family Alloxystidae which is solely hyperparasitic on aphidids and aphelinids which attack aphids (Andrews 1978). These hyperparasitoids are endoparasitic and oviposit into the primary parasitoid larva within their aphid host.

Seventeen families comprise the superfamily Chalcidoidea and eleven of these include hyperparasitic species. The host relationships of chalcids are varied; they attack the Lepidoptera, Diptera, Coleoptera, Hymenoptera and Hemiptera and may be endo- or ectoparasitic, solitary or gregarious. Individual chalcid species, however, are usually restricted to attacking one particular host stage.

Aphelinids are mostly primary parasitoids of Homoptera, but some attack the eggs of Lepidoptera and Orthoptera. In addition to some large genera in which all known species are primary ectoparasitoids (eg. Aphytis Howard) or endoparasitoids (Aphelinus Dalman) in both sexes, others exhibit different larval behaviour. This is connected either with peculiar host relationships (Azotus Howard) or with deviate ontogenies in the male sex (Coccophagus Westwood).

Hyperparasitism occurs either in both sexes or only in the male in different aphelinid species. In several species both sexes are secondary parasitoids attacking the primary parasitoids of scale insects and other Homoptera (eg. Marietta Howard), cerambycids (eg. Centrodora italica Ferriere) and Diptera (eg. Ablerus leucopidis Blanchard). The biology of several other species is more complicated: while teh female larvae are primarily endoparasitic, male larvae maybe primary ecto- or endoparasitoids or secondary parasitoids of chalcidoids. The latter are known as heteronomous parasitoids and may be subdivided into obligate autoparasitoids whose males develop on conspecific male or female larvae or pupae; facultative autoparasitoids whose males are parasitic on conspecifics or individuals of another species; and alloparasitoids whose males are parasitic only on other species (Walter, 1983). An example of autoparasitism is Encarsia (= Prospaltella) lahorensis Howard, which was recently introduced to California for the control of whitefly. Haploid eggs of P. lahorensis are deposited in late instar larvae or pupae of its own species, the male larvae develop first as endoparasites and then as ectoparasites. The sex ratio in this species depends on host availability (Viggiani 1981).

Most species in the family Perilampidae are hyperparasitic, usually attacking braconids, ichneumonids or tachinids in caterpillars (Askew 1970). The biology of Perilampus hyalinus Say is similar to that of the Trigonalidae. Females oviposit on food plants in the vicinity of a colony of caterpillars. On hatching, the planidial first instar larvae attack the caterpillars and search within them for primary

parasitoid larvae. If the caterpillar is unparasitised the planidia fail to develop (Smith 1912).

The family Pteromalidae includes many species which are hyperparasitic on aphids. Genera such as Asaphes, Pachyneuron and Coruna are ectoparasitic hyperparasitoids which venomize their hosts and attack, develop and pupate within mummified aphids.

2.12 Evolution of hyperparasitism.

Gordh (1981) suggested that, as hyperparasitoids occur in several taxa and have a variety of immature stages and oviposition behaviours, hyperparasitism must have evolved from primary parasitism on several occasions within the Hymenoptera. Many insects have defence reactions against parasitic larvae and the greater the taxonomic and physiological distance between the parasitoid and its host, the stronger the defence reaction. If a hymenopterous parasitoid accidentally oviposited in a species belonging to the same order as itself, it should be more likely to find it to be a suitable host than if it had oviposited in a species belonging to another order (Brues 1921). It is also conceivable that cleptoparasitism may have been a step in the evolution of hyperparasitism. Cleptoparasitism is a form of multiparasitism in which access to and paralysis of a host by a parasitoid species are essential before the host can be parasitised by the cleptoparasitoid, which, upon eclosion, destroys the egg or larva of the first parasitoid before feeding on the paralysed, primary host (Spadberry 1968).

For example, Rhyssa persuasoria (L.) is a parasitoid of siricids in wood, which is in turn cleptoparasitised by Pseudorhyssa sternata. Females of the latter species frequently observe R. persuasoria ovipositing and, when the primary withdraws its ovipositor, the P. sternata female explores the surface with its antennae to locate the drill shaft. The parasitoid then oviposits near the primary parasitoid egg on the already parasitised host. Although cleptoparasitoids often observe ovipositing R. persuasoria before locating the shaft, they can also find shafts several days after they have been drilled and in the absence of R. persuasoria females. It seems likely that they are attracted by secretions from the vaginal gland of the primary parasitoid. The first instar larvae of the cleptoparasitoid are able to attack and destroy all larval instars of the primary parasitoid; also P. sternata can develop to larval maturity on final instar larvae of R. persuasoria (Spadberry 1968)).

Another species, Temelucha interruptor, while not truly cleptoparasitic in that it can oviposit in unparasitised hosts, shows a clear preference for larvae of the pine shoot moth, Rhyacionia buoliana which have been previously parasitised by Orgilus obscurator. It seems likely that T. interruptor is adapted to finding the oviposition sites of O. obscurator rather than to finding R. buoliana larvae concealed in pine buds (Arthur et al 1964).

On the basis of these examples it is not difficult to imagine an evolutionary series beginning with multiparasitism by two or more parasitoid species, followed

by increasing dependence by one species on the host paralysis caused by a second species leading to cleptoparasitism and eventually, obligate hyperparasitism.

2.13 Biological characteristics of hyperparasitoids.

Hyperparasitoids show a variety of characteristics many of which are similar to those of primary parasitoids. Although the biology of many hyperparasitic species remains undocumented, a few general trends in life history strategies are apparent.

Primary Hymenoptera are particularly vulnerable to attack in the cocoon stage by hyperparasitoids as they tend to be exposed for long periods (Smith 1916). Hyperparasitism of primary parasitoids in the egg and adult stages, however, occurs much less frequently (Gordh 1981). Apanteles melanoscelus (Ratzeburg), for example, is a parasitoid of the gypsy moth, Porthetria dispar (= Lymantria dispar). Mature parasitoid larvae from the second generation overwinter in their cocoons and are exposed to attack by hyperparasitoids from July until the adults emerge the following spring. Thirty-five hyperparasitic species have been recorded from this host and the majority of these attack the cocoon stage (Muesebeck and Dohanian 1927). Similarly, parasitoids of the alfalfa weevil, such as Blathyplectes anurus (Thomson) and B. curculionis, have diapausing cocoon stages which are attacked by several hyperparasitic species (Day 1969, Simpson et al 1979). Hyperparasitoids, like parasitoids, may be either ectoparasitic or endoparasitic in the larval stage.

Endophagous species typically deposit their eggs within primary parasitoid larvae while the host is still alive. The parasitoid continues to develop until it reaches the cocoon-spinning stage. This type of behaviour is characteristic of Alloxystine species which attack primary parasitoids of aphids (Andrews 1978) and encyrtids, such as Cheiloneurus noxius, which attack mealybugs and scale insects (Weseloh 1968). Ectoparasitic species deposit their eggs on the surface of the primary parasitoid and the larvae feed externally on their host. Species with this type of behaviour often host feed and/or venomize their hosts. Hyperparasitoids are almost all ectoparasitic as they tend to attack hosts which are protected by cocoons or puparia. This contrasts with the type of larval feeding behaviour found in primary parasitoids, which are mainly endoparasitic (Muesebeck and Dohanian 1927, Hammond 1979, Gordh 1981). Hyperparasitoids which attack the parasitoids of aphids exemplify the relationship between endophagy and the host stage attacked. Species, such as Alloxysta victrix, which attack the larval stages of primary parasitoids while the aphids are still alive, are endophagous. While species which attack after the cocoon or 'mummy' stage has been formed, such as Asaphes californicus and Dendrocerus carpenteri, feed externally on the primary parasitoid larva or prepupa. Aphidencyrtus aphidivorus is an exception as the female hyperparasitoid can attack the primary parasitoid either while the aphid is alive or after the mummy is formed. In both cases, however, the A. aphidivorus larva is endoparasitic (Sullivan 1986, 1987).

Another general rule is that hyperparasitoids tend to go through more generations per year than their primary parasitoids, due to faster development and, in some cases, earlier emergence from overwintering (Hammond 1979). Fourteen out of seventeen hyperparasitoid species attacking Apanteles melanoscelus, for example, have at least two generations each year, while the host has no more than two. This parasitoid requires 28 days to develop from egg to adult; all but one of its hyperparasitoids have a faster developmental rate (Muesebeck and Dohanian 1927).
Many hyperparasitoids are also well synchronised with their hosts as they attack late in the development of the primary parasitoid and emerge later than hosts of the same generation. Emergence, therefore, tends to occur when suitable parasitoids are again available for attack (Hagen and van den Bosch 1968). Chua (1977, 1978) showed that while the spring emergence of the primary parasitoid, Diaeretiella rapae, is poorly synchronised with populations of its host, Brevicoryne brassicae, secondary parasitoids, such as Alloxysta fuscicornis, emerge after the parasitoid populations have become abundant. Also Tetrastichus galactopus (Ratzeburg), which attacks Apanteles glomeratus (L) in Pieris rapae, is highly synchronised with the first generation of the primary parasitoid (Nealis 1983).
Hyperparasitoids were originally thought to be much less host specific than primary parasitoids (Muesebeck and Dohanian 1927, Hagen and van den Bosch 1968, Beddington and Hammond 1977, Hammond 1979), but recently it has become apparent that there are several notable exceptions to this rule (Gutierrez 1970, van den Bosch 1981, Matejko and

Sullivan 1984, Sullivan 1986, 1987). Studies of host specificity have been hindered by a lack of taxonomic clarity in some taxa of the parasitic Hymenoptera. There are also problems of definition, as what is defined as 'broad oligophagy by one author may be 'polyphagy' when compared with a monophagous species or 'host specificity' in comparison with a polyphagous species.

It has been suggested that endoparasitoids have narrower host ranges than ectoparasitoids and it seems likely that this hypothesis could also apply to hyperparasitoids (Sullivan 1986, 1987). Ectoparasitic species such as Asaphes vulgaris Walker, are polyphagous and may develop as either secondary or tertiary parasitoids. Pachyneuron concolor (Foerster) may act either as a primary parasitoid attacking the puparia of aphidophagous Diptera or as a secondary parasitoid on encyrtid parasitoids in soft scales, mealybugs and coccinellid larvae. Host selection is based on locating a soft-bodied host with a hard, dry shell, independent of whether the host is a dipteran pupa in a puparium or a primary parasitoid in a mummified host (Rosen and Kfir 1983). Endoparasitic species such as A. aphidivorus and members of the genus Alloxysta are more host specific. A. megourae (Ashmead), for example, is host specific for the aphid parasitoid Aphidius smithi. Sensory structures on the ovipositor are used to discriminate between suitable and unsuitable hosts (Matejko and Sullivan 1980). Similar structures have also been found on the ovipositor of A. victrix. This species has two distinct phases in host selection; examination of aphids with the antennae and

probing of the aphid to detect any parasitoid larvae which may be present and determine their suitability for oviposition (Gutierrez 1970). In addition to the pronounced preferences shown by certain alloxystines for particular aphid-parasitoid combinations, encyrtid endoparasitic hyperparasitoids also show a certain degree of host specificity. Cheiloneurus noxius Compere attacks brown soft scales parasitised by the encyrtids Diversinervus elegans Silvestri, Aphycus stanleyi (Compere), A. luteolus Timberlake and Microterys flavus (Howard). Black scales containing A. stanleyi are also attacked. C. noxius females recognised the aphelinid parasitoids, Coccophagous scutellaris (Dalmain) and C. cowperi Girault as unsuitable hosts and did not oviposit in them. They also discriminate between suitable and unsuitable hosts at the probing stage of the oviposition process (Weseloh 1969).

It is possible, however, that some ectoparasitic species also have a limited ability to discriminate between suitable and unsuitable hosts. Matejko and Sullivan (1984) attributed the low success rate of the ectoparasitic hyperparasitoid, Dendrocerus carpenteri as a tertiary parasitoid, to a degree of host specificity which had not previously been suspected. Among primary parasitoids, there are several species which do not conform to the correlation between endoparasitism and host specificity. Askew and Shaw (1986) suggested that a classification of koinobionts and idiobionts was a more practical indication of host range. (Koinobionts permit the host to develop after oviposition by the parasitoid and themselves benefit from this continued development.

Idiobionts permanently paralyse or kill the host before the egg hatches, the host is then consumed in the location and state it was in when it was attacked). Many koinobionts are obligatory secondary parasitoids while idiobionts are often facultative. Askew and Shaw concluded that koinobiosis is a superior correlate to limited host ranges than endoparasitism, having examined the host ranges of chalcid parasitoids in a leaf miner community. It seems likely that the host ranges of koinobionts are restricted by their need to develop in close association with a living host. On this basis it seems reasonable to suggest that koinobiotic obligate secondary parasitoids will be found, on investigation of their biology, to be host specific. Idiobiotic hyperparasitoids will have comparatively wider host ranges and tend to act as facultative secondary parasitoids.

2.14 Hyperparasitoids and biological control.

The main interest in hyperparasitoids has stemmed from the broad ecological question of their influence on insect communities and, more specifically, their effect on the implementation of biological control programmes. The latter is the subject of debate and some authors remain unconvinced about the detrimental effect of hyperparasitoids. Occasionally, hyperparasitoids may themselves act as biological control agents. For example, Charips sp. have been used for the control of the parasitoid Lysiphlebus testaceipes in greenhouse trials for resistance in cereals to Schizaphis graminum (Burton et al 1977).

Similarly, Nesolynx thymus Girault is a hyperparasitoid of Tricholyga bombycis Beck., a parasitoid which causes serious losses of silkworms Bombyx mori L. (Kumar et al 1986). Traditionally, however, it has been the policy of classical biological control programmes (in which exotic parasitoids are released to control insect pests) to exclude secondary parasitoids (Doutt and de Bach 1964, Huffaker et al 1976, Waage and Hassell 1984, Sullivan 1986). Hyperparasitism may hinder the successful establishment of imported parasitoids or suppress their populations so that effective control is not achieved (Sickle and Weseloh 1973). The influence of hyperparasitism on the effectiveness of parasitoids used for biological control is, however, difficult to evaluate (Flanders 1943) and relatively few studies have considered the ecological importance of hyperparasitoids (Doutt and de Bach 1964, Zwolfer 1970, van den Bosch 1981, Rosen 1981). Generally, the impact of primary parasitoids on populations of phytophagous insects has been well documented but that of hyperparasitoids on populations of primary parasitoids is assumed, on the basis that hyperparasitoids possess similar attributes to those which make primary parasitoids effective control agents (Luck et. al. 1981). This implies that the phytophagous pest population ceases to be regulated by the primary parasitoid and specificity, synchrony and a high percentage of hyperparasitism are criteria by which the impact of hyperparasitoids can be judged. Direct evidence supporting this view is, however, lacking although circumstantial evidence suggests that hyperparasitoids can be deleterious (Luck et al 1981). The role played by hyperparasitoids varies greatly between insect communities.

Some primary parasitoids suffer heavy losses due to hyperparasitism while others are barely affected (Zwolfer 1970).

Examples which support the idea that hyperparasitoids have an economically significant detrimental effect on biological control programmes are surprisingly sparse in the literature. There are a few instances, however, which illustrate the negative effects of hyperparasitism. An encyrtid hyperparasitoid, Quaylea whittieri (Gir.), was liberated and established in California in 1901 in the mistaken belief that all encyrtid species are primary parasitoids. It was only when the black scale parasitoid, Metaphycus lounsburyi (How.) was introduced 18 years later that Q. whittieri was thought to have an economic effect. In areas where black scale was plentiful the parasitoid increased rapidly and control was achieved. Shortly afterwards, populations of the hyperparasitoid also increased and the pest again became numerous. It seemed obvious that the inability of the parasitoid to control black scale was due to the presence of the hyperparasitoid. Subsequently it has been shown that Q. whitteri has little effect on the biological control of scale insects and the ineffectiveness of M. lounsburyi is due to its lack of synchronisation with the life cycle of its host (Flanders 1943).

In 1961 Exenterus amictorius (Panzer) was introduced to control the pine sawfly, Diprion similis (Hartig) in Wisconsin. After a period of 10 years E. amictorius was found to be attacked by 11 species of hyperparasitoid, 9 endemic and 2 exotic. All of these species are polyphagous

and are thought to have a negative effect on the control of the pine sawfly (Mertins and Coppel 1973).

The aphidiine parasitoids of the potato aphid are attacked by a number of hyperparasitoids, including Asaphes vulgaris and Dendrocerus testaceimanus Kieffer. Total hyperparasitism has never been recorded but the possible numbers of the second primary parasitoid generation and, supposedly, the number of aphids which might have been parasitised are reduced by half (Dunn 1949). Hyperparasitism is also thought to be a major factor in reducing the impact of the parasitoid, Diaeretiella rapae, on its host, Brevicoryne brassicae (see later).

It has been frequently argued, however, that hyperparasitoids are not detrimental and may even contribute to the stability of insect communities. Nicholson (1933) in his classic paper on the balance of animal populations, proposed that, hyperparasitoids generally have little effect on phytophagous host densities, although they may increase them slightly. It seemed improbable that a hyperparasitoid could completely free a phytophagous insect from the control of a parasitoid. Flanders (1943) argued that hyperparasitism is a form of mutualism which may prevent outbreaks of phytophagous insects by regulating the populations of primary parasitoids. Hyperparasitism was thought to have a dampening effect on parasitoid populations, preventing them from annihilating the host and so causing their own extinction. Beddington and Hammond (1977) and May and Hassell (1981) produced mathematical models to describe host-parasitoid-obligate hyperparasitoid systems and both

concluded that such systems are most likely to be stable when the searching efficiency of the hyperparasitoid exceeds that of the parasitiod. Luck et al (1981) also constructed a model of the relationship between parasitoid and hyperparasitoid populations, based on the Hassell and Varley (1969) modification of the Nicholson-Bailey equation. They concluded that, under certain conditions, the presence of a hyperparasitoid may improve a biological control system, altering it from one in which the pest exhibits periodic outbreaks to one of continuous subeconomic densities. They emphasised that their models, although used widely to investigate host-parasitoid behaviour, are not very realistic.

There are a few examples of biological control programmes in which hyperparasitoids, although present, do not have a detrimental effect and, in some cases, may even be stabilising. Muesebeck and Dohanian (1927) studied the hyperparasitoids of A. melanoscelus which they considered to be largely responsible for the maintenance of a proper relationship between the parasitoid and its host.

The larch sawfly, Pristiphora erichsonii (Hartig), is a major pest of larches in North America. In the 1950's a parasitoid, Olesicampe benefactor Hinz, was released for the control of the larch sawfly. The parasitoid lays its eggs in the first instar larvae of the host and there they are attacked by an ichneumonid hyperparasitoid, Mesochorus dimidiatus Holmgren. O. benefactor provides effective control of the sawfly despite the abundance of the

hyperparasitoid. When sawfly populations are large the rate of hyperparasitism by M. dimidiatus exceeds that of parasitism by O. benefactor. At low host population levels the two rates are approximately equal while at very low sawfly densities, O. benefactor rates exceed those of M. dimidiatus. This relationship should tend to stabilise the interrelationships between the sawfly and the parasitoids, although the direction of population change will still be influenced by density independent mortality factors (Ives 1976).

In 1968 an Iranian ecotype of the parasitoid Trioxys pallidus (Haliday) was introduced to California to control the walnut aphid, Chromaphis juglandicola (Kallenbach), after a previous attempt with a French ecotype had failed. The Iranian ecotype became established and spread rapidly through the walnut groves of California and successful control of the walnut aphid was achieved 3 years after the introduction of the parasitoid (Messenger 1975, van den Bosch et al 1979). Soon after T. pallidus became established it was attacked by a number of native hyperparasitoids including Asaphes sp., Pachyneuron sp., Dendrocerus sp., Aphidencyrtus sp. and Alloxysta sp. In a small scale study of a non-commercial walnut grove Frazer and van den Bosch (1973) found that hyperparasitism did not prove a threat to the biological control of C. juglandicola. Similarly in larger studies, Messenger (1975) and van den Bosch et al (1979) concluded that hyperparasitoids do not impair the efficiency of T. pallidus. At the end of the season the hyperparasitoids increase so that nearly all the primaries are attacked.

Nevertheless, parasitism of the early spring brood of aphid reaches up to 98% as the major hyperparasitoids are polyphagous, resulting in a lag in hyperparasitism. The end of season build up of hyperparasitoids is not detrimental and may even prevent the very efficient T. pallidus from overexploiting its host population.

The weight of evidence in the literature, therefore, seems to favour the idea that hyperparasitoids do not have an economically significant impact on biological control (although their ecological impact may be significant). Until this has been proven for all hyperparasitoids, however, it is reasonable to take steps for their exclusion.

2.2 THE BIOLOGY OF *Brevicoryne brassicae*, *Diaeretiella rapae* AND *Alloxysta fuscicornis*.

2.21 *Brevicoryne brassicae*

The cabbage aphid, *Brevicoryne brassicae* (L.) is an economically important pest of cruciferous crops with a world-wide distribution (Fullaway 1915, Petherbridge and Mellor 1935, Todd 1955, Hafez 1961, Pimental 1961, Hughes 1971, Oatman and Platner 1972). Sinigrin or mustard oil plays an important role in host selection (Bonnemaison 1965) and, therefore, it mainly attacks plants belonging to the family Cruciferae. These include several crops and also wild crucifers such as wild turnip which act as resevoirs for the aphid and its parasitoids (Akinlosotu 1971). *B. brassicae* infestations cause stunting of plants, curling of leaves and the production of honeydew reduces their market value. This aphid is also a vector of several virus diseases of cruciferous crops (Bonnemaison 1965).

In the spring, the host plants are infested by alatae (winged forms) and these produce apterae (wingless forms) which increase rapidly (Raworth *et al* 1984). The aphid has four nymphal instars and, while the plant is actively growing, the predominant forms are the wingless, parthenogenetic females which exploit the food supply to its limit. Rapid embryonic and nymphal development cause telescoping of generations and are the main factors contributing to the fast rate of population increase (Hughes 1963). Dense colonies of aphids accumulate (Hayamizu 1982) and, as the population density increases, alatae are produced which

disperse to neighbouring plants (Hughes 1963, Raworth et al 1984). Cabbage aphids tend to show a bimodal population curve with peaks in the spring and autumn (Bonnemaison 1965, Hughes and Gilbert 1968, Chua 1977). In cold climates sexual forms are produced in the autumn. The oviparae lay eggs on the aerial parts of the host plant, these overwinter and hatch into parthenogenetic fundatrices the following spring (Hughes 1963). In milder climates, however, the sexual cycle is suppressed and parthenogenetic reproduction continues throughout the year (Petherbridge and Mellor 1936, Hughes 1963, Bonnemaison 1965). In England B. brassicae overwinters as parthenogenetic virginoparae during mild winters (Chua 1977), although eggs have been recorded by some authors (Petherbridge and Mellor 1936).

2.22 Diaeretiella rapae

Diaeretiella rapae (M'Intosh 1855) is the only primary parasitoid attacking B. brassicae (Petherbridge and Mellor 1936, George 1957, Hafez 1961, Hughes 1963, Paetzold and Vater 1965, Hagen and van den Bosch 1968, Oatman and Platner 1972, Chua 1978, Raworth et al 1984, Ayal 1987). Its distribution is cosmopolitan and it occurs, with a few exceptions, wherever its host is found (Schlinger and Hall 1960, Hafez 1961, Bonnemaison 1965, Mackauer and Stary 1967, Stary and Schlinger 1967, Hagen and van den Bosch 1968, Akinlosotu 1971).

D. rapae has been recorded as reducing the populations of B. brassicae by a significant amount (Fullaway 1915, Shembel 1922, Schlinger and Hall 1960, Pimentel 1961, Pandey et al 1984). More frequently, however, the parasitoid fails to

have a significant effect on the populations of its host (Petherbridge and Mellor 1936, Paetzold and Vater 1965, Stary 1966, Hagen and van den Bosch 1968, Lowe 1968, Daiber 1971, Oatman and Platner 1972, Chua 1978). This has been attributed to a number of causes; the longer developmental time of D. rapae in comparison to its hosts, the asynchrony of the parasitoid and aphid populations, the high mortality of parasitoids in the mummy stage and the high incidence of superparasitism (Hafez 1961, Hagen and van den Bosch 1968, Daiber 1971, Chua 1978). The majority of authors, however, consider hyperparasitism to be the main factor responsible for reducing the impact of D. rapae on aphid populations (Todd 1956, Hafez 1961, Sedlag 1964, Paetzold and Vater 1965, Hagen and van den Bosch 1968, Lowe 1968, Daiber 1971). The host specificity of the parasitic Hymenoptera results from four steps in the host selection process:

(a) Host habitat finding; the habitats of the host and parasitoid must coincide.

(b) Host finding; the parasitoid must be able to locate the host within the habitat.

(c) Host acceptance; having encountered a prospective host the parasitoid must be stimulated to attack it.

(d) Host suitability; the parasitoid progeny must be able to develop within the host (Salt 1935, Doutt 1959, Stary 1964).

It is thought that host taxa and habitat are both important in delimiting the host range of a parasitoid species (Gardenfors 1986). The host range of the aphidiids, which are all parasitoids of aphids, is restricted to units of their hosts which are taxonomically clearly defined

(Mackauer 1965). Habitat is, however, also of major significance in restricting host specificity of this group. Many aphidiine species appear to prefer one or a few habitats and within these they may be limited by their searching behaviour to specific plant taxa (Stary and Schlinger 1967). Consequently, they will be restricted to aphids on these plants, although other potentially suitable hosts may occur nearby (Gardenfors 1986). For example, B. brassicae is attacked throughout the season by D. rapae in steppe-type habitats (Stary 1964).

Stary (1966) defined six types of parasitoids based on their host specificity. These ranged from type 1 whose specificity was restricted to a single host species (these are termed monophagous) through type 3, which are species restricted to two or more genera of the same host group (oligophagous), to type 6 in which the parasitoid attacks host genera of various host groups. The mode of host life plays the most important role in this case (polyphagous). D. rapae is an 'oligophagous-polyphagous' parasitoid on this scale, belonging to type 4. It attacks many aphid species of the subfamily Myzinae and is mainly restricted to aphids which feed on cruciferous and chenopodiaceous plants (Stary and Schlinger 1967). (It is probably significant that both D. rapae and its main host, B. brassicae, are attracted by cabbage oils (Read et al 1970, Bonnemaison 1965)). Although D. rapae attacks at least 18 aphid species (Schlinger and Hall 1960, Stary 1976), its preferred host is B. brassicae (Hafez 1961, Akinlosotu 1971). Wilson and Lamdin (1987) demonstrated that, although there were no significant

differences in the longevity, developmental time or percent successful emergence of D. rapae from B. brassicae and Myzus persicae, the parasitoid clearly preferred to oviposit and laid more female eggs in the former species.

D. rapae is an endophagous parasitoid (i.e. the larvae develop and feed within the host). Female parasitoids deposit their eggs directly into the adipose tissue of live aphids (Spencer 1926) using a reduced ovipositor which permits only superficial penetration of the aphid body (Broussal 1966). The oval, elongate eggs absorb liquid rapidly after oviposition and hatch 48 to 72 hours later. The first instar is curved in shape with a long spiny cauda. This stage is active and attacks the host embryos with well-developed, sclerotized mandible and cytolytic enzymes. The first instar larva has a thick cuticle which prevents self-digestion.

D. rapae is a solitary parasitoid (i.e. only one adult emerges per host) and at this stage the oldest larva inhibits the development of any supernumery larvae present by biochemical means. After 48 hours at 20°C the larva moults to the second instar. This has neither a cauda or mandibles and lies in the host haemocoel feeding on liquids which are ingested using the muscular pharynx. The third instar is formed after 24 hours and is similar in morphology. When a further 24 hours have passed the larva again moults to the fourth and final instar. In this stage the mandibles are again present. The larva becomes very active and feeds voraciously on the remaining host tissues. The aphid continues feeding, and may even reproduce, until

this parasitoid instar is reached, so providing the parasitoid with an uninterrupted nutrient supply. When the contents of the aphid have been completely consumed the larva spins a cocoon within the aphid skin. The aphid is cemented to the leaf through a slit in the ventral surface. Pupation occurs inside this 'mummy' (Spencer 1926, Broussal 1966, Couchman and King 1977). Adults emerge through a circular hole cut in the mummy and the generation time is 14 days at 20°C (Vater 1971).

Mating and oviposition can occur shortly after emergence. D. rapae is arrhenotokous, so virgin females lay male eggs only. It is also pro-ovogenic i.e. newly emerged females contain their full complement of mature eggs (Spencer 1926, Hafez 1961, Broussal 1966). Adults feed mainly on honeydew and it has been found that this increases their longevity (Spencer 1926, Hagen and van den Bosch 1968). Similar to other aphidiids D. rapae is multivoltine and, in temperate climates, hibernates in the prepupal stage within the aphid mummy (Spencer 1926, Hafez 1961, Hagen and van den Bosch 1968). D. rapae has also been reported to have a summer diapause in California (Schlinger and Hall 1960). Emergence of adults occurs throughout the year with peaks in April and May (Hafez 1961, Chua 1978). Dispersal occurs by flight and in parasitised alate aphids (Hafez 1961, Vater 1971, Chua 1977).

2.23 Alloxysta fuscicornis

Several hyperparasitoids are associated with B. brassicae and D. rapae, including Alloxysta fuscicornis (Westwood), Asaphes vulgaris Walker, A. suspensus (Nees), Dendrocerus carpenteri (Curtis), Pachyneuron minutissimum Forster and Lygocerus aphidovorus K. (George 1957, Hafez 1961, Lowe 1968, Akinlosotu 1971, Chua 1978). A. fuscicornis is the most numerous of these species and occurs, in association with D. rapae and B. brassicae, throughout the world (Hafez 1961, Akinlosotu 1971, Oatman and Platner 1972, Evenhuis 1974, Beardsley 1985). A. fuscicornis differs from the other hyperparasitoids listed as it is an obligate endoparasitoid while they attack either D. rapae or A. fuscicornis (tertiary hyperparasitism) and develop ectoparasitically (the larvae feed externally on their host).

The taxonomy of the family Alloxystidae has been problematic. The Alloxystidae and Charipidae are considered by some taxonomists to be families of the superfamily Cynipoidea (van Achterberg 1982, Evenhuis and Barbotin 1987, Evenhuis and Kiriak 1988. The Alloxystidae are all hyperparasitic on aphids through the Aphididae and Aphelinidae. They include three genera; Phaenoglyphis Forster, Alloxysta Forster and Lytoxysta Kieffer. Evenhuis (1972) suggested that all the alloxystid hyperparasitoids of B. brassicae through D. rapae, mentioned in the literature, belong to one species. He stated that this species should be known as Alloxysta brassicae Ashmead (Evenhuis 1974). This species was subsequently synonymized and is now known as Alloxysta fuscicornis (Evenhuis 1982).

There is, however, still some debate about the status of this species, as its morphology closely resembles that of A. victrix (Westwood) (Andrews 1978). In the past they have been separated on the basis of head coloration and antennal segment lengths (Fergusson 1986). Evenhuis (1972) reared many hyperparasitic species from mummies for which the aphid and aphidid parasitoid species were known. He concluded that colour characters are, to a large extent, specifically constant. Fergusson (1986), however, on examining this character in a large number of specimens found it to be variable and unreliable for species determination.
A. fuscicornis was almost always associated with the Cruciferae/Myzinae/D. rapae complex and recorded from Rosa sp./Aphidius sp. (common hosts of A. victrix) only infrequently (Andrews 1978). Fergusson (1986) found that the morphological characters previously used to distinguish these two species break down if a large number of specimens are examined and synonymized A. fuscicornis with A. victrix. Evenhuis (pers. comm. 1986) disagrees with this view and considers that Fergusson paid insufficient attention to important characteristics such as the patterns of pubescence on the pronotum and propodeum. Also, Fergusson based his conclusions mainly on specimens collected from the field rather than rearing them from well known hosts in order to assess intra-specific variability. For these reasons, I have adopted Evenhuis' classification of A. fuscicornis, which is based on rearing hyperparasitoids from their hosts.

In the past hyperparasitoids were considered to be largely polyphagous (Hagen and van den Bosch 1968, Gutierrez and van den Bosch 1970a, Sullivan 1986) but during the last twenty years a surprising degree of host specificity has been shown to exist in certain endoparasitic species (van den Bosch 1981, Sullivan 1986). There is, obviously, an additional step in the host selection process of hyperparasitoids, in comparison to that of primary parasitoids (i.e. they must accept not only the direct (primary parasitoid) but also the indirect host (aphid)). Host specificity in the Alloxystidae is, therefore, not a simple association between the secondary and primary parasitoid. The association is influenced by a preference for certain aphid species and, possibly, for certain host plants (Andrews 1978). Evenhuis (1971) reared many Alloxystine species from aphid mummies collected in the field. The majority of these species exhibited a characteristic association of an aphid host, a primary aphidid parasitoid and an Alloxystine hyperparasitoid. Several species are very host specific, specialising on one particular primary parasitoid species. A. citripes (Thomson), for example, is a specialised hyperparasitoid of Trioxys pallidus, which in turn is a specialised parasitoid of Callaphididae, such as Tuberculoides annulatus (Hartig) on oak and Pterocallis alni (De Geer) on alder (Evenhuis 1976). A. victrix appears to be more polyphagous as it attacks several Aphidius species which parasitise Macrosiphum and related genera (Evenhuis 1976).

It seems likely that the primary parasitoids, with which the endoparasitic Alloxystidae are more closely associated than their aphid hosts, will play a major role in determining hyperparasitoid host specificity. There are two distinct steps in the host selection process of A. fuscicornis. Firstly, the aphids must be located within the habitat and accepted for probing. This step is a coarse mechanism based on an examination of the aphid with the antennae (Gutierrez 1970d). For example, A. victrix was found to prefer one aphid species, Acyrthosiphon pisum (Harris), to another, Therioaphis trifolii (Monell) (Gutierrez 1970c). Secondly, the hyperparasitoid must accept or reject any primary parasitoid larvae which may be present in the aphid haemocoel. This step is carried out by means of sensory structures on the ovipositor tip (Gutierrez 1970d) and A. victrix exhibited an ability to discriminate between primary parasitoid larvae of several species in the haemocoels of two aphid species (Gutierrez 1970c).

A. fuscicornis females oviposit directly into parasitoid larvae within their living aphid hosts (Haviland 1921, Gutierrez 1970b, Andrews 1978). A. fuscicornis is considered to be a modified pro-ovogenic species as females emerge with a limited egg supply and more eggs are developed subsequently. It is interesting to note that, in this respect, A. fuscicornis is intermediate between D. rapae, which is completely pro-ovogenic, and the tertiary parasitoids, A. vulgaris and P. minutissimum, which are synovogenic (all the eggs are formed after emergence) (Broussal 1966). Alloxystine eggs are oval in shape with a short peduncle or stalk which is reduced, suggesting that it

has lost its use which may have been either for respiration or attachment (Haviland 1921, Clausen 1940, Fergusson 1986). Eggs which are deposited in the aphid haemocoel do not develop (Gutierrez 1970). Two or three days after oviposition the first instar larva ecloses and begins to feed within the primary parasitoid larva (Gutierrez 1970). The first instar larvae have chitinous segmental plates and a distinct cauda (Haviland 1921, Fergusson 1986). The mouthparts consist of two slender mandibles Subsequent instars lack chitinous plates and the mandibles are large and simple (Haviland 1921, Clausen 1940).

The A. fuscicornis larva develops within the host haemocoel without destroying it until the parasitoid reaches the prepupal stage and spins its cocoon (Spencer 1926). In the fifth and final instar (Vater 1971) the hyperparasitoid consumes the remains of its host (Gutierrez 1970) and pupates within the D. rapae cocoon (Spencer 1926).

A. fuscicornis overwinters as a mature larva within the host cocoon (Dunn 1949) and adults emerge in April or May of the following year (Chua 1978). During the summer months the generation time is about 13 days (Sullivan 1972) and, on emergence, the adults feed on flower nectar (Andrews 1978). Males emerge before females so that the sex ratio of the population in early spring is male biased. This bias decreases with time, however, and eventually the females become numerically dominant. It has been shown that D. rapae is poorly synchronised with its host, as emergence occurs before the aphid population on Brussels sprouts has built up to a significant level (Chua 1978). But the infestation of

early potato and Brussels sprouts plants by M. persicae helps the parasitoid to find an appropriate host, in addition to B. brassicae on the seed plants early in the season. It is possible that an early population of the parasitoid would build up on these early crops and eventually migrate to new cruciferous crops (Hafez 1961). A. fuscicornis, however, arrives at the Brussels sprouts plants when D. rapae has reached a sizeable population (Chua 1978).

3. REPRODUCTIVE STRATEGIES

A wide range of reproductive strategies occur within the parasitic Hymenoptera; some parasitoids emerge with a full complement of mature eggs (pro-ovogenesis) while in other species oviposition does not occur until some time after emergence (synovogenesis). In the latter case the parasitoid may have to feed before oviposition can take place and eggs may continue to mature throughout adult life. Associated with this range of strategies is a range of fecundities, both in terms of total number of eggs produced and daily rate of egg production. In the Ichneumonidae the number of ovarioles per ovary is directly related to the overall fecundity and the rate of egg production of a parasitoid species, and there are a wide range of fecundities and ovariole numbers among different species. The number of eggs a female can lay in a lifetime is dependent on several factors, which can be divided into two categories: those that affect the probability of discovering the host and ovipositing in it and those that determine the probability of survival once the egg has been laid (Price 1975). Parasitoid fecundity is also closely correlated with the host stage attacked; ichneumonids which parasitise the most abundant and vulnerable stages of a host have large numbers of ovarioles while those attacking the later, and less common instars, have progressively smaller numbers of ovarioles per ovary (Price 1972).

Host availability depends on both host abundance and accessibility. Frequently a host which is readily available is also vulnerable as many other mortality factors are

likely to act upon it. The probability of survival of the parasitoid on or in the host is, therefore, often inversely proportional to host availability (Price 1972). Host availability depends on the host stage attacked (the egg stage is always more abundant than the pupal stage), effective defence mechanisms, concealment in leaf rolls or webs and the general year-to-year abundance of the host species. When parasitoids are ranked according to the host stage attacked and this is plotted against their potential fecundities (mean number of ovarioles per ovary) a trend is evident. The higher the seasonal abundance of the host, the greater is the potential fecundity of the subfamily or tribe. Several modifications of ovary structure and egg production parallel the increase in ovariole number per ovary as, with increasing host abundance, number of mature oocytes and the potential for storage of eggs in the oviduct increase and the size of eggs decreases (Price 1972, 1974, 1975).

An explanation of reproductive strategies may be framed in energetic terms as the energy allocated to egg production clearly depends on the energetic content of the host and the division of this between maintenance, body building and egg production. Cody (1966) stated, with reference to birds, that a given quantity of energy available for reproduction must be optimally allocated between three energetic drains: eggs, avoidance of predation and competition. This statement could be qualified, when it is applied to parasitoids, to include a fourth energetic drain: the energy expended whilst searching for hosts.

Many parasitoids feed in the adult stage, so supplementing the energy obtained from the host (Askew 1971).
Obligate hyperparasitoids must always attack hosts which are less 'available' than hosts of primary parasitoids in the same system. Their hosts are often (a) less abundant, as they occur within a later stage of the herbivorous insect and (b) less accessible, as not all members of an insect population will be parasitised and hyperparasitoids must, therefore, find parasitised individuals within a healthy population. The latter statement does not necessarily apply to facultative hyperparasitoids whose hosts may be as or more abundant than those of the primary parasitoid.
On this basis it seems likely that an obligate hyperparasitoid will have a lower potential fecundity and hence fewer ovarioles per ovary than primary parasitoids in the same system.

This chapter is divided into four main parts. The first outlines the culturing methods which were used throughout the laboratory experiments in this study. In the second part the daily fecundity, longevity schedules and number of ovarioles per ovary are determined for D. rapae and A. fuscicornis. These basic aspects of parasitoid biology are important in determining the foraging behaviour which may be adopted by these species. This is developed in the rest of the chapter by considering two basic factors of parasitoid biology which affect larval mortality and thus, the number of eggs which reach maturity: the availability of hosts in terms of the number of instars in which development can occur and the rate of development within these instars.

3.11 Culturing.

Cultures were started from samples collected from a Brussels sprouts plot at Silwood Park, Berkshire, in October 1984. Fresh material was added periodically to the cultures from field populations. Aphid colonies were established on small potted Brussels sprouts plants (9 to 10 leaves) in the laboratory, by placing adult aphids on previously uninfested plants and allowing them to remain there for two or three days. After this time the adult aphids were removed leaving first instar nymphs which formed the basis of the culture. Contamination of cultures by aphids which had been parasitised in the field was thus avoided. The plants were watered every two to three days and once a week one plant was replaced.

D. rapae adults were acquired from the field by collecting aphid mummies and allowing the adults to emerge in a Petri dish. D. rapae adults were separated from any hyperparasitoids present and placed in a cage containing four Brussels sprouts plants which were heavily infested with B. brassicae. Once a week a fresh plant from the aphid culture was introduced and plants were removed as they were required for the hyperparasitoid culture.

Cultures of A. fuscicornis were started and maintained in a similar manner. Adults were separated from other parasitoids and hyperparasitoids emerging from B. brassicae mummies collected from the field and introduced to cages containing plants infested with both unparasitised and parasitised aphids. Plants from the D. rapae culture were introduced at intervals.

It was essential to avoid cross-contamination between cultures of these three species. Cages were, therefore, kept in separate controlled temperature rooms (at 20 and 25 °C) and checked regularly.

3.12 Method of parasitising aphids for use in experiments with A. fuscicornis.

Many of the experiments described in this thesis required a known number of parasitised aphids to be exposed to the hyperparasitoid. As it is difficult to distinguish accurately between parasitised and unparasitised aphids before mummy formation without dissection, a method was devised to parasitise a high proportion of B. brassicae. Ten aphids from the stock culture were placed on a small piece of leaf in a Petri dish and allowed to settle for 30 minutes. Two female parasitoids were then introduced to the dish for 24 hours. After this time the parasitoids were removed and the aphids were carefully transferred to a Brussels sprouts plant and allowed to develop at 20°C for five to six days before exposure to A. fuscicornis.
This method was tested by exposing ten groups of ten aphids to D. rapae females as described above. The aphids were dissected six days after being exposed and it was found that 95% were parasitised.

3.2 Fecundity and longevity schedules.

The following procedure was carried out to determine the fecundity and longevity schedules of A. fuscicornis and D. rapae.

Newly emerged parasitoids were obtained by carefully removing mummies from the D. rapae culture and allowing the adults to emerge in a Petri dish. Twenty, second to third instar aphids were placed on a leaf disc in a Petri dish with a newly emerged female parasitoid. A drop of honey solution was provided on the lid of the dish. The aphids were replaced at 24-hour intervals until the parasitoid died. After exposure to the parasitoid each group of aphids was kept in a separate Petri dish for three days and then dissected. In this way the daily fecundity and longevity of ten individual parasitoids was determined. Similarly, a newly emerged mated female hyperparasitoid was placed in a Petri dish with 20 parasitised aphids. The aphids were again replaced every 24 hours until the wasp died. This was also repeated with ten female hyperparasitoids.

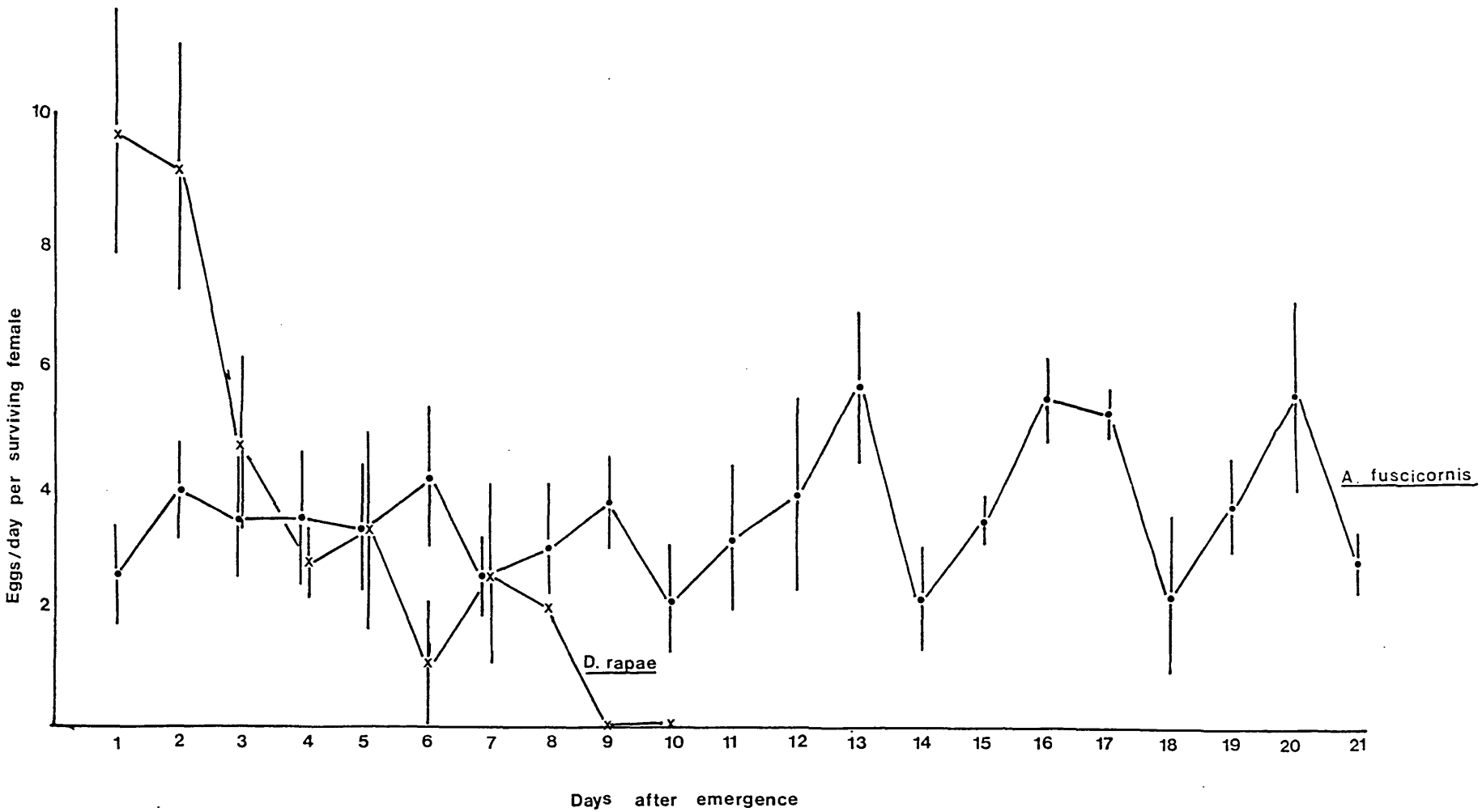
The number of ovarioles per ovary was determined by dissecting several females of each species.

Results.

D. rapae females were found to have only one ovariole per ovary containing in excess of 100 mature eggs. A. fuscicornis females, however, had 10 ovarioles per ovary with two or three mature eggs per ovariole.

Both species oviposited from the first day after emergence (Figure 1), but in D. rapae most eggs were deposited within

Figure 1: Mean daily fecundity



the first few days following emergence while in A. fuscicornis the rate of oviposition oscillated until the hyperparasitoid died. The hyperparasitoid had a significantly ($p<0.001$) greater mean longevity than the parasitoid (13.9 ± 1.82 S.E. and 4.9 ± 0.69 S.E days, respectively, $n = 10$ for both species), but there was no significant difference between the mean lifetime fecundities of these species (46.60 ± 10.95 S.E. and 27.70 ± 4.66 S.E. eggs per parasitoid, respectively). D. rapae had a significantly ($p<0.05$) faster rate of parasitism than A. fuscicornis, with 5.83 (± 0.87) eggs deposited per female per day as opposed to 2.99 (± 0.56) eggs per female per day for A. fuscicornis.

3.3 Availability of hosts and rate of development.

The number of hosts available to a parasitoid will depend, not only on their overall abundance, but also on the number of instars within which the parasitoid can develop and the time for which these instars persist, and on factors such as the synchrony of the parasitoid with the host. D. rapae attacks all the instars of B. brassicae, although as the parasitoid ages a preference for second and third instars over first, fourth and adult apterae and alatae becomes increasingly apparent (Hafez 1961, Broussal 1966). A. fuscicornis females also attack all the larval instars of D. rapae, up to the mummy stage, but there is a clear preference for third and fourth instars over earlier stages (Broussal 1966). Parasitoid eggs may fail to complete their development in some host instars, however, so the success of

parasitism varies between instars, affecting the availability of hosts to the parasitoid.

The view that egg production is adapted to counter, and so provides a measure of, the relative hostility of the environment in which organisms live is common in the literature. This 'balanced mortality' hypothesis is often used to explain the high fecundity of many parasites and marine organisms (i.e. the maintenance of the population is ensured when the probability of survival of an individual is low (see Price 1974 for a review)). The survivorship of parasitoids in the larval stage is considered to be closely linked to that of the host and the probability of survival of a parasitoid can, therefore, be estimated from the host survivorship curve (Price 1974). This is only true, however, when mortality factors act on a host irrespective or whether or not it is parasitised. McAllister and Roitberg (1987) demonstrated, that, in some climates, pea aphids, Acyrthrosiphon pisum, parasitised by Aphidius ervi, had a higher chance of falling off the host plant (in response to predators) than unparasitised individuals in the same population. In this case, parasitoid larvae have a greater chance of mortality than their unparasitised hosts.

The mortality factors which act on D. rapae and A. fuscicornis in the larval stages can be divided into two groups depending on whether they affect the aphid before or after mummy formation. The first group includes predators such as coccinellids, syrphids, chrysopids and cecidomyiids (and of course A. fuscicornis for D. rapae), while the second group is mainly comprised of parasitoids which can

act either at the secondary or tertiary level. Obviously climatic factors, such as heavy rain, fall in both groups, although mummies may be less susceptible than live aphids as they are more firmly fixed to the leaf surface.

The major predators of aphids are syrphids and coccinellids, although chrysopids may also be important (Hagen and van den Bosch 1968, Akinlosotu 1973, Laska 1984). These predators attack parasitised and unparasitised live aphids indiscriminately but reject moribund aphids and mummies (Akinlosotu 1973). It is unlikely that they could distinguish parasitised and hyperparasitised aphids.
A complex of hyperparasitoids attack parasitised aphids after mummy formation: these include Pachyneuron minutissimum. Dendrocerus carpenterii, Asaphes suspensus and A. vulgaris. The first two species are incidental as their main hosts are aphids other than B. brassicae (Chua 1978). Asaphes spp. are known to attack mummies containing A. fuscicornis and D. rapae indiscriminately (Hafez 1961, Sullivan 1972), although the ability of Asaphes to parasitise A. fuscicornis successfully decreases during the four days prior to emergence of the adult hyperparasitoid (Sullivan 1972). The impact of these hyperparasitoids on the D. rapae and A. fuscicornis populations is thought to be low due to the small numbers of adults emerging from field collected mummies (Chua 1977).
Laska (1984) compared the impact of parasitoids and predators on B. brassicae populations by estimating the amount of aphids (in terms of numbers and quantity (mg)) killed during 24 hours at 20°C.

This was calculated as mummies developed in a removed sample and daily aphid consumption. Predators were found to be a more important mortality factor than parasitoids (85.9 and 14.1% of total aphid loss, respectively). D. rapae and A. fuscicornis will, therefore, become less vulnerable to predation when they reach the mummy stage and it would be advantageous for them to spend comparatively less time developing prior to mummy formation.

The following experiment tests the hypothesis that success of parasitism may not be equal in all host instars and compares the time from egg to mummy formation in D. rapae and A. fuscicornis.

Method.

Adult aphids were carefully placed on an uninfested Brussels sprouts plant. Twenty-four hours later they were removed leaving first instar aphids on the plant. Each first instar aphid was exposed separately to an experienced D. rapae female which was observed until it had attacked the aphid, the aphid was then transferred to a fresh plant. The parasitised aphids were placed on plants at 20°C in groups of ten and observed daily. The time to mummy formation and the number of mummies formed were recorded. The mummies were removed from the plant with a small piece of leaf intact and placed in a Petri dish. Time to emergence and number of adults emerging were recorded. This was replicated six times and repeated with second, third and fourth instars and adult aphids (4, 6, 8 and 10 days, respectively, after removing the initial adults from the plant).

Similarly, second instar aphids were exposed to D. rapae, as described at the beginning of this chapter. Each aphid was subsequently exposed to a female hyperparasitoid and observed until it had been probed for more than 30 seconds. Aphids were exposed to A. fuscicornis 4, 6, 7, 8 and 10 days after exposure to the primary parasitoid (first, second, third and fourth instars and mummies, respectively). The aphids were kept on a plant at 20°C and the times from egg to mummy formation and egg to emergence and the number of mummies formed and adults (of both species) emerging were recorded. Approximately six groups of ten parasitised aphids were exposed for each parasitoid instar.

Results.

D. rapae larvae developed successfully to the adult stage within all host instars but a lower proportion of attacks by D. rapae on fourth instars and adult aphids resulted in successful parasitism (i.e. emergence of D. rapae adults) than on first, second or third instars (Table 1). Attacks by A. fuscicornis on D. rapae larvae were significantly more successful on second, third and fourth instars than on first instars (Table 1). Although hyperparasitoid females probed D. rapae mummies, all of these developed normally to produce D. rapae adults.

Development of D. rapae larvae from egg to adult in second, third and fourth instars and adults was significantly faster than in first instars. Also, A. fuscicornis developed significantly faster in fourth instars of D. rapae than in first instars (Table 2).

Table 1: Success rate of oviposition in different host instars (analyzed with GLIM).

D. rapae

Host instar	mean proportion of successful attacks	deviance estimate	± S.E.
1	0.56[a]	0.2296	0.2406
2	0.57[a]	0.1069	0.3556
3	0.51[a]	- 0.1295	0.3287
4	0.24[b]	- 0.1382	0.3353
adult	0.35[b]	- 0.8486	0.3359

A. fuscicornis

Host instar	mean proportion of successful attacks	deviance estimate	± S.E.
1	0.49[a]	- 0.3610	0.2716
2	0.77[b]	1.489	0.4404
3	0.63[b]	0.9557	0.4132
4	0.87[b]	0.1796	0.440

Table 2: Time for development from egg to adult in different host instars (days).

D. rapae

Host instar	mean development time	deviance estimate	± S.E.
1	16.28[a]	16.29	0.3833
2	13.67[b]	- 2.619	0.5643
3	14.37[b]	- 1.911	0.5249
4	13.66[b]	- 2.619	0.5643
adult	13.83[b]	- 2.452	0.5643

A. fuscicornis

Host instar	mean development time	deviance estimate	± S.E.
1	15.00[a]	15.00	0.4436
2	14.28[a]	- 0.714	0.6493
3	14.12[a]	- 1.00	0.6493
4	13.25[b]	- 1.75	0.6493

Table 3: Time from egg to emergence in preferred host instars (days)

	D. rapae	A. fuscicornis
mean time	14.07	13.68
S.E.	± 0.96	± 1.07

p = N.S.

Table 4: Time from egg to mummy formation in preferred host instars (days)

	D. rapae	A. fuscicornis
mean time	8.86	4.12
S.E.	± 0.81	± 1.29

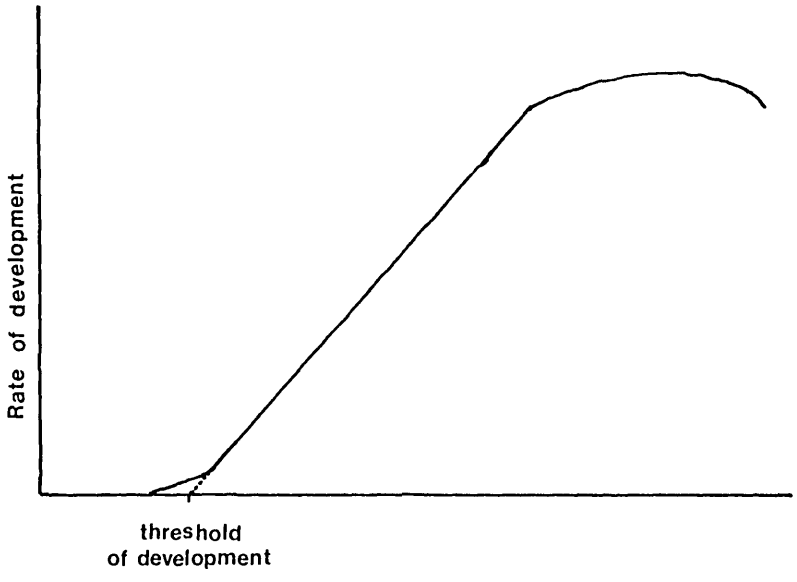
$p < 0.001$

There were no significant differences in the time taken for development from egg to adult by D. rapae and A. fuscicornis in their preferred host instars (second and third, and third and fourth, respectively) (Table 3). On average, however, D. rapae took twice as long to develop from the egg to the mummy stage as A. fuscicornis ($p<0.001$) (Table 4).

3.4 Rate of development of D. rapae and A. fuscicornis.

Traditionally, the development period of insects has been measured as a thermal constant which is an expression of the amount of heat required for an insect to complete a particular stage of development (Howe 1967, Andrewartha and Birch 1954, Messenger 1959, Campbell et. al. 1974). The relationship between temperature and rate of development is described by a logistic curve (Andrewartha and Birch 1954, Lamb 1961, Campbell et. al. 1974) as shown in Figure 2. Rate of development is frequently expressed as the reciprocal of the duration of the stage being studied and may be multiplied by 100 to give percent development per unit time. The reciprocal scale cannot be used for comparisons between the same stage in different species or different stages in the same species, however, as the slope of the curve is a function of the duration of the particular stage under consideration (Andrewartha and Birch 1954). Development is considered to cease below a certain theoretical temperature (the threshold of development) which is found by extrapolating the linear portion of the graph.

Figure 2: Relationship between temperature and rate of development



In practice, the relationship is not linear near the threshold and slow development may continue below this temperature (Messenger and Fitters 1959). Similarly, near the upper lethal limit development is slower than expected (Scopes and Biggerstaff 1977). The linear model is, however, a valid approximation when temperatures normally experienced by the insects in the field are within the linear portion of the curve (Raworth et. al 1984).

The product of the mean temperature above the threshold and the time of development is constant within the linear portion of the graph. This is the thermal constant (day °C) and is a characteristic of individual species. It may be determined by subtracting the calculated threshold temperature from the mean experimental temperature and multiplying by the number of days required for development (Andrewartha and Birch 1954, Scopes and Biggerstaff 1977).

The aim of this experiment was, therefore, to determine the developmental thresholds and thermal constants for D. rapae and A. fuscicornis from the egg to the first instar as a means of comparing their rates of development.

Method.

Thirty aphids (second- to third-instars) were exposed individually to a D. rapae female. They were observed until oviposition had taken place and then transferred to an uninfested Brussels sprouts plant which was placed in Watkins-Doncaster cage. The aphids were kept at 15, 20 or 25°C and dissected after 48 hours.

These temperatures were chosen as they fall between the lower and upper developmental limits for D. rapae (Lamb 1961, Akinlosotu 1973, Raworth et. al. 1984). This was repeated and the aphids were dissected 54, 60, 66, 72, ... hours after oviposition until the median development time was determined. (Hochberg et. al. 1986).
This was repeated using an A. fuscicornis female and parasitised aphids.

Results.

Figure 3 shows the relationship between rate of development and temperature for both species. It can be seen that A. fuscicornis has a faster development rate at all temperatures. The threshold temperatures for development were found by extrapolation of the regression line (see Table 5) and the thermal constant was calculated as follows:

Thermal constant = (mean experimental temperature - threshold temperature) x hours required for development at mean temperature

The thermal constants are indicated in Table 5. Although the developmental thresholds for both species were the same, the thermal constant for A. fuscicornis was less than that of D. rapae due to the faster developmental rate of the former.

Figure 3: Determination of thermal constants

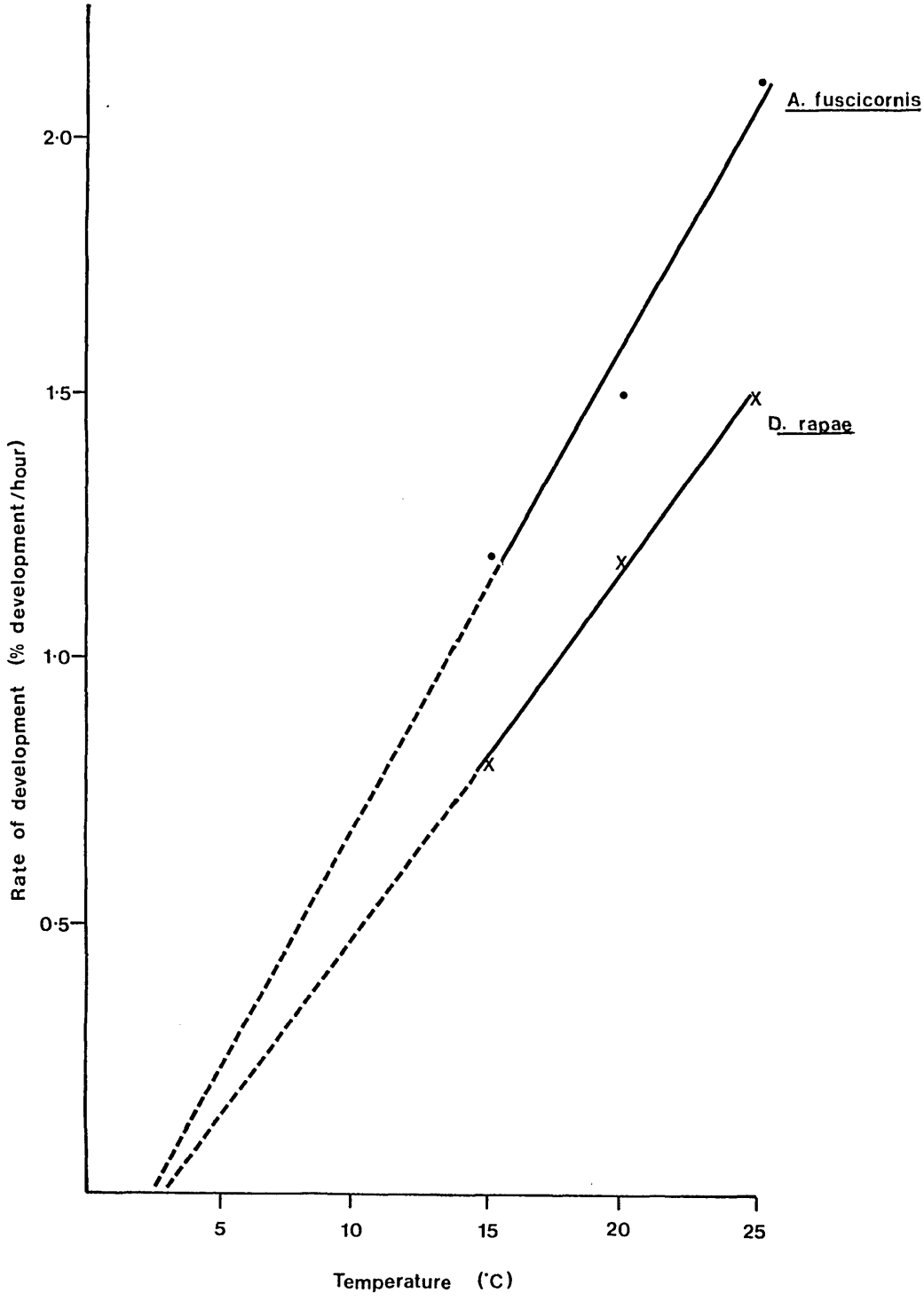


Table 5: Calculation of thermal constants.

D. rapae

threshold of development = 2.5°C

mean temperature = 20°C

temperature above threshold = 17.5°C

development time at 20°C = 84.75 hours

thermal constant = 17.5 x 84.75

= 1483.12 h °C

A. fuscicornis

threshold of development = 2.5°C

mean temperature = 20°C

temperature above threshold = 17.5°C

development time at 20°C = 62.50 hours

thermal constant = 17.5 x 62.50

= 1093.75 h °C

DISCUSSION.

In comparison to the values of 13.9 and 4.9 days and 5.83 and 2.99 eggs/female per day, recorded for the longevities and fecundities of A. fuscicornis and D. rapae, respectively, Hafez (1961) recorded a mean lifetime fecundity of 83 eggs per D. rapae female and a longevity of 8.64 days, Akinlosotu (1973) recorded a mean longevity of 4.8 days and Atwal et. al. (1967) a longevity of 5.1 days. Broussal (1966) recorded a maximum longevity of 13 days for D. rapae and 34 days for A. fuscicornis (as Charips ancylocera) with females of both species beginning to oviposit directly after emergence.

It seems logical to assume that the host population of D. rapae is more abundant than that of A. fuscicornis (see Chapter 5 for details of host distributions). It is also likely that it is more accessible. Firstly because hyperparasitoids must find parasitised individuals within a healthy population and, secondly, because of the behaviour of A. fuscicornis, which must probe both parasitised and unparasitised aphids to detect parasitoid larvae. Price (1972) suggested that the accessibility of a host may be inferred from the length of the parasitoid's ovipositor. Parasitoids attacking exposed hosts have short ovipositors while those with concealed hosts have long ovipositors. Price demonstrated that there is a decreasing trend in the number of ovarioles per ovary with an increasing ratio of ovipositor to body length. The fact that D. rapae has an extremely reduced ovipositor (Broussal 1966) while in A. fuscicornis the ovipositor is much longer, despite this

parasitoid's smaller body size, also supports the idea that D. rapae searches for hosts which are more easily accessible than those of A. fuscicornis.

Furthermore, as D. rapae belongs to a lower trophic level than A. fuscicornis, its larval food supply must have a higher energy content than that of the hyperparasitoid, so less energy may be available to A. fuscicornis (possibly leading to its smaller body size). Both species were observed to feed on aphid honeydew as adults, but, unlike several other parasitic and hyperparasitic species (Muesebeck and Dohanian 1972, Clausen 1940, Askew 1971), neither feed directly on their hosts. Feeding on honeydew is known to increase the longevity and fecundity of many insects (Zoebelein 1956) and it is likely that this applies to A. fuscicornis and D. rapae.

These results appear to disagree with Price's (1972, 1974, 1977) hypothesis that ovariole number and hence potential fecundity are related to the abundance and accessibility of hosts. D. rapae appears, upon dissection, to have only one ovariole in each ovary, while the hyperparasitoid has ten ovarioles per ovary. It is likely, however, that D. rapae is an exception to Price's hypothesis, as its ovaries are a modified form. Other members of the Aphididae (eg. Aphidius) are known to lack ovarioles although there is some differentiation of the follicles within the ovaries (Richards and Davies 1977) and it seems likely that D. rapae belongs to this group.

D. rapae is a pro-ovogenic species (i.e. it emerges with a full complement of mature eggs) while A. fuscicornis is intermediate between a pro-ovogenic and a synovogenic species as it emerges with some mature eggs, but more develop during the wasp's lifetime (Broussal 1966).

It seems likely, therefore, that D. rapae is well adapted to exploit large aphid colonies soon after emergence as a large number of hosts could be parasitised in quick succession. The hosts of A. fuscicornis occur in smaller groups, however, so it is obviously an advantage for the hyperparasitoid to mature only a few eggs at a time, thus saving energy and avoiding wastage of eggs.

The greater longevity of the hyperparasitoid in comparison to the parasitoid may compensate for the greater handling time involved in distinguishing parasitised and unparasitised aphids before oviposition can occur (see Chapter 4).

Attempts by D. rapae at parasitism may be less successful in fourth instar and adult aphids than in earlier instars because older aphids are protected to a greater extent by their waxy covering. It is possible that the 'preference' shown by D. rapae for the second and third instars of its host, as recorded by previous authors (Hafez 1961, Broussal 1966) is due to unsuccessful parasitism rather than a behavioural preference by the parasitoid for particular host instars.

Parasitism by A. fuscicornis was less successful in the first than in the other larval host instars. It is possible that, oviposition by A. fuscicornis in first instars of D. rapae was unsuccessful because the larva was small in

comparison to the aphid and was therefore, difficult for the hyperparasitoid to locate. Also, parasitoid larvae at this stage of development are fairly active in comparison to later instars (Couchman and King 1977) and may be able to move away from the hyperparasitoid's ovipositor. Although there was no significant difference in the times taken by D. rapae and A. fuscicornis to develop from the egg to the adult stage, D. rapae spent more time before reaching the mummy stage. This species is, therefore, probably more vulnerable to predation than A. fuscicornis, which spends the greater part of its larval development within a mummy. (Also, D. rapae is subject to an additional mortality factor in comparison to A. fuscicornis). The ability to escape predation in this way is probably one of the main advantages which A. fuscicornis gains from the hyperparasitic mode of life.

The value of the developmental threshold found for D. rapae for egg to first instar was similar to that found by other authors for egg to adult (Table 6). Developmental thresholds and thermal constants are modified by acclimatisation, variations in temperature during exposure, environmental factors other than temperature and stage of development of the individual (Messenger 1959). Raworth et. al. (1984), however, found that there was no significant difference between the developmental thresholds for the different instars of B. brassicae.

Thresholds also differ between different aphid species and their parasitoids and between populations of one species from different areas (Campbell et. al. 1984).

Table 6: Developmental thresholds for *B. brassicae* and *D. rapae* (egg to adult)

B. brassicae	*D. rapae*	Author
6.5	6.5	Hafez, 1961
5	7	Hughes, 1963
3.2	2.7	Akinlosotu, 1973
7.1	3.5	Campbell *et.al.*, 1974
4.7	4.9	Campbell *et.al.*, 1975
6.7	-	Raworth *et.al.*, 1984

(This probably causes some of the variation between the developmental thresholds recorded by different authors in Table 6). The cabbage aphid, for example, has relatively high developmental thresholds in warm climates and lower thresholds in colder areas (Campbell et. al. 1974). Generally, developmental thresholds of parasitoids are higher than those of their hosts (Campbell et. al. 1984, Campbell and Mackauer 1975), and in the spring the build-up of the parasitoid population will be delayed until average temperatures increase and the host population is well established. This is not, however, always true of D. rapae and B. brassicae (Table 6), and may explain the poor synchronisation of the parasitoid with its host population as observed by Chua (1978). It might be expected on this basis that A. fuscicornis would have a higher developmental threshold than D. rapae (van den Bosch 1981), especially as there is a lag between the emergence of these two species in the spring (Hafez 1961, Chua 1978). This was not, however, shown to be the case as the developmental thresholds of the parasitoid and hyperparasitoid are the same. Interestingly, the hyperparasitoids, Dendrocerus niger and Asaphes lucens have higher developmental thresholds than their host Aphidius smithi (Campbell et al. 1974, Campbell and Mackauer 1975).

It has been shown for some species that development is slower at constant temperatures than at fluctuating temperatures with the same mean (Messenger and Flitters 1959, Messenger 1964). Generally, however, the effects of fluctuating temperature and the corresponding constant temperature on the rate of development are equivalent within

the range where the relationship between temperature and the rate of development is linear (Andrewartha and Birch 1954, Messenger 1959, Gilbert and Gutierrez 1973, Campbell et al. 1974, Hochberg et al. 1986). At lower temperatures development is accelerated over that which would be predicted on the basis of constant temperature conditions while at higher temperatures development is retarded. At intermediate temperatures, however, development proceeds at approximately the same rate as would be expected relative to constant temperature regimes (Messenger 1959.)

In summary, A. fuscicornis and D. rapae have different reproductive strategies, D. rapae has a large number of mature eggs available but a short longevity, while A. fuscicornis has fewer eggs available at any time but is longer lived. D. rapae, therefore, appears to be adapted to exploit a host population which occurs in large colonies while the hyperparasitoid is adapted for a host which occurs in smaller, more widespread groups. D. rapae probably also has a higher potential fecundity in order to compensate for the greater vulnerability of immature stages to predation. A. fuscicornis has a faster developmental rate in the egg to first instar and this probably contributes to the shorter time spent before the developing larva is protected by a mummy, so minimising the risks of predation.

4. SEARCHING EFFICIENCY

In this chapter basic parameters such as searching efficiency and handling time were determined for both species from functional response experiments as a means of comparing basic foraging behaviour. The study of parasitoid searching efficiency is continued in the second part of the chapter in experiments which relate rates of parasitism to light intensity and temperature.

4.1 Functional responses.

The functional response is defined as the response of a parasitoid to changes in host density in terms of the number of hosts attacked (Holling 1959 a, b). Three types of functional response are common in the literature on insect parasitoid population dynamics. The first is described by a linear increase in the number of hosts parasitised to a maximum when the parasitoid runs out of eggs and/or time. A type II response takes into account the reduction in time available for searching for hosts due to the time needed for oviposition and post-ovipositional cleaning and resting (handling time). This response rises to a plateau at a continually decreasing rate and has been described by Rogers (1972b) in the 'random parasite equation' as:

$$N_a = N_t \left[1 - \exp.\left(\frac{-a' T P_t}{1 + a' T_h N_t}\right)\right]$$

where N_a, the number of hosts attacked, is based on the Poisson distribution of potential encounters, N_t is the number of hosts present, a' is the instantaneous search rate, T is total time available, P_t is number of parasitoids

present and T_h is handling time. This assumes random search for hosts so allowing for their depletion during the course of foraging.

Type III functional responses are described by a sigmoid curve and arise when one or more components of searching activity are dependent on host density, contrasting with the random parasite equation in which a' and T_h are constant at all host densities (Hassell et al. 1977).

Functional response curves are a characteristic feature of parasitoid - host interactions and are important in determining the individual effectiveness of parasitoids and hence the level of parasitism inflicted on a host population (Hassell and Waage 1984). Mathematical models of the population dynamics of host-parasitoid-obligate hyperparasitoid systems predict that, in order for such a system to be stable the searching efficiency of the hyperparasitoid is likely to be greater than that of the primary (i.e. the ratio of a_2 (the hyperparasitoid search rate) to a_1 (the primary search rate) is likely to be greater than 1 (Beddington and Hammond 1977, May and Hassell 1981)).

It is important to realise, however, that the values for the parameters derived from functional response experiments under laboratory conditions may not be the same in a more complex field situation. A group of hosts placed on a small leaf disc in a Petri dish may be considerably easier for a parasitoid to locate than the same hosts scattered over a plant in the field (on which non-host species may also be present). Also in laboratory experiments, temperature, light

intensity and wind speeds will usually be constant over the experimental period, while in the field the changing nature of these factors may be reflected in a fluctuating parasitoid search rate. When the search rate of a parasitoid is reduced at low host densities due to increased complexity of the system or the use of non-preferred host instars or species a Type III, rather than a Type II, response may be obtained. Cheng (1985) demonstrated that the type of functional response exhibited by D. rapae females depends on the aphid instar. Also, Taylor (1988) showed that the type of functional response found for Bracon hebetor Say did not differ significantly between different sizes of two host species, Agnasta kuhniella and Plodia interpunctella, but were very significantly different between these two species. In experiments on parasitism where all the host densities were present simultaneously, Jones and Hassell (1988) obtained similar patterns of parasitism for Trybliographa rapae (Westw.) with its host, Delia radicum (L.), in both the laboratory and field, and with hosts on small discs and whole plants.

The apparent absence of a stabilising density dependent functional response in many parasitoids may be due to experimental procedures in which the number of hosts found at low densities is higher than in a field situation where parasitoids leave sites after searching unsuccessfully for some time (van Lenteren and Bakker 1976). Despite these shortcomings, functional response curves provide a useful basis for comparing the searching processes of D. rapae and A. fuscicornis.

Method.

(a) D. rapae

Approximately ten adult cabbage aphids were taken from the main culture and placed in a clip cage on the upper leaf of a small Brussels sprouts plant (9 to 10 leaves) in a Doncaster-Watkins cage. Twenty-four hours later the adult aphids were removed and the first instar nymphs were allowed to develop for five days, after which time they had reached the second to third instar (Chua 1975). This aphid instar was used because previous authors (Hafez 1961, Akinlosotu 1973) have found D. rapae to prefer it. The clip cage and any excess nymphs were removed so that a patch of four aphids was left on one leaf of the plant. A newly emerged (during the previous 48 hours) mated D. rapae female, which had been fed on honey, was allowed to forage in the cage for 24 hours. After a further three days the aphids were dissected and the number which had been parasitised was recorded.

This procedure was repeated using aphid densities of 8, 16, 32, 64 and 128/plant. Approximately five replicates were carried out at each density.

(b) A. fuscicornis.

First instar B. brassicae nymphs were obtained as described above and placed on leaf discs in groups of ten in individual Petri dishes. One D. rapae female was introduced to each dish and allowed to attack the aphids for 24 hours. The aphids were then placed on one upper leaf of a Brussels sprouts plant within a clip cage. Three days later, when the

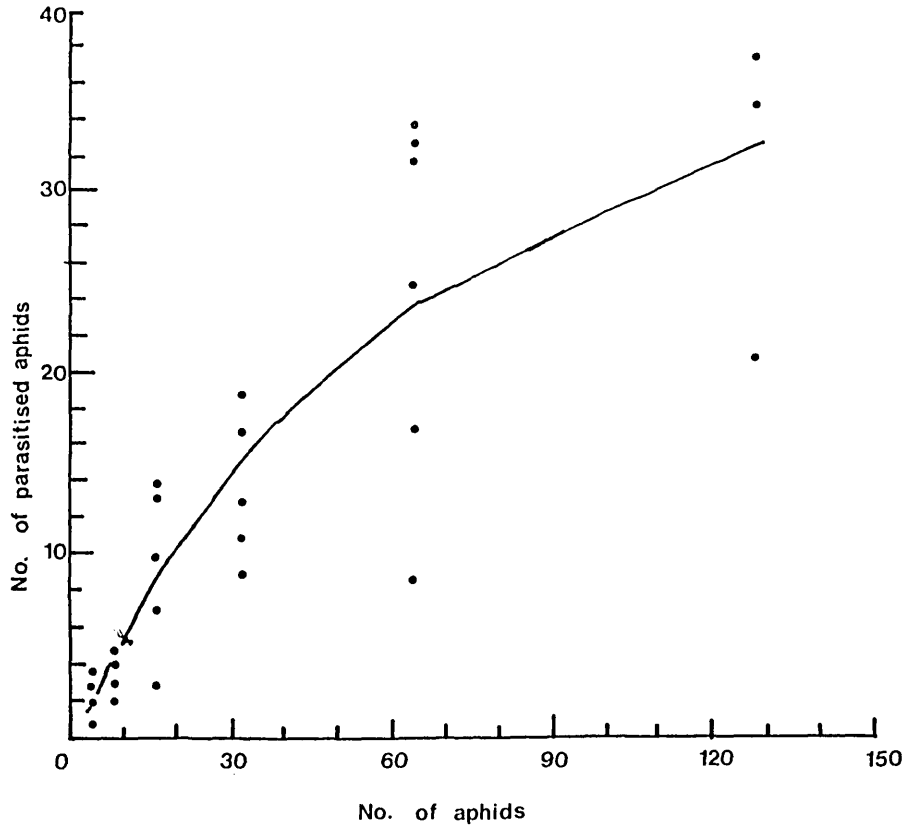
aphids were in the second to third instar and the parasitoid larvae were in the first to second instar, the clip cage was removed and a fed A. fuscicornis female was introduced. The wasp was allowed to forage for 24 hours. After allowing three days for the hyperparasitoid larvae to develop, the aphids and parasitoid larvae within them were dissected. As it is difficult to obtain a group of aphids all of which are known to be parasitised, it was not possible to replicate all the host densities. Instead a range of densities from 2 to 53 were exposed to the hyperparasitoid.

Results.

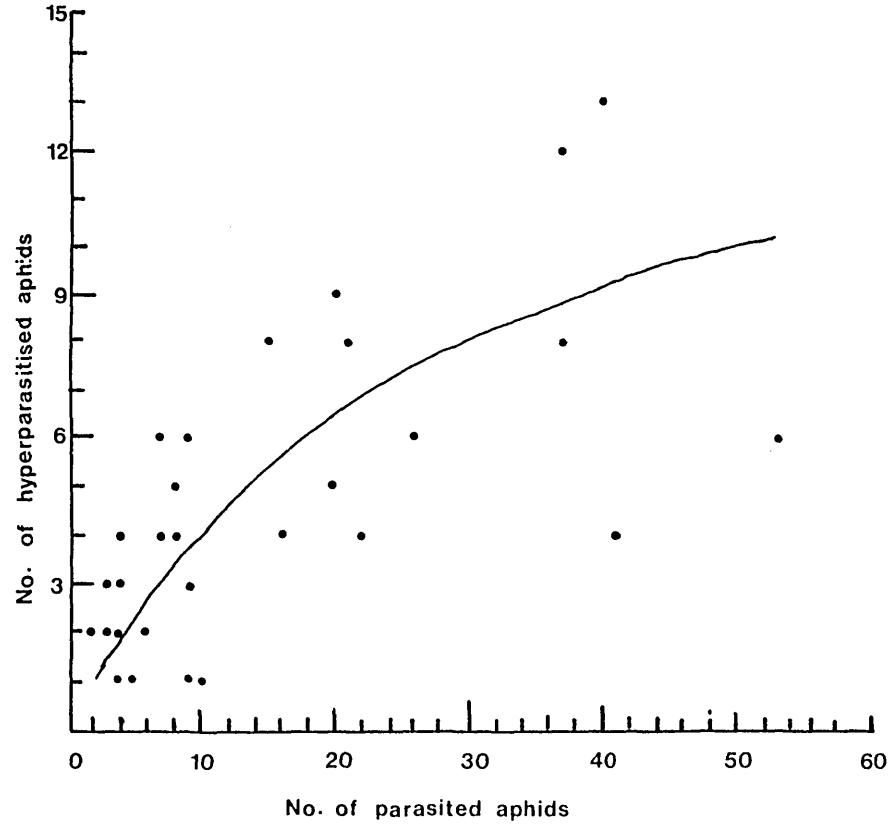
Although some authors (eg. Trexler et al. 1988) have suggested that analyses using angular transformation and logit analysis are most effective at determing functional responses, in this analysis the conventional method of fitting the model described by the random parasite equation directly to the untransformed data using a non-linear least squares technique was employed. A significant fit was obtained for the data for both species (r^2 = 0.796 for D. rapae and 0.554 for A. fuscicornis ($p<0.01$)) and estimates of a' and T_h were calculated (see Figure 4 and Table 7). There was no significant difference between the values of a' obtained for D. rapae and A. fuscicornis, but the hyperparasitoid had a significantly ($p<0.05$) longer handling time than the parasitoid.

Figure 4 Functional responses

(a) D. rapae



(b) A. fuscicornis



4.2 Response of D. rapae and A. fuscicornis to temperature and light intensity.

The number of hosts attacked per parasitoid is directly related to the total time available for searching (see equation 1). Total time available is determined not only by the overall adult longevity of a species but also by the relationship between searching activity and environmental factors such as temperature and light intensity. It was shown previously that the long handling time of A. fuscicornis is compensated by its long adult life-span. This compensation could be augmented by an ability to search at low temperatures and / or light intensities.

The ability to detect hosts in the dark obviously depends on the importance of visual cues in the host selection process. Vision, as a component of host location, has occasionally been demonstrated in insect parasitoids, particularly in conjunction with host movement (Weseloh 1981). Perilitus coccinellae (Schrank), for example, is attracted to its hosts (adult coccinellids) by their movement and odour, size and colour of the moving object are further stimuli to host recognition (Richerson and DeLoach 1972). Similarly, Drino bohemica Mesn., a tachinid parasitoid of sawfly larvae, is attracted to moving feathers (resembling its hosts in shape) in the presence of host odour (Monteith 1956).

Table 7: Values of a' and T_h derived from the random parasite equation (± S.E.) (cage size/hour and hours, respectively)

	a'	T_h	a_2/a_1
D. rapae	0.044 ± 0.013	0.456 ± 0.089	0.787
A. fuscicornis	0.034 ± 0.014	1.590 ± 0.435	

The following experiment was carried out to investigate the ability of D. rapae and A. fuscicornis to search for and attack their hosts at different temperatures and in the presence and absence of light.

Method.

This experiment had a two-way ANOVA design. Twenty aphids were placed on a leaf disc in each of six Petri dishes and allowed to settle for 30 minutes. After this time three of the dishes were covered with aluminium foil to exclude light and one experienced, mated D. rapae female was introduced to each dish. Two dishes (one covered and one uncovered) were left at each temperature (10, 15 or 20°C) for one hour, after which time the parasitoid was removed. The aphids were kept at 20°C for three days and then dissected to determine the number which had been parasitised. This was replicated ten times at each temperature and light treatment.
This procedure was repeated using 20 parasitised aphids and one experienced, mated A. fuscicornis female per dish. Ten replicates were again carried out for each treatment combination.

Results.

A two-way analysis of variance revealed that, for D. rapae there is no significant interaction between the two treatments; the main effects can, therefore, be considered separately. There is a significant ($p<0.01$) difference between the number of aphids parasitised in at least two of the temperatures and between the number of aphids

parasitised in the presence and absence of light ($p<0.01$). As can be seen from Table 8, significantly ($p<0.05$) more aphids were parasitised at 20 than at 15 or 10°C. Also significantly ($p<0.05$) more were parasitised in the light than in the dark. When data for A. fuscicornis were analysed a significant ($p<0.05$) interaction between the two treatments was found (i.e. the hyperparasitoid responds differently to different temperatures in the presence and absence of light). It is invalid, therefore, to compare the main treatment effects directly, rather a comparison should be made between the different treatment combinations. The results for A. fuscicornis are summarised in Table 9. Significantly ($p<0.05$) fewer aphids were hyperparasitised at 10°C than at 15 or 20°C in the light.

There was, however, no significant difference between the number parasitised at 15 and 20°C either in the presence or absence of light. There was no significant difference in the number hyperparasitised in the dark at different temperatures. The number hyperparasitised in the light was significantly ($p<0.05$) different from that hyperparasitised in the dark at 15 and 20°C. At 10°C there was no significant difference.

Table 8: Number of aphids parasitised at different temperatures and light intensities.

	10°C	15°C	20°C	means
light	3.10	5.60	8.10	5.60
dark	0.10	0.50	1.90	0.83
				95% LSD = 1.49
means	1.60	3.05	5.00	95% LSD = 1.83

95% LSD for treatment combinations = 1.106

Table 9: Number of aphids hyperparasitised at different temperatures and light intensities.

	10°C	15°C	20°C
light	0.10	2.30	1.80
dark	0	0	0.50

95% LSD for treatment combinations = 1.106

Discussion.

Both Type II and Type III functional responses have been obtained for D. rapae and A. fuscicornis by previous authors. Akinlosotu (1973) found a Type II response for D. rapae using 'half-grown' aphids. Chua (1979) obtained Type II responses of both species using their preferred host stages. Cheng (1985) found both Type II and Type III responses for D. rapae using second and third, and first and fourth B. brassicae instars, respectively. Pandey et al. (1984) obtained a Type III functional response with D. rapae and third instar nymphs of the mustard aphid, Lipaphis erysimi, possibly a less preferred host species than B. brassicae.

These results are similar to those for other parasitoid species, where both Type II and Type III responses have been derived under different experimental conditions (van Lenteren and Bakker 1976, 1978, Hassell et al. 1977).

The hypothesis that the searching efficiency of the hyperparasitoid is likely to be greater than that of the primary in order for a host-parasitoid-obligate hyperparasitoid system t be stable (Beddington and Hammond 1977, May and Hassell 1981) is supported by the examples which are summarized in Table 10. This does not always apply to the D. rapae - A. fuscicornis relationship. Although Hammond (1979) found the searching efficiency of A. fuscicornis to be greater than that of D. rapae with a ratio of 9.4, Chua (1979) found a value of search rate fc the hyperparasitoid which was less than that of the parasitoid. The present study confirms the latter result as $a_2/a_1 = 0.785$ (Table 7).

Table 10. Ratio of searching efficiency of parasitoids and hyperparasitoids (a_1 and a_2, respectively) (after Hassell, 1978).

Host	Parasitoid	Hyperparasitoid	$a_2:a_1$	Author
Operophtera brumata	Cyzencis albicans	Phygadeuon dumetorum	22.4	Hassell 1969
Coccus hesperidium	Microterys flavus	Marietta exitiosa	3.4	Kfir et.al 1976
Coccus hesperidium	Microterys flavus	Cheiloneurus paralia	4.4	Kfir et.al 1976
Pristiphora erichsonii	Olesicampe benefactor	Mesochorus dimidiatus	1.0	Ives 1976

Differences in the experimental set-ups used might account for the different values for the ratio of hyperparasitoid:parasitoid searching efficiency, as A. fuscicornis and D. rapae may respond differently to changes in experimental set-up. This seems unlikely, however, as all three experiments were carried out on a Brussels sprouts plant within a Doncaster-Watkins cage. Chua trimmed the leaves of the plants so reducing their surface area and used second to third instar B. brassicae nymphs as hosts for D. rapae and fourth instar D. rapae larvae as hosts for A. fuscicornis. There may also have been differences in factors such as temperature, relative humidity and photoperiod. A. fuscicornis was found to have a much greater handling time than D. rapae, probably because the hyperparasitoid must detect parasitoid larvae within the aphid haemocoel before oviposition and probes both parasitised and unparasitised aphids. The shorter handling time of D. rapae increases the time available for search and the likelihood of locating further hosts. It is misleading, however to consider handling time in isolation as many parasitoid species compensate for a long handling time with greater longevity (Hassell 1978). Handling time, which may have a negative effect on stability, will be of minor importance in this respect if $T^h/T << 1$ (Hassell and May 1973). This was shown to be the case for D. rapae and A. fuscicornis as values of 0.0038 and 0.0048, respectively, were calculated for the ratio of T^h to T (using mean values of longevity calculated in Chapter 3). It appears, therefore, that the long handling time of A. fuscicornis is compensated by the

long adult life-span of this species, which may in turn be an adaptation to the relative ease of locating its hosts.

For both species there is some evidence that searching activity is reduced at low temperatures and light intensities. The activity of D. rapae females increases with temperature. Akinlosotu (1973), in a similar experiment, showed that temperature affected the host-finding activities of D. rapae females, reaching an optimum at 20°C, above which activity decreased. Only a few aphids were attacked in the dark but this number was again greater at higher temperatures. In A. fuscicornis the situation is more complicated, but both temperature and light appear to affect activity. The hyperparasitoids become almost inactive at 10°C, even in the presence of light. There was no significant difference in the number of hosts attacked in the dark at different temperatures. It appears, therefore, that in the absence of light the number of hosts attacked by D. rapae is greatly reduced, while the number attacked by A. fuscicornis is negligible. This may be because these parasitoids become inactive in the dark or because visual cues have an important role at this stage of the searching process. Both species respond to an increase in temperature in the light by an increase in the number of hosts attacked. Presence or absence of light is, however, known to be unimportant to the searching activity of various other parasitoid species. The hyperparasitoids of Apanteles melanoscelus were found to oviposit almost as readily in darkness as in daylight (Muesebeck and Dohanian 1927). Rotheray (1979, 1981) tested five parasitoids of

aphidophagous syrphid larvae and found that there was no significant difference in the number of larvae parasitised in light or dark conditions, although visual cues may have a minor role in host selection.

5. AVOIDANCE OF SUPERPARASITISM BY *D. rapae* AND *A. fuscicornis*.

Superparasitism was first defined by Fiske (1910) as occurring when an individual host is attacked by two or more primary parasitoid species or by one species, more than once. Usually, however, superparasitism is defined as the act of laying an egg in a host which is already parasitised by a parasitoid of the same species (Waage 1986, Hubbard *et al.* 1987), while parasitism of one host by parasitoids of different species is known as multiparasitism. Although superparasitism has been recorded frequently among the parasitic Hymenoptera (Waage and Godfray 1985) the ability of parasitoids to recognise hosts already parasitised by themselves or by conspecifics (i.e. host discrimination) is also a common phenomenon (Salt 1961, van Lenteren 1981, Bakker *et al.* 1985). The avoidance of superparasitism involves two distinct faculties, the ability to refrain from oviposition when suitable hosts are not available and the ability to discriminate between healthy and parasitised hosts (Salt 1961).

As *D. rapae* and *A. fuscicornis* are known to have different potential fecundities, longevities and host distributions, it is of interest to consider the incidence of superparasitism in their populations. Also, the searching efficiency of *A. fuscicornis* could be increased if it could distinguish not only parasitised and hyperparasitised aphids but also unparasitised aphids which have and have not been previously probed.

Collection of data on host discrimination in the field is time consuming (van Lenteren et al. 1976), the following laboratory experiment was, therefore, carried out to consider host discrimination in D. rapae and A. fuscicornis.

Method.

(a) A. fuscicornis.

As parasitoids which have not previously encountered unparasitised hosts superparasitise more frequently than 'experienced' individuals (van Lenteren 1976), the wasps used were standardised by placing them in a Petri dish with twenty hosts (unparasitised aphids for D. rapae, parasitised aphids for A. fuscicornis) for one hour, two to three days before the experiment.

Ten aphids which had been parasitised five to six days previously (as described in Chapter 3) were placed on a leaf disc in a Petri dish and allowed to settle for 30 minutes. A map of the leaf disc was drawn and the position of each aphid was marked on it; in this way the number of times a hyperparasitoid encountered any aphid could be recorded. One standardised A. fuscicornis female was introduced to the Petri dish. The observations were recorded using a 'Rustrak' event recorder: number of aphids which were probed the first time they were encountered, probing time, number of previously probed aphids which were probed on subsequent encounters and probing times for subsequently encountered aphids. A hyperparasitoid was considered to have 'encountered' an aphid if it touched it with its antennae. The observations stopped when the wasp had been off the leaf for more than one minute.

The above procedure was replicated with ten hyperparasitoids and the aphids were dissected two days later to detect superparasitism.

This was repeated using ten parasitised and ten unparasitised aphids, the unparasitised aphids were distinguished by marking their hind legs with a water-soluble marker. In addition to the above observations the following were recorded: number of unparasitised aphids which were probed on the first encounter, number which were probed on subsequent encounters and the respective probing times.

(b) D. rapae.

A similar experiment was carried out using standardised D. rapae females and ten unparasitised aphids. Number of aphids attacked following the first encounter, number attacked on subsequent encounters, number of jabs per aphid on each encounter and time spent attacking each aphid were recorded. The experiment was replicated ten times and the aphids were dissected two or three days later.

Results.

An arcsin transformation was used to calculate 95% confidence intervals for the mean proportion of aphids which were probed on first and subsequent encounters. A. fuscicornis females probed significantly ($p<0.05$) more aphids on the first than on subsequent encounters (Table 11). This was also true when unparasitised aphids were present ($P<0.05$).

Table 11: Avoidance of superparasitism by *A. fuscicornis* (95% C.I. for mean proportion probed were calculated using an arcsin transformation).

(a) with parasitised aphids only.

	1st encounter	subsequent encounters
mean proportion probed	0.985	0.16
upper and lower limits	0.93 - 0.99	0.037 - 0.346
mean probing times (± 95% C.I.)	137.74 ± 30.22	43.89 ±27.35

(b) with both parasitised and unparasitised aphids.

	parasitised aphids		unparasitised aphids	
	1st encounter	subsequent encounters	1st encounter	subsequent encounters
mean proportion probed	0.973	0.215	0.853	0.241
upper and lower limits	0.90 - 0.99	0.07 - 0.41	0.65 - 0.98	0.05 - 0.51

Aphids were probed for significantly shorter ($p<0.05$) times on subsequent than on first encounters. Interestingly, unparasitised aphids were also significantly ($p<0.05$) less likely to be probed on subsequent than on first encounters. D. rapae females also probed significantly ($p<0.05$) fewer aphids on encountering them for the second or third time than on the first encounter (Table 12). There was no significant difference, however, between the number of stabs in first and subsequently encountered aphids or between the length of time spent attacking these aphids.

On dissecting the aphids from all three experiments, it was found that, when only parasitised aphids were exposed to A. fuscicornis, 5.88% of those that were parasitised contained more than one hyperparasitoid larva. When unparasitised and parasitised aphids were exposed to the hyperparasitoid together no superparasitism was detected.

D. rapae showed a lower avoidance of superparasitism with 40% of the aphids which were parasitised containing more than one parasitoid larva.

Table 12: Avoidance of superparasitism by *D. rapae*

(95% C.I. for mean proportion probed were calculated using an arcsin transformation).

	1st encounter	subsequent encounters
mean proportion attacked	0.933	0.676
upper and lower limits	0.85 - 0.98	0.475 - 0.848
mean no. jabs/aphid (± 95% C.I.)	2.40 ± 0.36	2.32 ± 0.75
mean attack time (secs ± 95% C.I.)	12.76 ± 6.24	9.84 ± 4.05

Discussion.

D. rapae females, therefore, have a greater tendency to parasitise hosts twice than A. fuscicornis. Females of the primary parasitoid are known to lay only one egg per oviposition (Hafez 1961), but two or more females frequently attack one host simultaneously (although not in this experiment as only one female was present at a time). This has not been recorded for A. fuscicornis, probably because there is insufficient room for more than one female in an aphid at a time. Matjeko and Sullivan (1980), however, often observed four or five females of Alloxysta megourae ovipositing at the same time in one aphid. All the hyperparasitoids probed simultaneously for the primary parasitoid larva and invariably, although several eggs were laid, only one adult emerged from each host. Superparasitism also occurs in Alloxysta pleuralis, but no more than one female has been observed ovipositing at a time, even if two females encounter the same aphid at the same time (Singh and Srivastava 1987). Within the confines of this experiment, it is possible that superparasitism arises from: (a) a female re-encountering a host before a mark has become apparent, (b) an inability to distinguish parasitised hosts or (c) an increasing tendency to oviposit despite encountering only parasitised hosts for sometime. This explanation is unlikely as parasitoids were free to leave the patch. Both external and internal markers occur among other parasitoid species. In scelionids and trichogrammatids an external marker is applied to the host with the ovipositor.

These external markers may only persist for a few hours, suggesting that the chemical used is unstable or slightly volatile (Strand 1986). Dufour's gland is the source of an external marker in various parasitoid species (Hubbard et al. 1987).

Internal marking could be caused by the injection of a substance during oviposition, substances released by the egg after oviposition, a change in the concentration of body fluids or formation of new substances by the host as a reaction to parasitism (van Lenteren 1976). Internal markers are often latent, becoming apparent to the parasitoid several hours after oviposition and persisting throughout development (Strand 1986).

In V. canescens the parasitoid can discriminate between unparasitised and parasitised hosts shortly after oviposition due to a specific chemical marker which is injected when the egg is laid. This chemical has been shown to originate in Dufour's gland and its activity declines with time (Hubbard et al 1987). On the other hand, in A. nigripes the relatively long time threshold for discrimination suggests that an egg or parasitoid injected substance is likely to be the marker. The two or more hours required for the marker to become apparent would, however, probably be enough time for biochemical changes to occur within the host haemolymph (Cloutier 1984).

Viruses which are transmitted by parasitoids to their hosts have been implicated as possible mediators in this process (Stoltz and Vinson 1979). Changes in the host could also be triggered by the insertion of the ovipositor and/or injected

material independently of oviposition success.
Alternatively, the stimulus for discrimination could be a marker which is gradually released by the parasitoid egg (Cloutier et al. 1984).
As A. fuscicornis avoided previously encountered hosts after antennal contact in approximately 80% of encounters and as previously encountered hosts were probed for a shorter time, it seems likely that the hyperparasitoid can detect both an internal and an external mark in hyperparasitised aphids. Previously probed unparasitised aphids are also avoided so it is possible that at least the external mark occurs as a result of probing rather than oviposition.
D. rapae avoided approximately 40% of parasitised aphids after antennal contact, suggesting that there may be an external mark. The presence of an internal mark is doubtful, however, as parasitoid females spent the same length of time attacking parasitised and unparasitised aphids and also stabbed them the same number of times. It is possible that this avoidance of superparasitism by D. rapae was due to the behaviour of the aphid and not to a marker. Recently parasitised aphids appeared to react more violently to oviposition attempts (by kicking and swinging away from the parasitoid) than unparasitised individuals.
It seems likely that the internal marker used by the hyperparasitoid is injected during oviposition as it is apparent within minutes. The use of both an external and an internal marker by A. fuscicornis may appear superficially to be unnecessary. External marking may, however, have evolved as a means by which a female can rapidly discriminate and avoid duplication of her own reproductive

effort. Small differences in oviposition time can result in a large competitive disadvantage for a superparasitising female's progeny, especially in solitary species. External marks are likely to have a short persistence in the field while internal marks remain throughout development and so are apparent long after the ovipositing female has left the patch (Strand 1986).

The avoidance of superparasitism has traditionally been considered to be advantageous for parasitoid species. Four main reasons have been suggested for this:

(a) It prevents wastage of eggs. This is especially important in egg-limited parasitoids (Rogers 1972a, van Lenteren 1976, Bakker et al. 1985).

(b) It avoids wastage of hosts, as hosts are sometimes killed by frequent parasitoid attacks (van Lenteren 1976, Bakker et al. 1985).

(c) It saves time, if laying an egg takes longer than discriminating between healthy and parasitised hosts (van Lenteren 1976, Bakker et al. 1985).

(d) If the ability to discriminate initiates migration from the patch after a number of probes in parasitised hosts, this should result in a more efficient distribution of parasitoid eggs (Rogers 1972a, van Lenteren 1976, 1981, Bakker et al. 1985). Alphen and Galis (1983), however, pointed out that there is no data to support the hypothesis that encounters with parasitised hosts have a detrimental effect on patch time.

Superparasitism is, therefore, often interpreted as a deficiency in the parasitoid's physiological and sensory

systems (Hubbard et al. 1985), especially among solitary parasitoids where the value of superparasitism is less obvious than among gregarious species (Waage 1986). The tendency to avoid superparasitism is, however, rarely absolute (van Lenteren 1981, Cloutier 1984, Bakker et al. 1985) with superparasitism occurring frequently in insect populations. In some circumstances superparasitism may be advantageous, even for solitary species.

(a) If the probability of raising offspring by superparasitism is greater than zero, it may pay to oviposit in hosts already parasitised by other females; so parasitoids may stay in a patch and superparasitise. This decision could be adaptive if the time taken to travel between host patches is long or if dispersal is associated with a high risk or mortality. For example, Leptopilina heterotoma strongly avoids superparasitism when only one female is present in a patch, but the incidence of superparasitism increases when more than one female is present (van Alphen and Vet 1986). Superparasitism may also be advantageous, for a parasitoid which is not egg limited, if it takes more time and/or energy to discriminate and reject a host than to oviposit (Waage 1986).

(b) By superparasitising newly found hosts, parasitoid females experiencing a generally low rate of encounter with hosts would increase the probability that it is one of their own offspring which survives larval competition (Cloutier 1984).

(c) There is some evidence that superparasitism in solitary endoparasitoids reduces the effectiveness of the host immune response allowing more parasitoids to survive per host

(Sharpiro 1969, Bakker et al. 1985, Waage 1986). For example, Puttler (1974) showed that encapsulation of parasitoid eggs occurred less frequently in superparasitised weevil larvae than in larvae were only one egg was present.

(d) Another aspect of superparasitism is the possibility of influencing the sex ratio of the adults emerging from a host or group of hosts in such a way that the possibility of the superparasitising females leaving many grandchildren is increased. In local mate competition the genetic contribution to future generations could be large when only a small number of male producing eggs are added to a patch which has already been exploited. Under these circumstances, a reduction of searching efficiency, expressed as number of eggs laid per unit time, does not necessarily mean that the fitness gain per unit time also decreases, as the small investment of a few male eggs may give a substantial profit (Bakker et al. 1985, van Alphen and Vet 1986). Several authors have shown that superparasitising eggs are more frequently male than female (Waage and Godfray 1985). Superparasitism should be more common, therefore, when the proportion of hosts encountered which are already parasitised is high, when discrimination time is long compared to oviposition time, when rate of host finding is low or when parasitoids have a high fecundity.

A number of reasons could be used to explain the difference in host discrimination between D. rapae and A. fuscicornis. Firstly, it is possible that the primary parasitoid relies on an internal marker, such as a biochemical change in the host haemolymph, which takes too long to become apparent to

have been detected in this experiment. The internal marker used by the hyperparasitoid probably becomes apparent almost immediately.

Superparasitism by D. rapae may reduce the host immune response so allowing at least one egg to escape encapsulation. It is likely, however, that the eggs of A. fuscicornis are also subject to encapsulation by D. rapae, as the eggs of a related species, A. victrix, suffer weak encapsulation in certain parasitoid larvae, including D. rapae (Gutierrez 1970a).

Akinlosotu (1973) suggested that D. rapae females use multiple attacks on aphids to break up dense colonies so gaining access to aphids in the centre. The mode of oviposition employed by A. fuscicornis may make it easier for the hyperparasitoid to attack aphids in the middle of the colony. The presence of unparasitised aphids in a colony may also contribute to the avoidance of superparasitism by the hyperparasitoid by reducing the probability of encountering a parasitised aphid more than once.

Due to the activity of unparasitised aphids there may be little time for D. rapae to sense a previous egg using the ovipositor and it may not be worth the effort to subdue the host to check. With A. fuscicornis this is less likely to be a problem due to the mode of oviposition.

6.1 FIELD DISTRIBUTIONS OF THE HOSTS OF *D. rapae* AND *A. fuscicornis*.

To understand the foraging behaviour of *D. rapae* and *A. fuscicornis* it necessary first to have detailed knowledge of the distribution of their host populations in space and time, as this distribution defines the context in which they forage.

B. brassicae forms dense aggregations, which include all developmental stages, on brassica plants (Hayamizu 1982). The distribution of these colonies on different areas of the Brussels sprouts plants is non-random, with aphid colonies occurring more frequently at preferred feeding sites. *B. brassicae* prefers the young leaves of brassicas and may, therefore, be most frequent on the group of tightly curled leaves at the top of the stem (van Endem 1965, Hayamizu, 1982).

The efficiency of the parasitoid's foraging strategy will, therefore, be increased if certain areas of the plant are searched non-randomly in a way which coincides with the expected distribution of the aphids (Ayal 1987). This chapter examines whether the hyperparasitoid increases its efficiency by preferentially searching areas in which parasitised aphids are most numerous, which is obviously a function of both the aphid distribution and parasitoid foraging behaviour.

Many parasitoid species are suitable for laboratory studies, partly due to their small size, but, for the same reason, they are difficult to observe in the field.

The resulting lack of field data means that there is little on which to base patterns of host abundance and distribution in laboratory experiments (van Alphen and Vet 1986). The distributions of colonies of healthy aphids and groups of parasitised and hyperparasitised aphids within colonies were therefore studied in the field.

Several models have been developed to describe the optimal strategy which should be adopted by parasitoids foraging for a host with a patchy distribution (Hassell and May 1974, Charnov 1976, Cook and Hubbard 1977, Hubbard and Cook 1978, Comins and Hassell 1979, McNair 1982). A foraging parasitoid must make two decisions; which patches to visit and how long to spend on each patch (see Chapter 7). Iwasa et al. (1981) compared several simple decision rules for determining when to leave a patch (Gibbs 1962, Krebs 1973, Hassell and May 1974) and demonstrated that the optimal strategy depends critically on the spatial distribution of the host. When the distribution of hosts between patches is uniform, with equal numbers of hosts in each patch, an optimised fixed number strategy (with parasitoids attacking the same number of hosts in each patch) gave the highest capture rate. When the variance in the number of hosts per patch was large, however, the latter strategy was the least efficient. It is of interest, therefore, to determine the variance between the aphid colony sizes as this will have implications for the foraging strategy adopted by D. rapae. The strategy adopted by A. fuscicornis will be influenced not only by the variance of aphid colony sizes but also by the numbers of parasitised aphids within these colonies.

A sampling programme was carried out to examine the field distributions of unparasitised and parasitised aphids (i.e. hosts of *D. rapae* and *A. fuscicornis*, respectively).

Methods.

The sampling programme was conducted in a plot of Brussels sprouts, which had been planted the previous spring at Silwood Park, Berkshire. The plot consisted of 40 rows with 40 plants per row, which were divided into 20 sub-plots with 80 plants each. Every five days, from 27th August to 21st October 1985, each sub-plot was sampled by removing all the aphids from one plant which had been chosen at random. (Each plant was sampled no more than once during the season). Previous authors (Church and Strictland 1954, van Emden 1963, Akinlosotu 1973) used a 'three leaf' method to estimate aphid populations in the field. Three leaves were removed from a number of plants which were chosen at random and the number of aphids per leaf was counted. It is more accurate, however, to examine all the leaves of a plant as the aphids are not distributed evenly and the distribution changes during the season (Chua 1975, Cheng 1985). The latter method was chosen here as an accurate estimate of the size and structure of each aphid colony was required. Brussels sprouts plants have 20 to 30 leaves at this stage of growth and can be divided into three main areas (Raworth *et al* 1984). The first ten leaves from the ground were classified as 'lower', the next ten as 'middle' and remainder as 'upper'. The tightly curled leaves in the centre of the upper leaves were referred to as the 'crown'.

The position of each aphid colony on the plant was noted, then the entire colony was removed from the plant and placed in a vial containing 30% alcohol. The aphids were dissected and the following observations were recorded: number and position of colonies, number of aphids per colony, instar of each aphid (1, 2, 3, 4, apterous or alate adult), number and instar of any parasitoid larvae present (egg, 1, 2, 3, 4, early, late or empty mummy) and number and instar of any hyperparasitoid larvae present (egg, 1, 2, 3, early, late or empty mummy). The instars of D. rapae were distinguished by differences in their morphology, in particular their size and shape. The first instar is caudate and sickle shaped with a large head, while second and third instars are both hymenopteriform in shape. The cauda is reduced in the second instar and the head is blunter in shape than in the first instar. The third instar differs from the second in that the cauda is very much reduced and lacks spines, the body is curved and the head is shorter. In the fourth instar the cauda is no longer present and the head is slightly more pronounced than in the previous two instars. Each instar is, of course, larger than the preceding one and by the fourth instar the larva completely fills the aphid haemocoel (see Couchman and King 1977 for a more detailed description of larval morphology).

Instars of A. fuscicornis were identified in a similar manner from descriptions of their morphology in Haviland (1921). The first instar in this case has a distinct head and cauda and differs from the following instar in head shape. In the third instar, the cauda is greatly reduced and the body becomes distended.

For both species 'late' mummies were considered to be those in which the meconium had been expelled and sclerotization was advanced. In 'early' mummies the larval characteristics were still predominant. Empty mummies were distinguished by the shapes of the emergence hole and meconium. Empty mummies of the primary parasitoid have circular emergence holes with a cap attached and a meconium consisting of 15 to 20 cigar-shaped bodies. Emergence holes in A. fuscicornis are irregular and the cap is absent, the meconium consists of four circular bodies which are often linked together (Hafez 1965). Acid Fuschin was used to detect hyperparasitoid eggs within parasitoid larvae.

Results.

The population trends of B. brassicae, D. rapae and A. fuscicornis during September and October 1985, are illustrated in Figures 5 and 6. At the beginning of the sampling period there was an average of six aphids per plant, in comparison to densities of 1470 and 33 aphids per plant as sampled by Chua in 1973 and 1974, respectively (Chua 1975), and up to 100 aphids per plant sampled by Cheng in 1981 and 1982 (Cheng 1985).

The aphid population increased rapidly until it reached a peak in mid-October. B. brassicae populations generally have two peaks; a minor peak in mid-July followed by a major peak in September or October (Hafez 1961, Hughes 1963, Akinlosotu 1973, Chua 1979). The eventual decline in aphid numbers at the end of the season has been attributed to the onset of cold weather (Chua 1975), a decline in reproductive rate due

Figure 5 Population trends of B. brassicae, D. rapae and A. fusicornis

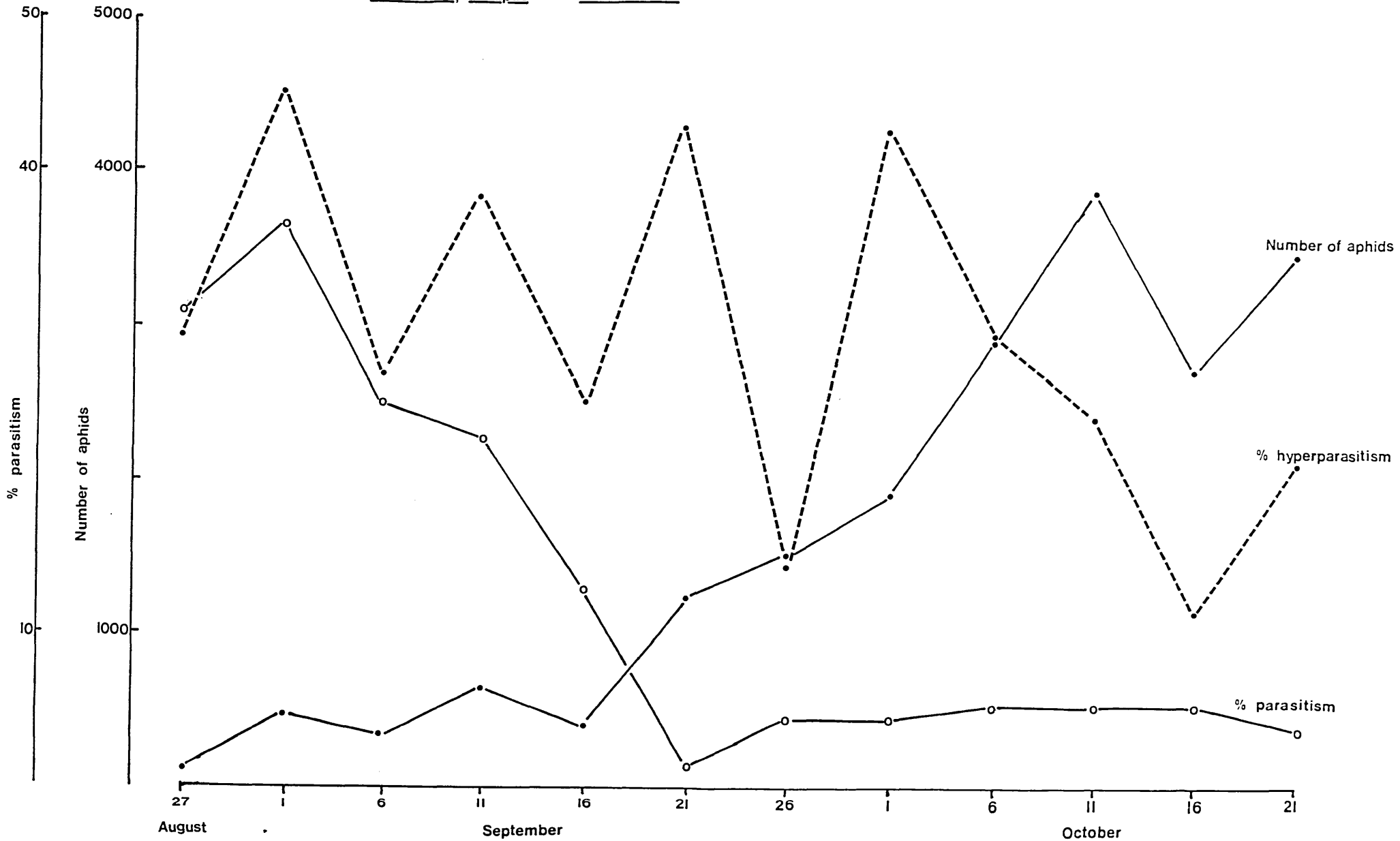
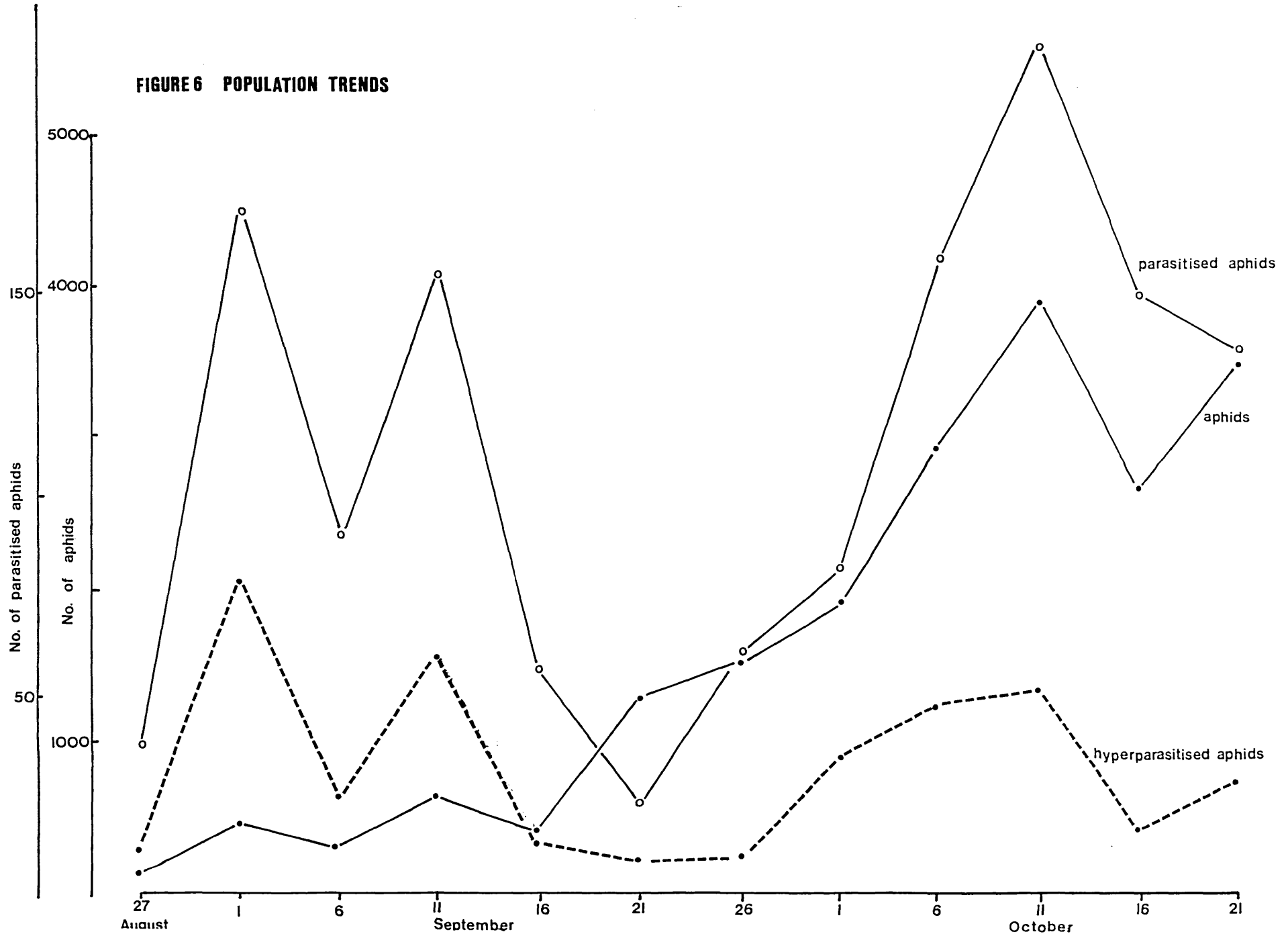


FIGURE 6 POPULATION TRENDS



to overcrowding (Hughes 1963) and the effect of predators (Raworth et al 1984). It seems unlikely that this decline is due to the affects of parasitism by D. rapae because percentage parasitism was less than 10% from the middle of September and remained roughly at this level until the end of October, while aphid numbers continued to increase until the second week of October (Figure 5). The number of parasitised aphids fluctuated, however, with peaks at the beginning and end of the sampling period (Figure 6). The decline in percentage parasitism may be due to the greater rate of increase of the aphid in comparison to the parasitoid population.

Overall percentage parasitism of the D. rapae population does not appear to be solely related to trends in percentage parasitism of B. brassicae, although the number of hyperparasitised aphids closely follows the number which are parasitised (Figure 6). In August and September percentage hyperparasitism fluctuated between successive samples, which may reflect successive generations, as the generation time of A. fuscicornis is 11 days (Vater 1971). The eventual decline of hyperparasitism is probably due to a combination of factors; a decrease in hyperparasitoid activity due to low temperatures, the decrease in percentage parasitism by D. rapae so that fewer hosts are available and an increase in aphid colony size, making location of hosts more difficult.

In order to determine the degree of dispersion or aggregation of host colonies, which may have a major influence on parasitoid searching strategy, the mean host colony size and its variance were examined for each sampling

date. The relationship between these two parameters has been shown to obey a power law for many species (Taylor et al. 1978) which is expressed by:

$$s^2 = ax^b$$

where s^2 is variance, x is the mean and b is an index of aggregation which is characteristic and constant for a species (Southwood 1978). b is determined by plotting log variance versus log mean and fitting a linear regression i.e.:

$$\log s^2 = \log a + b \log x$$

High values of b may indicate strong contagion, but if the regression line crosses the Poisson line ($s^2 = x$) this indicates a change to a more even distribution at low densities. If the population is randomly dispersed (i.e. follows a Poisson distribution) the mean will equal the variance and therefore departures of the coefficient of dispersion s^2/x from unity are a measure of the departure from the Poisson and from randomness (Southwood 1978). The relationship between mean and variance of host colony sizes for both species (B. brassicae colonies and groups of parasitised aphids for D. rapae and A. fuscicornis, respectively) was described by plotting log variance versus log mean (Figure 7). A significant relationship ($p<0.01$) between the variance and the mean was obtained for both host colony types, but there was no significant difference between the values of b. Calculations of variance:mean ratios for colonies of B. brassicae and groups of parasitised aphids revealed that ratios for aphid colonies

FIGURE 7 LOG VARIANCE VERSUS LOG MEAN FOR HOST COLONIES

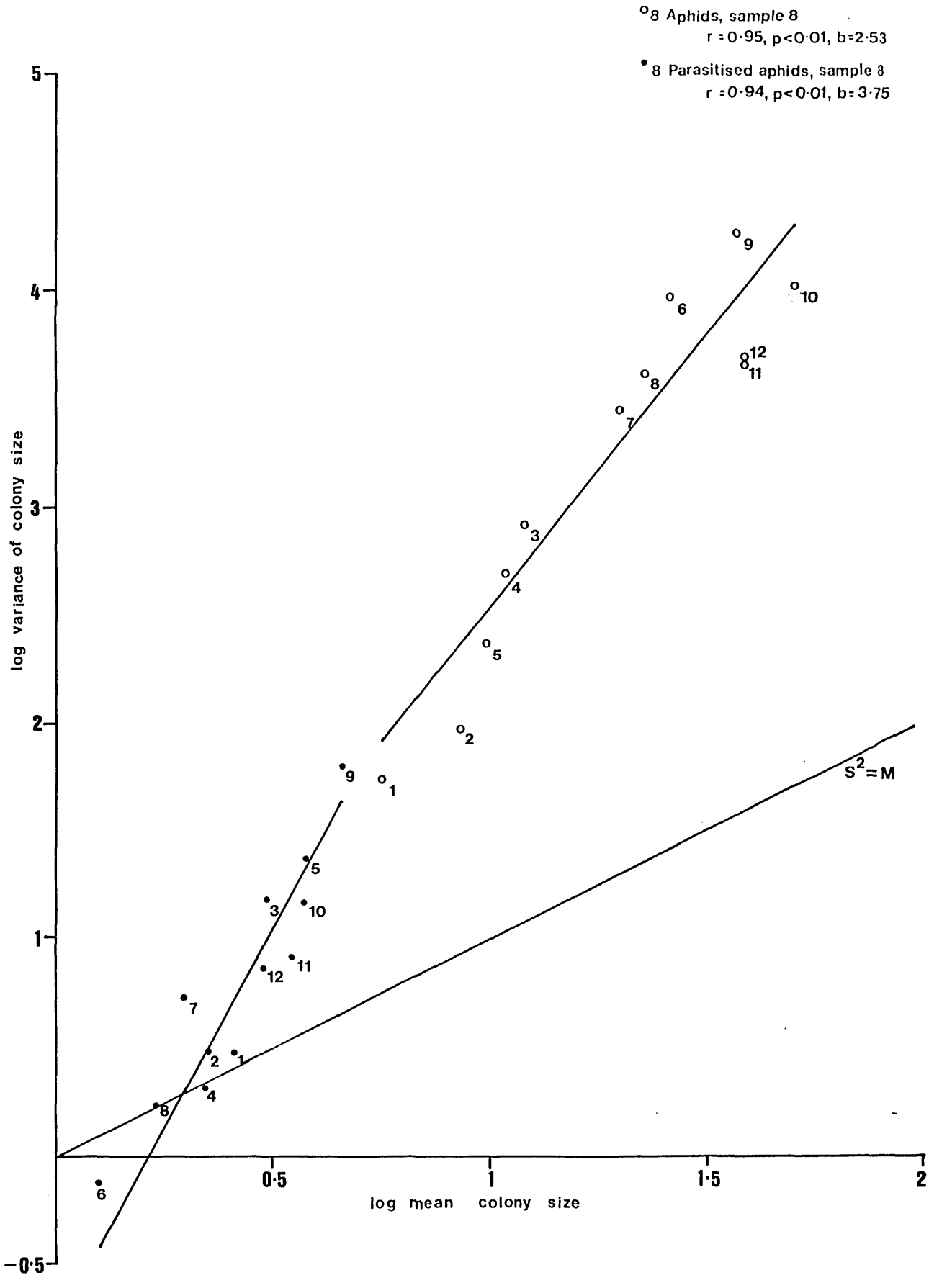


Table 13: Variance:mean ratios for aphid colonies and groups of parasitised aphids

Sample No.	Aphids	Parasitised aphids
1	9.56	0.96
2	7.27	1.46
3	64.06	7.54
4	46.85	1.39
5	25.49	6.43
6	377.20	0.19
7	142.75	2.59
8	183.00	1.14
9	519.99	13.99
10	226.19	4.72
11	121.76	2.45
12	133.08	0.94

were generally several times greater than the corresponding value for groups of parasitised aphids (see Table 13). This suggests that D. rapae searches for hosts which have a more aggregated distribution than those of the hyperparasitoid.

At the beginning of the sampling period aphid colonies were mainly small in size (less than ten aphids per colony) (Figure 7), but as the season progressed mean aphid colony sizes and the variance of colony sizes increased. Small aphid colonies (less than 10 aphids) remained the most common size class throughout the sampling period.

Host 'colonies' of A. fuscicornis (i.e. groups of parasitised aphids) had a distribution which differed from that of the hosts of the primary parasitoid in its variance and mean. This distribution results from the oviposition behaviour of D. rapae which rarely attacks more than ten aphids in a colony regardless of its size. Groups of parasitised aphids occurred mainly in the one to ten size class throughout September and October. Mean group size was more constant than that of aphid colonies (Figure 7) and variance within samples tended to be lower. The variance:mean ratio for parasitised aphid group size also remained relatively constant during the sampling period compared with the ratio for aphid colony size. The mean number of aphid colonies per sample was significantly greater ($p<0.001$) than the mean number of parasitoid 'colonies'. In this case, however, the regression line crosses the Poisson line, suggesting a more even distribution at low densities (Southwood 1978).

The data from the sampling programme was analysed further to examine the relationships between time (sampling date) and colony position and parameters such as number of aphid

colonies, aphid colony size (excluding mummies), number of colonies attacked (colonies in which one or more aphids contained a first instar parasitoid larva) and number of aphids attacked per colony (number of aphids with first instar parasitoid larvae). A similar analysis was carried out for the number of groups of parasitised aphids (within aphid colonies), group size, number of groups of parasitised aphids attacked (number of groups with one or more parasitised aphids with first instar hyperparasitoid larvae) and the number of parasitised aphids attacked per group. The analysis was carried out using GLIM (Royal Statistical Society, London 1977). This method fits a linear model to the data and the amount of variance about the model due to various factors is calculated. The estimates of deviance from the mean and standard errors produced are contained in Appendix 1.

The means of numbers of aphid colonies on different days are shown in Figure 8. The number of aphid colonies increases with time; sampling days 2, 4, 6, 7, 8, 9, 10, 11 and 12 had significantly ($p<0.05$) more colonies than day 1, and days 8, 9, 10, 11 and 12 had more colonies than day 2. Aphid colonies also increased in size as the season progressed (Figure 9) and on days 9, 10, 11 and 12 the mean colony size was significantly ($p<0.05$) different from that on day 1. The number of aphids attacked per colony showed only a slight increase during the sampling period (Figure 10). Only the last sample (21st October) had significantly ($p<0.05$) more aphids attacked per colony than the first sample (27th August). Similarly, only on the 21st October were

FIGURE 8 MEAN NUMBER OF HOST COLONIES (±S.E.)

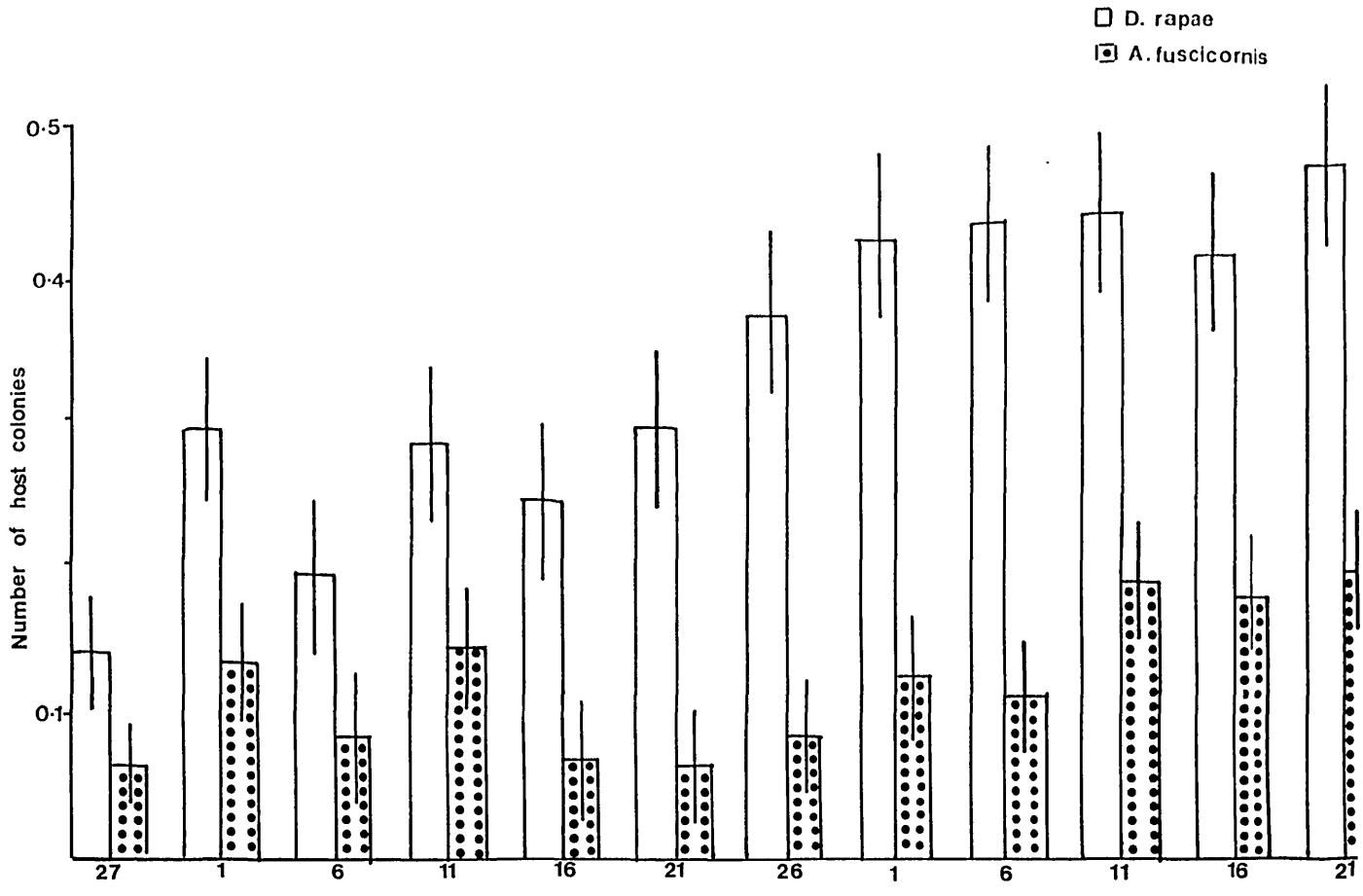


FIGURE 9 MEAN NUMBER OF HOSTS/COLONY (±S.E.)

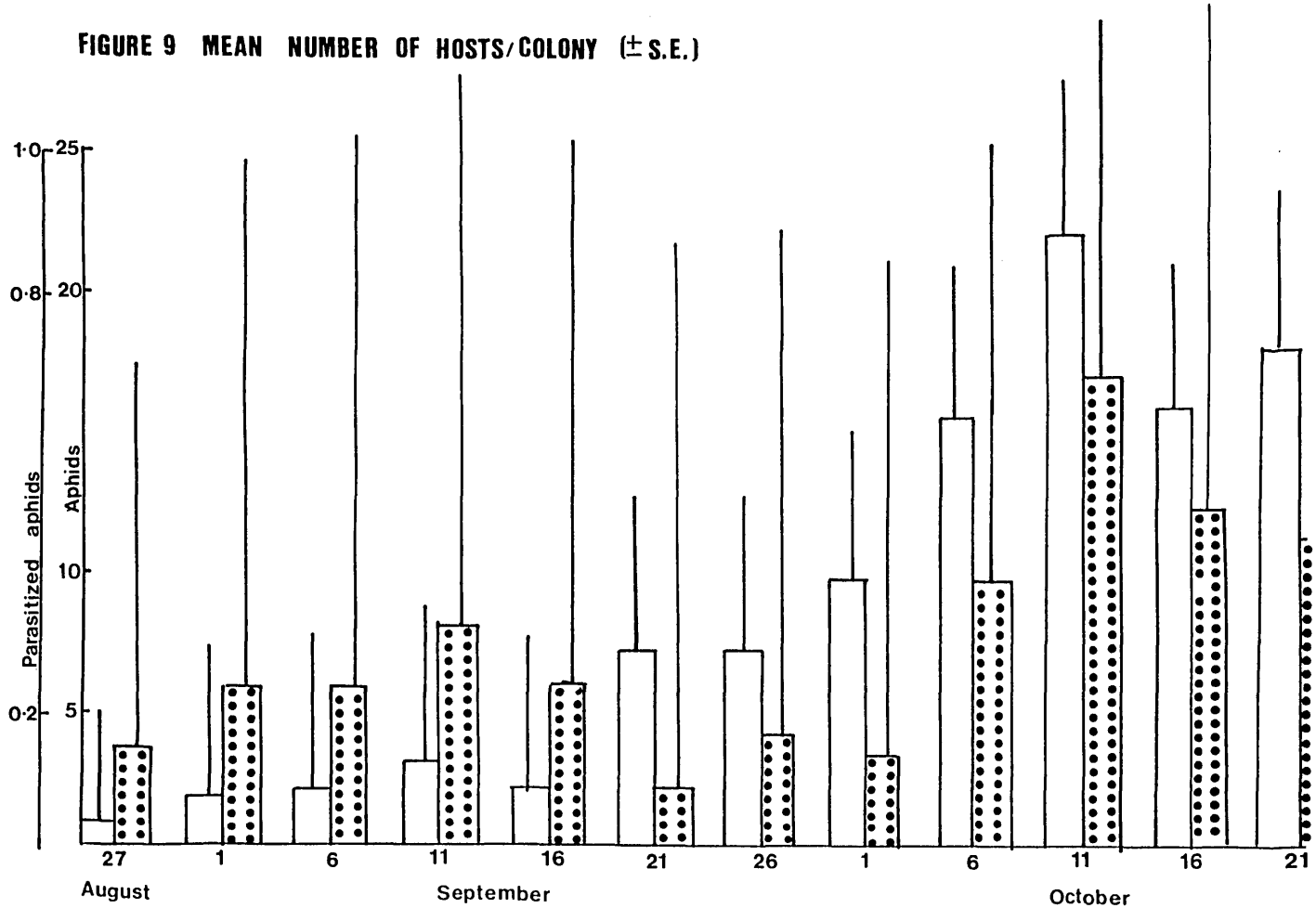


FIGURE 10 NUMBER OF HOSTS ATTACKED/COLONY (±S.E.)

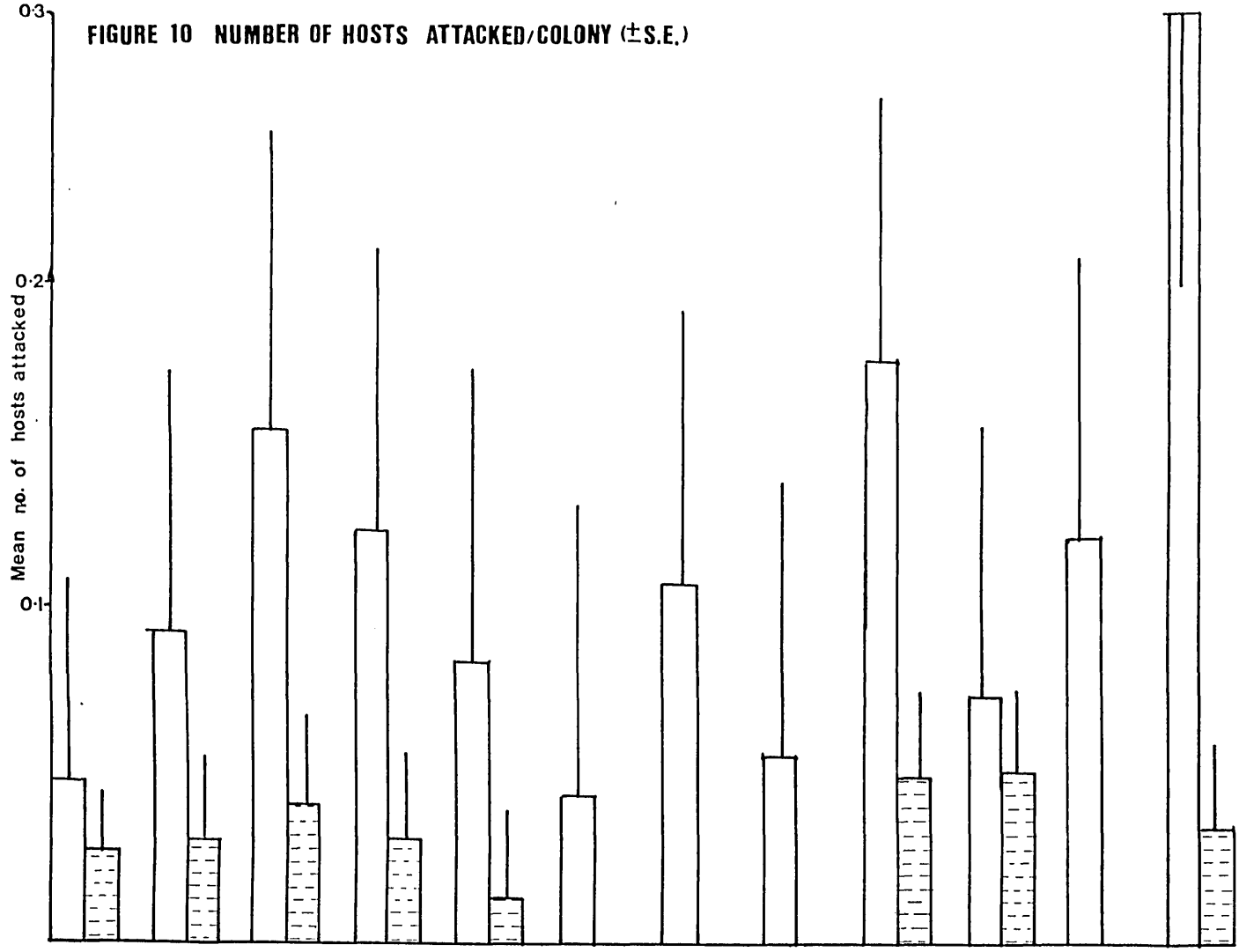
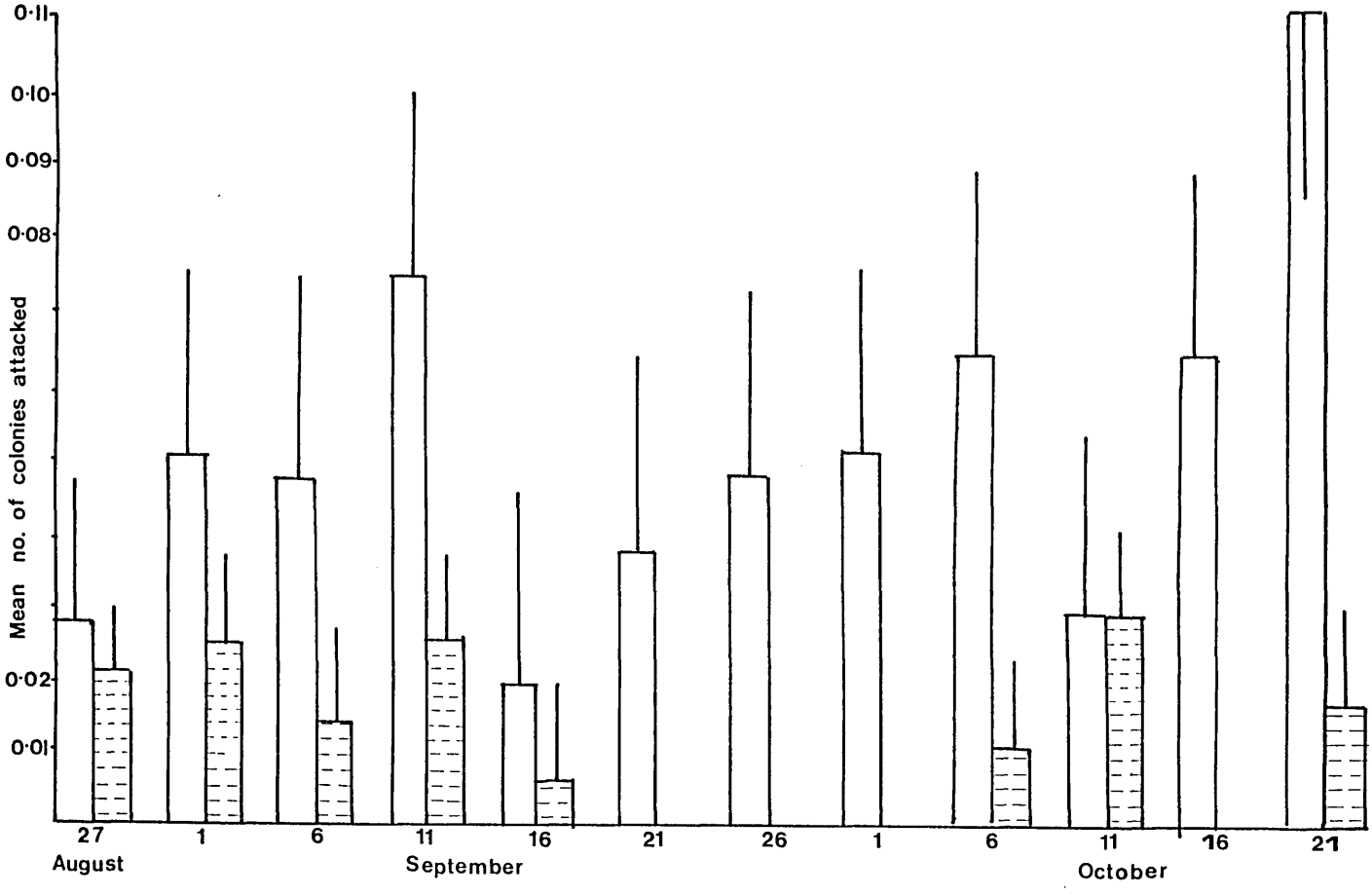


FIGURE 11 NUMBER OF HOST COLONIES (±S.E.)



significantly ($p<0.05$) more aphid colonies attacked by the parasitoid than on the 27th August (Figure 11).

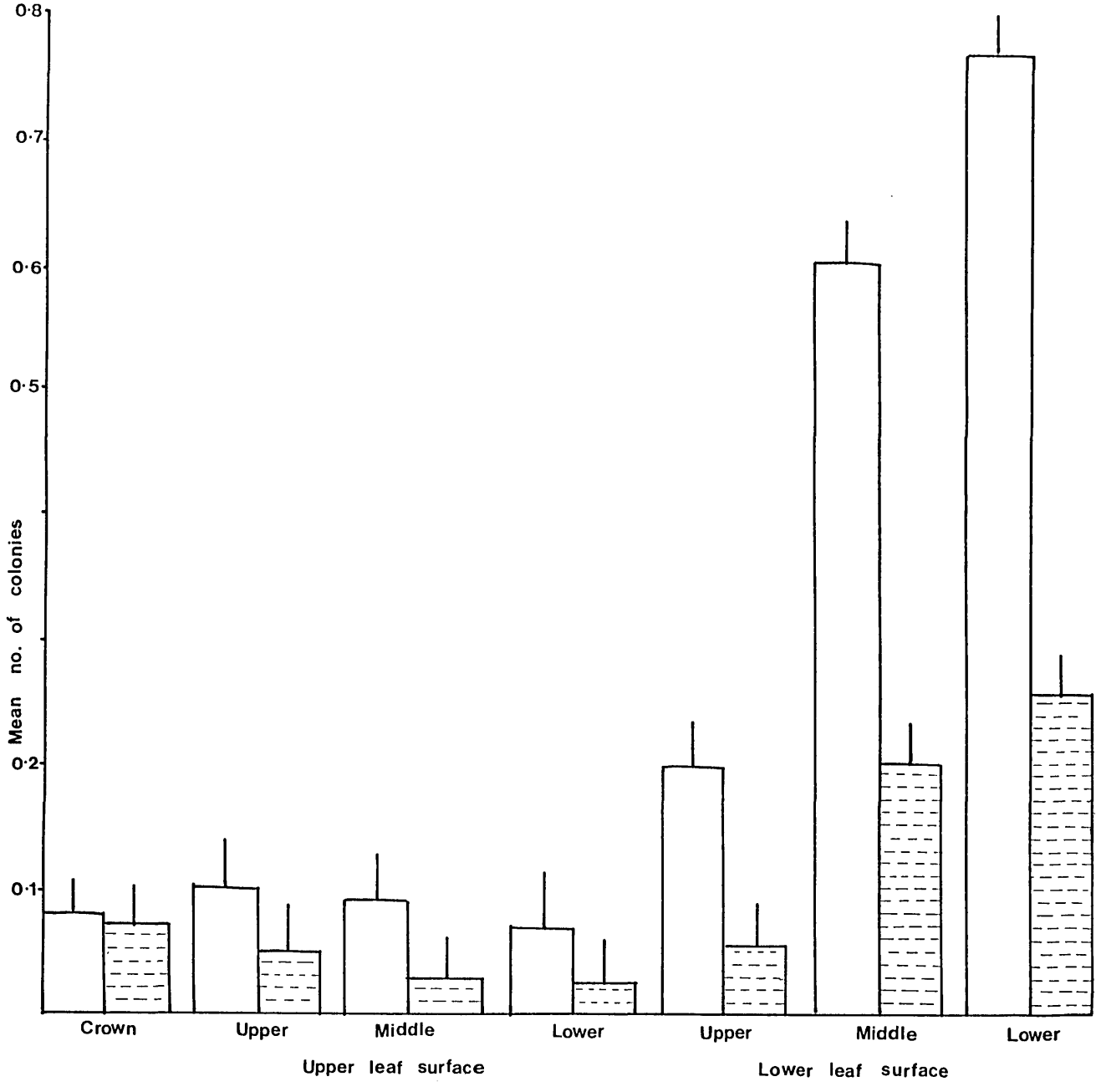
There were also significantly ($p<0.05$) more groups of parasitised aphids within aphid colonies at the end than at the beginning of the sampling period (Figure 8); samples 10, 11 and 12 are significantly ($p<0.05$) greater than sample 1. The mean number of parasitised aphids per group, however, did not increase significantly ($p<0.05$) (Figure 9). This suggests that although aphid colonies increase in both numbers and size during the season. groups of parasitised aphids within these colonies increase only in numbers and not in size. A decreasing proportion of the aphid population must, therefore, be available to the hyperparasitoid for oviposition as the season progresses.

The mean number of parasitised aphids attacked by the hyperparasitoid and the mean number of groups of parasitised aphids attacked did not increase significantly ($p<0.05$) with time (Figures 10 and 11, respectively). Neither was there any significant decrease in hyperparasitism, despite the increasing difficulty for the hyperparasitoid to locate parasitised aphids.

Aphid colonies were recorded as being at one of seven positions on the plant; on the crown, upper surface of the upper, middle or lower leaves or on the undersurface of the upper, middle or lower leaves.

Significantly ($p<0.05$) more aphid colonies occurred on the undersurfaces of upper, middle and lower leaves than on the crown or the upper leaf surfaces (Figure 12). Colonies were most numerous on the undersurfaces of lower leaves. Aphid colonies on the undersurfaces of middle and lower leaves

FIGURE 12 NUMBER OF COLONIES AT EACH POSITION (± S.E.)



were also larger than colonies on other parts of the plant (Figure 13).

There were no significant differences between the number of aphids attacked by D. rapae per colony at each position (Figure 14) but significantly ($p<0.05$) fewer colonies were attacked on the upper surface of the middle and lower leaves than on the crown or undersurfaces of the middle and lower leaves (Figure 15). Similarly, more groups of parasitised aphids occurred on undersurfaces of lower and middle leaves than at other positions (Figure 12). On the undersurfaces of the middle leaves, however, groups of parasitised aphids were significantly ($p<0.05$) larger than at any other position on the plant (Figure 13). Also significantly ($p<0.05$) more parasitised aphids were attacked on the undersurfaces of middle leaves than elsewhere on the plant (Figure 14). There was no significant difference between the numbers of groups of parasitised aphids attacked by the hyperparasitoid at different positions (Figure 15).

There was a significant interaction between days and positions for all parameters, except the number of aphid colonies and groups of parasitised aphids attacked. In the former this indicates that the effects at different positions are different on different days.

The parasitoid and hyperparasitoid must, therefore, search for host populations which differ in their distributions both in time and in space.

FIGURE 13 SIZE OF HOST COLONIES AT EACH POSITION (± S.E.)

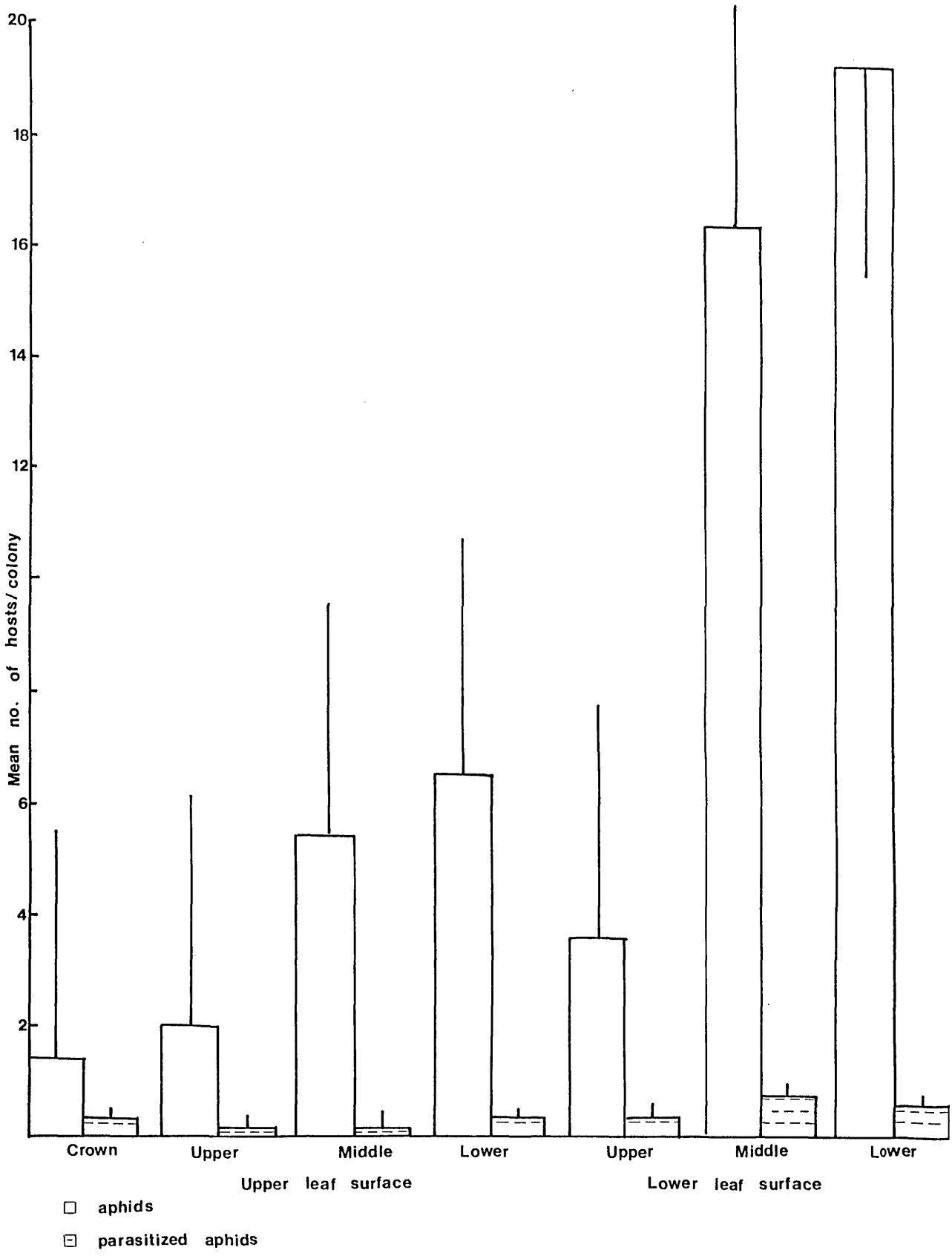


FIGURE 14 MEAN NUMBER OF HOSTS ATTACKED/COLONY (±S.E.)

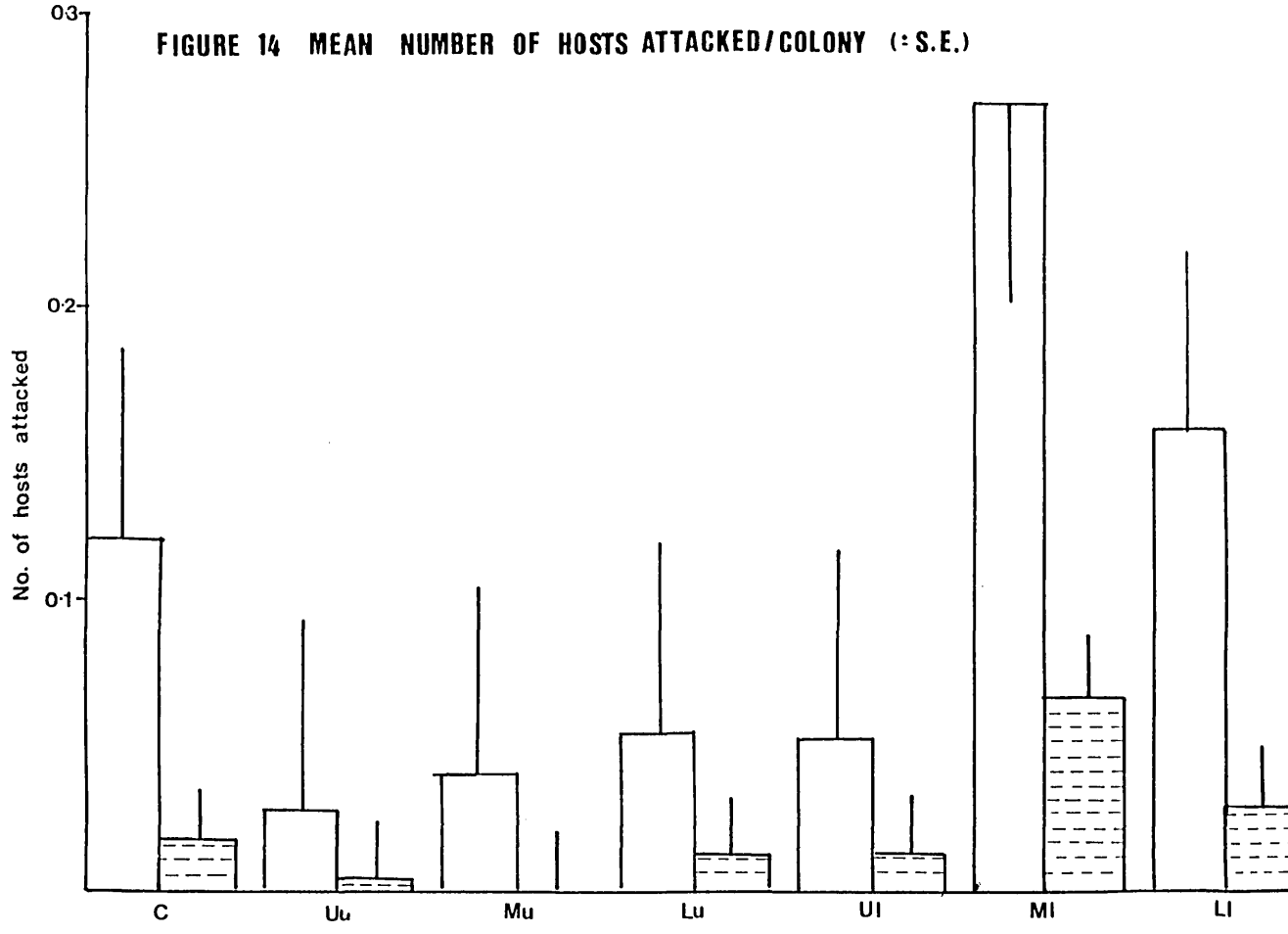
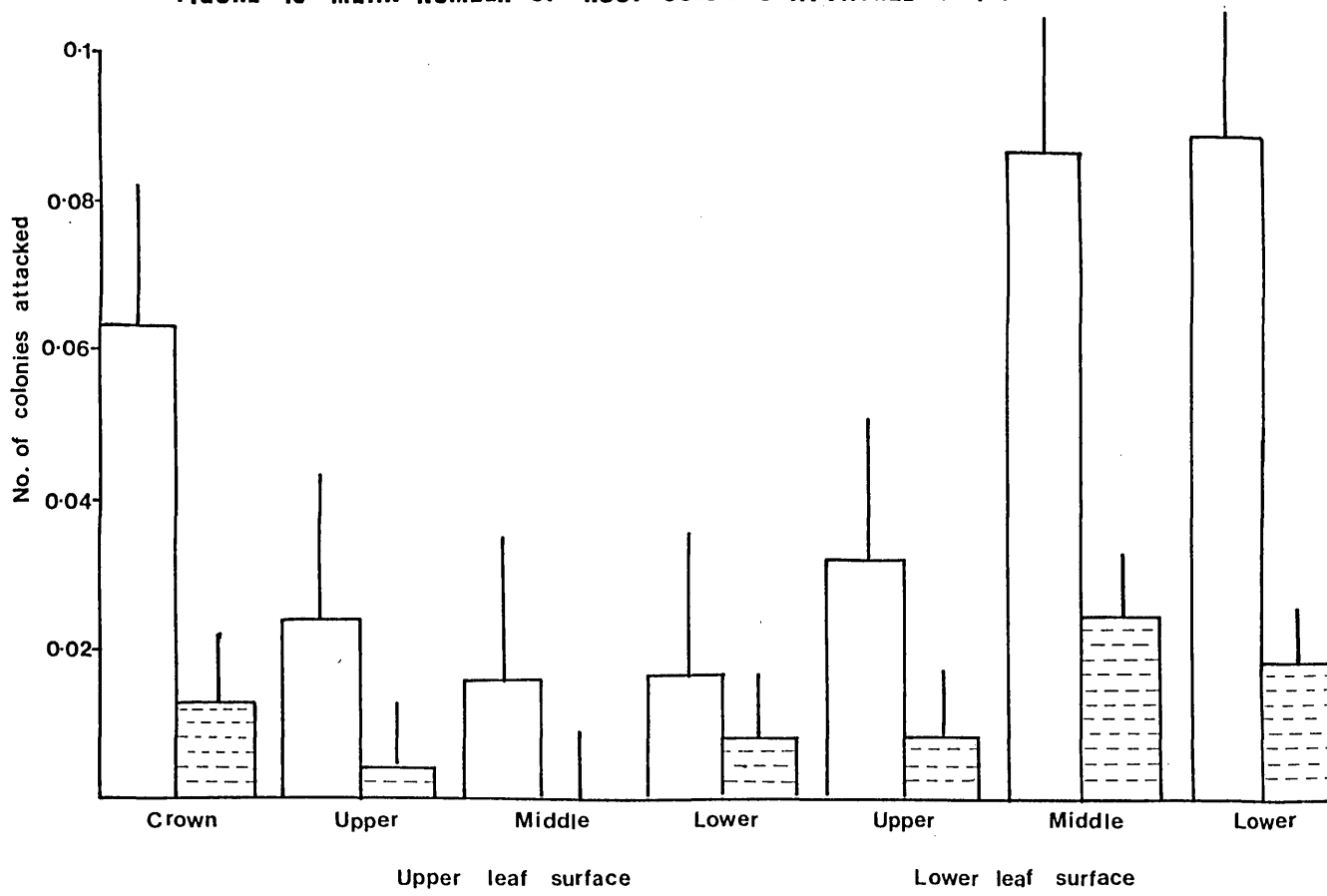


FIGURE 15 MEAN NUMBER OF HOST COLONIES ATTACKED (±S.E.)



This difference may result in differences in foraging behaviour of the two species. The responses of the parasitoid and hyperparasitoid to host colonies of varying size and quality was considered in the following experiment.

6.2 AGGREGATIVE BEHAVIOUR OF *D. rapae* AND *A. fuscicornis* IN THE FIELD.

Models of parasitoid-host interactions have predicted that spatial heterogeneity, especially the concentration of parasitoid attacks in areas of high host density, is a contributing factor to the stability of interacting populations (Hassell and May 1974, Hassell 1978, Hassell 1982). Many parasitoids are known to respond to spatial variations in host density by foraging aggregatively (i.e. spending relatively more time in patches of high host density than areas of low host density (Morrison 1986)). This aggregative behaviour has been demonstrated for a number of parasitoid species, both in the laboratory (Akinlosotu 1973, Hassell 1978, Hassell 1982) and in the field (Waage 1983, Smith and Maelzer 1986). Aggregative behaviour is not necessarily, however, reflected in the resulting spatial pattern of parasitism as parasitoids which aggregate in patches of high host density may show either positive or negative density dependent or density independent patterns of parasitism (Hassell 1982, Morrison 1986). The total foraging time allocated to a patch is a sum of two components; active searching time and the time spent in non-searching activities, such as handling hosts, resting, etc.

The overall spatial pattern of parasitism resulting from the parasitoid's foraging behaviour will depend on both the aggregative response over all patches and on the factors limiting the rate of parasitism within a patch.
As A. fuscicornis forages for parasitised aphids within aphid colonies and has been shown to waste time handling both healthy and parasitised aphids, it is of interest to determine whether or not it has an aggregative response to aphid colonies of different sizes and also to different sizes of groups of parasitised aphids within a fixed colony size.
Most studies of aggregative behaviour in parasitoids have been carried out using artificial laboratory systems. Few studies combine direct field observations on the distribution of searching parasitoids with measurement of the resulting patterns of parasitism (but see Waage 1983 and Smith and Maelzer 1986).

The following experiments were carried out in the field to observe the responses of D. rapae and A. fuscicornis to aphid colonies of different sizes and colonies of fixed size with varying numbers of parasitised aphids per colony.

Method.
Two experiments were carried out in a plot of Brussels sprouts (roughly 1200 plants) which had been planted at Silwood Park the previous spring and which had 20 to 30 leaves. The experiments were conducted in September and October 1986, when the populations of both parasitoid species were at their peak.

Twenty-five Brussels sprouts plants were dug up and placed in large polythene pots. All the aphids, syrphid larvae, caterpillars, etc. were removed from each plant and the plants were arranged in a 5 x 5 'Latin square' design within the Brussels sprouts plot. Each plant was reinfested with either 1, 5, 10, 40 or 100 unparasitised aphids (with 5 plants per density). The aphids were placed on the upper surface of one of the upper leaves of each plant and the leaf was carefully covered with a piece of muslin which was tied at the petiole to prevent access by predators or parasitoids. The aphids were allowed to settle overnight and the muslin was removed the following morning. The number of parasitoids and hyperparasitoids on each plant was recorded at ten minute intervals throughout the day until both species had stopped searching. The observations were continued the next day (weather permitting) and then the aphids were removed from the plants. After allowing 48 hours for any parasitoid larvae present to develop, the aphids were dissected.
This procedure was repeated three times and six days of observations were recorded.

The second experiment was similar in design except that twenty aphids were placed on each plant and of these 0, 1, 4, 8 or 16 had been parasitised at least three days previously, the remaining aphids were unparasitised. Plants were again observed at ten minute intervals and the numbers of parasitoids and hyperparasitoids on each plant were recorded.

Table 14: Experiment 1. Mean numbers of parasitoids/day (± S.E.)

Day	Weather	*D. rapae*/plant	*A. fuscicornis*/plant
1	mostly cloudy	4.32 ± 1.34	0.72 ± 0.77[a]
2	cloudy a.m. no wind	4.96 ± 1.34	1.72 ± 0.77[a]
3	sunny intervals	4.96 ± 1.34	2.28 ± 0.77[a]
4	sunny intervals	5.56 ± 1.34	3.08 ± 0.77[b]
5	sunny + warm	6.28 ± 1.34	2.44 ± 0.77[b]
6	cloudy a.m. windy	2.72 ± 1.34	1.36 ± 0.77[a]

Table 15: Experiment 2. Mean numbers of parasitoids/day (± S.E.)

Day	Weather	*D. rapae*/plant	*A. fuscicornis*
1	sunny intervals	6.6 ± 1.0[a]	1.6 ± 0.59[a]
2	cloudy, no wind	1.48 ± 1.0[b]	2.08 ± 0.59[a b]
3	sunny	1.32 ± 1.0[b]	0.68 ± 0.59[a c]
4	cloudy a.m.	1.72 ± 1.0[b]	1.8 ± 0.59[a]

The procedure was repeated three times but, due to adverse weather, only four days of observations were recorded.

Results.

These results were also analysed using GLIM. Table 14 shows the number of D. rapae and A. fuscicornis individuals observed per plant on each of six days of the first experiment. Analysis with GLIM showed no significant difference in the number of D. rapae observed on different days.

Significantly ($p<0.05$) more A. fuscicornis, however, were observed on days 4 and 5 than on days 1 and 6. Also, in the second experiment significantly ($p<0.05$) fewer primary parasitoids were observed on days 2, 3 and 4 than on day 1 (Table 15) and for the hyperparasitoid significantly ($p<0.05$) more individuals were observed on day 2 than on day 3. These differences in numbers of wasps observed each day are obviously due to different weather conditions, for example, most hyperparasitoids were observed on days 4 and 5 in the first experiment and these were the sunniest days on which observations were recorded. Although hours of sunshine appear to be important, the wind speed also influences the number of wasps searching each day, more A. fuscicornis were observed on day 2 than day 3 of the second experiment, although the latter was sunnier it was also more windy. It is interesting to note that D. rapae and A. fuscicornis do not appear to respond in the same way to changes in weather.

Table 16: Number of parasitoids/plant with varying numbers of unparasitised aphids (± S.E.)

No. unparasitised aphids	D. rapae/plant	A. fuscicornis/plant
1	2.53 ± 0.87[a]	0.53 ± 0.52[a]
5	3.20 ± 1.24[a]	0.50 ± 0.73[a]
10	3.97 ± 1.24[a]	1.70 ± 0.73[a]
40	8.03 ± 1.24[b]	4.17 ± 0.73[b]
> 100	6.27 ± 1.24[b]	2.77 ± 0.73[b]

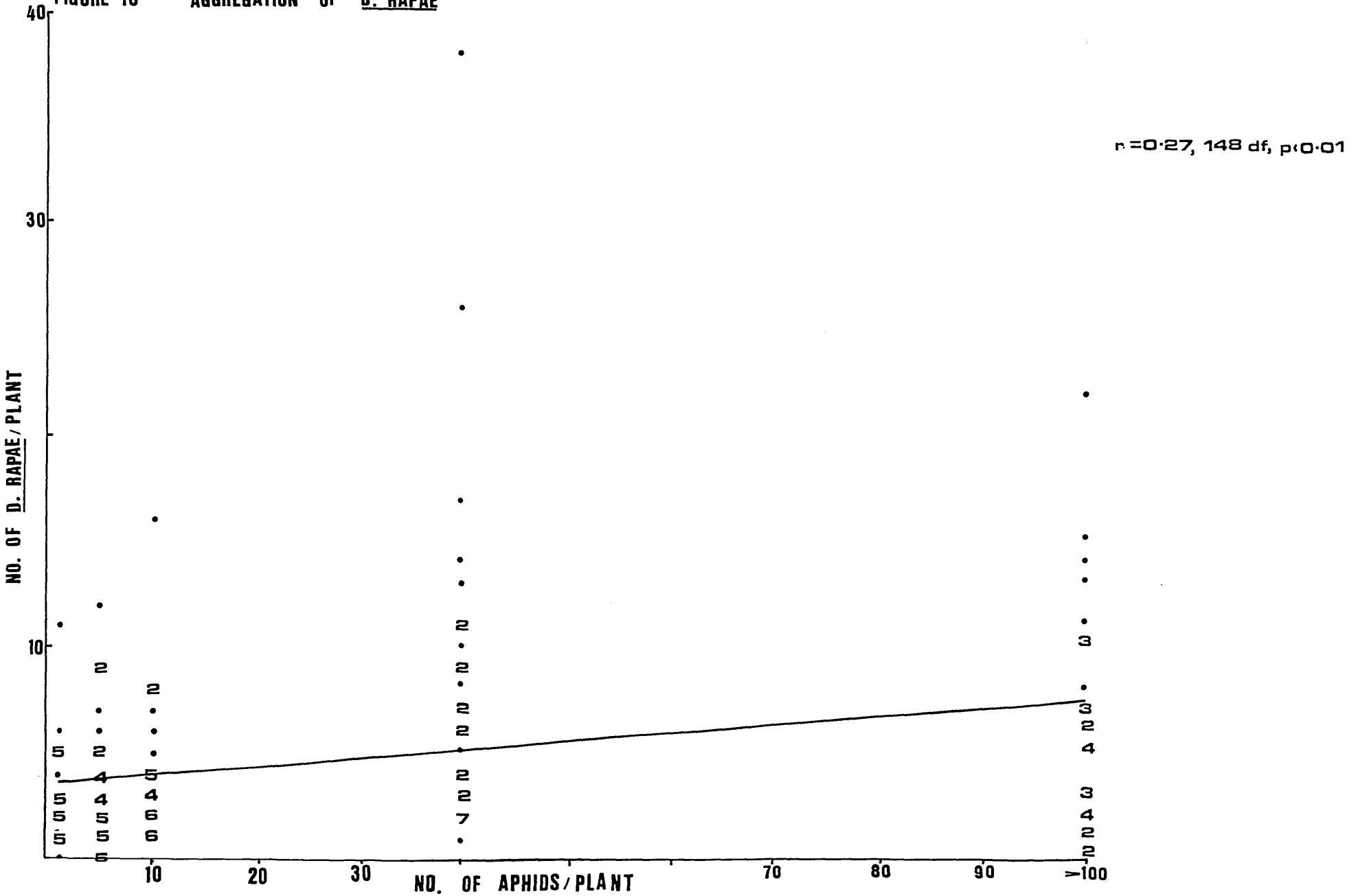
Table 17: Aggregation of adult parasitoids in response to different densities of parasitised aphids (± S.E.)

No. parasitised aphids	D. rapae/plant	A. fuscicornis/plant
0	2.0 ± 0.93[a]	0.40 ± 0.48[a]
1	2.05 ± 1.32[a]	1.35 ± 0.67[a]
4	2.45 ± 1.32[a]	1.40 ± 0.67[a]
8	2.60 ± 1.32[a]	2.05 ± 0.67[b]
16	4.80 ± 1.32[b]	2.50 ± 0.67[b]

Smith and Maelzer (1986), in a similar experiment observed more parasitoids of the red scale during a period of warm weather than during a succeeding period of cool, wet weather.

In the first experiment significantly ($p<0.05$) more D. rapae were observed on plants with the highest densities of unparasitised aphids (40 and 100 plus aphids per plant) (Table 16). Figure 16 shows the number of primary parasitoids observed per plant for different aphid densities. A linear regression had a significantly ($p<0.01$) positive slope, indicating positive aggregation of wasps in relation to host density. It is worth noting, however, that the slope of the line is slight, so that the mean number of parasitoids expected at high densities is less than twice that expected at low densities. This tendency for aggregation is not reflected in the resulting pattern of parasitism (Figure 17) and there is no evidence of either positive or negative density dependence. A. fuscicornis also aggregates in response to increasing densities of unparasitised aphids (Table 16), significantly ($p<0.05$) more hyperparasitoids were observed at the highest densities. Again, a linear regression was significant ($p<0.01$) with a positive slope (Figure 18), although the slope was small. D. rapae had a slight aggregative response to high densities of parasitised aphids but this was only significant at the highest density (16 out of 20 aphids parasitised) (Table 17). A regression of the number of observations versus density of parasitised aphids was significant ($p<0.05$), but this significance was due to one point at the highest density (Figure 19).

FIGURE 16 AGGREGATION OF D. RAPAE



r=0·27, 148 df, p<0·01

FIGURE 17 DISTRIBUTION OF PARASITISM BY D. RAPAE

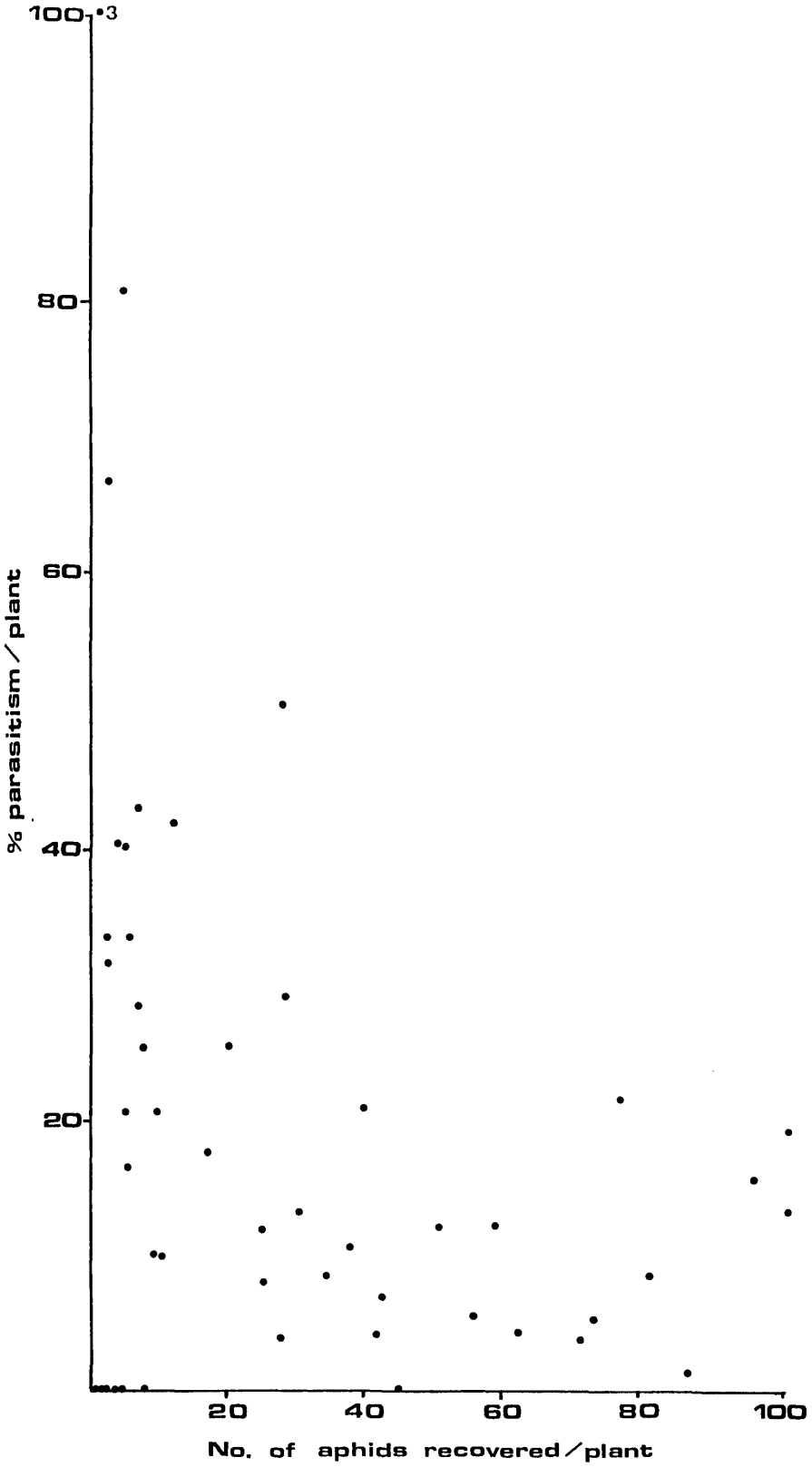


FIGURE 18 AGGREGATION OF A. FUSCICORNIS IN RESPONSE TO UNPARASITISED APHIDS

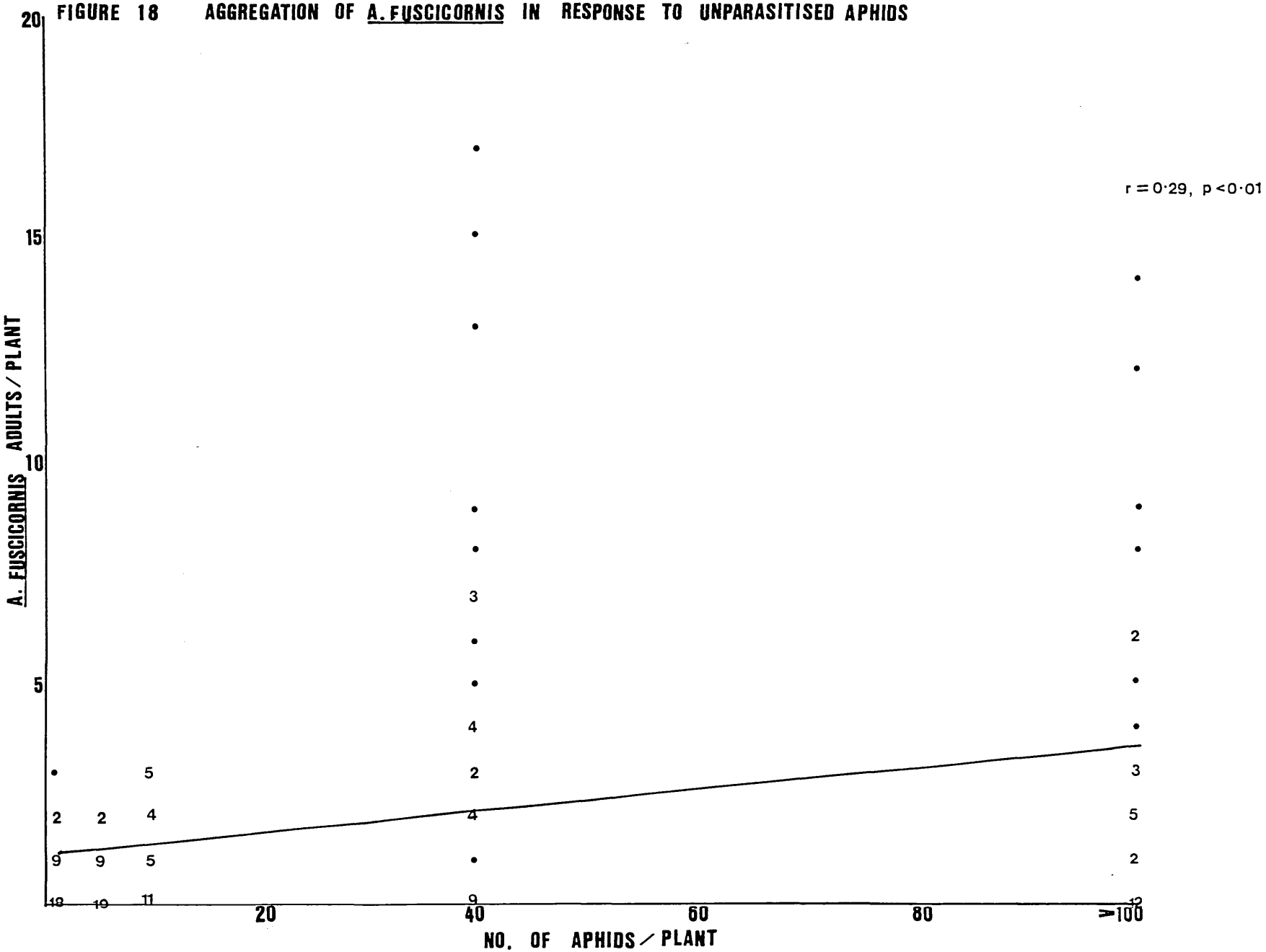
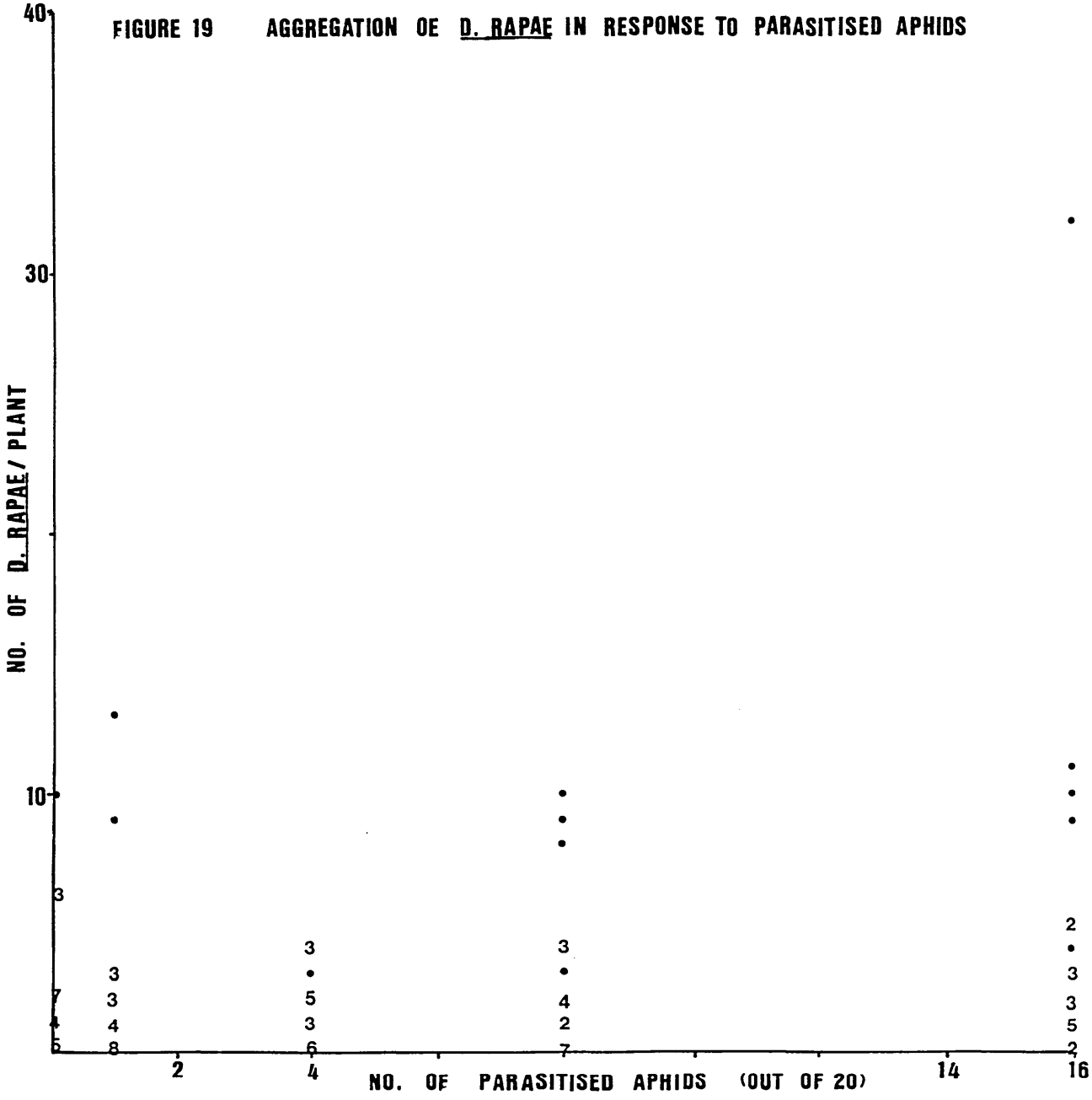


FIGURE 19 AGGREGATION OE D. RAPAE IN RESPONSE TO PARASITISED APHIDS



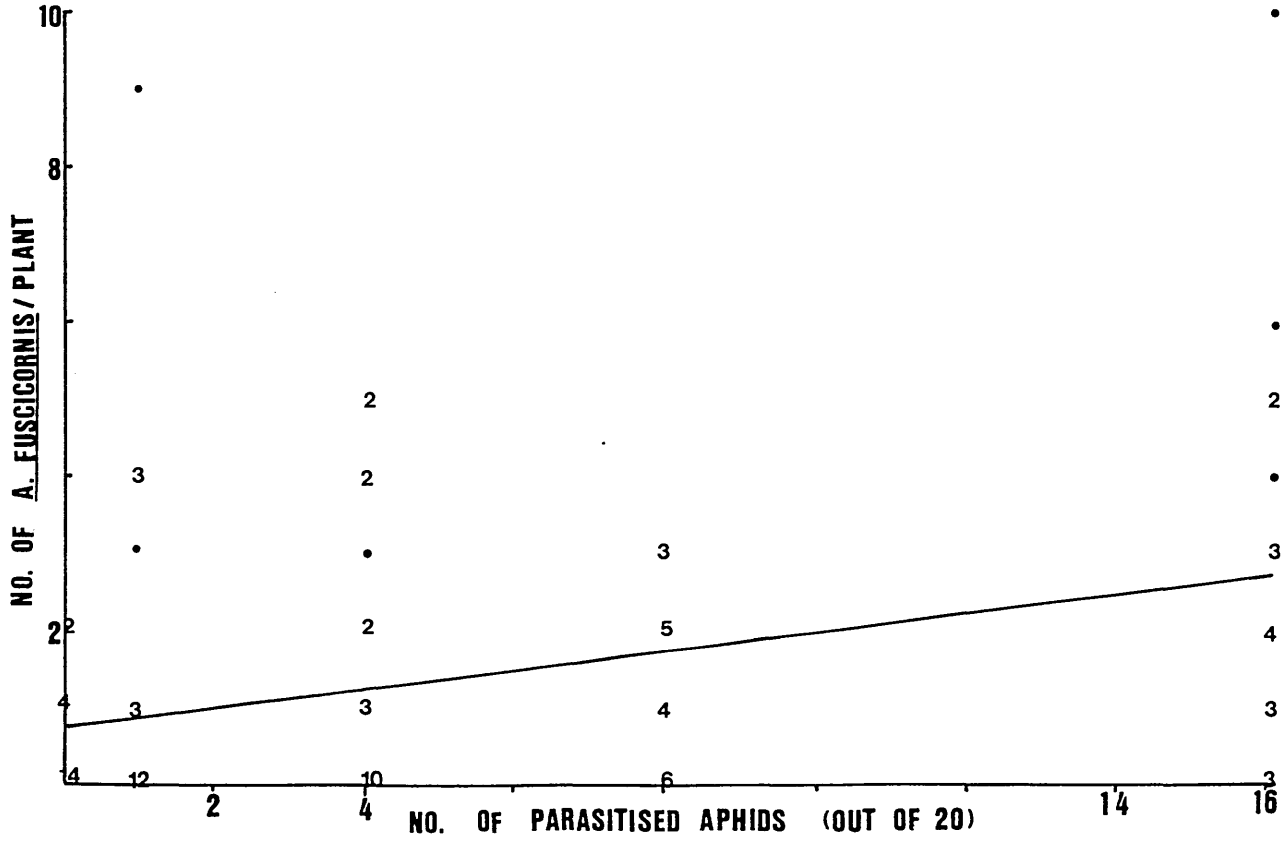
When the analysis was repeated without this point the regression was not significant.

Significantly ($p<0.05$) more hyperparasitoids were observed at the two highest host densities (8 and 16 out of 20 aphids parasitised) than when no parasitised aphids were present (Table 17). There was no significant difference, however, between the lowest and highest densities of parasitised aphids. A regression of the number of A. fuscicornis observed and host density was also significant ($p<0.01$), indicating some aggregation at higher densities (Figure 20). Again, there was no evidence of density dependent parasitism as a result of aggregative behaviour (Figure 21).

Discussion.

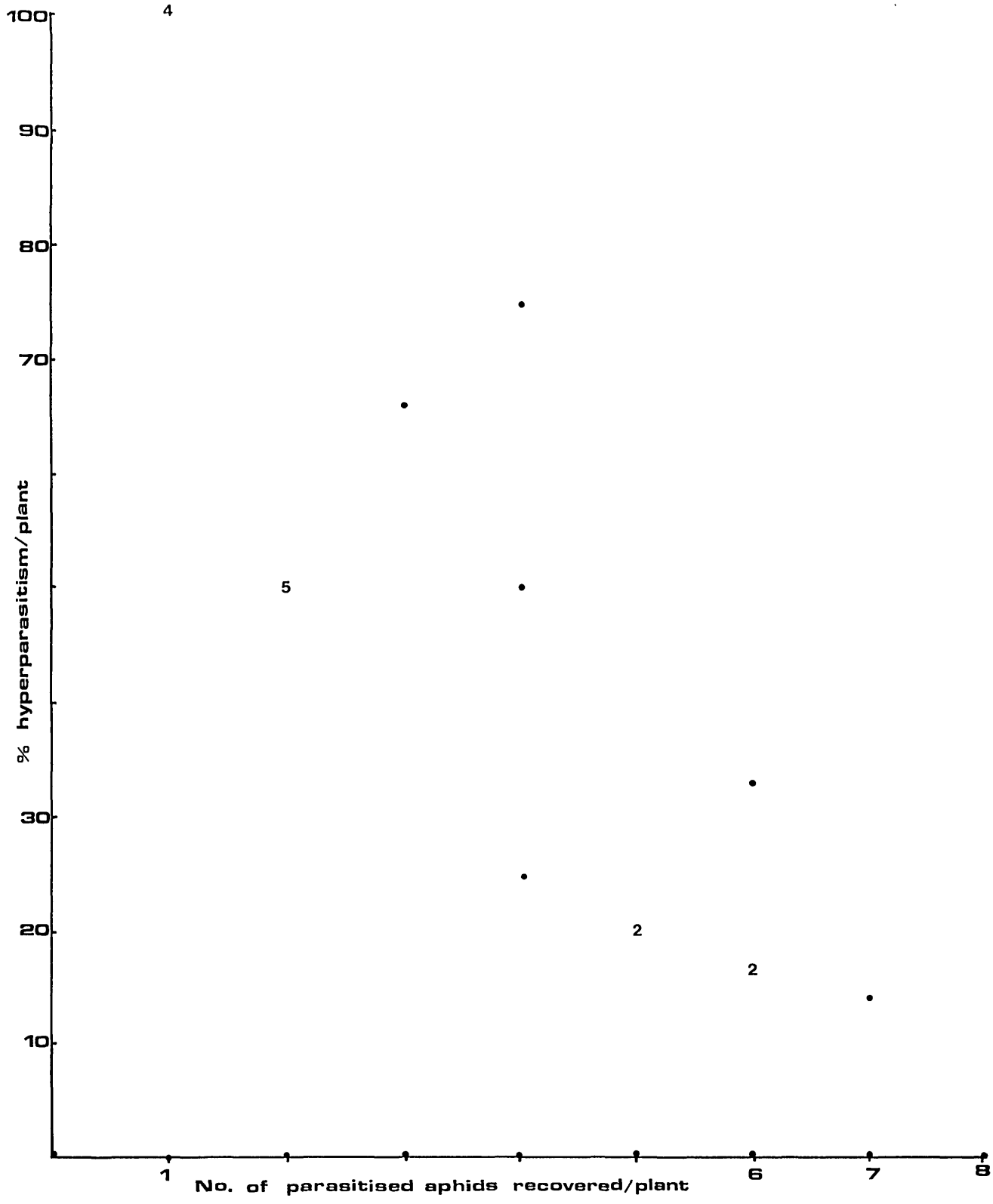
In the first section of this chapter, the low populations of aphids recorded at the beginning of the sampling period were probably due to the high rainfall and low temperatures prevailing throughout the summer of 1985. Low temperatures prolong the development time of B. brassicae (Akinlosotu 1973, Raworth et al 1984) so reducing the intrinsic rate of increase of the population. Heavy rain also has a detrimental effect on aphid populations (Hughes 1963). Hafez (1961) attributed the decline of percentage parasitism by D. rapae to two main factors; the effect of hyperparasitism and the limited egg supply and relative decrease in parasitoid activity at high host densities. The downward trend in the rate of parasitism may also be caused by changes in prevailing temperatures. As B. brassicae is reproductively active at lower temperatures than D. rapae (Akinlosotu 1973) aphid populations continue to increase

FIGURE 20 AGGREGATION OF A. FUSCICORNIS IN RESPONSE TO PARASITISED APHIDS



r = 0·29, p<0·01

Figure 21 Distribution of parasitism by A. fuscicornis



while those of the parasitoid are declining or static. Numerous authors have cited hyperparasitism as a major contributing factor in the decline of D. rapae populations at the end of the season (George 1957, Hafez 1961, Akinlosotu 1973, Oatman and Platner 1973, Chua 1975). Chua (1977) sampled D. rapae and A. fuscicornis adults, using sticky traps, from July until November. Populations of the primary parasitoid peaked in late September and those of the hyperparasitoid in mid-October. In the present study numbers of parasitised and hyperparasitised aphids suggested that the two populations peaked at approximately the same time. Chua also showed that A. fuscicornis emerged later in the spring than D. rapae, suggesting that the hyperparasitoid is better synchronised with its host population than D. rapae is with the aphid population.
As the host colonies of D. rapae and A. fuscicornis differed throughout the sampling period in their variance and mean (Figure 7), the hyperparasitoid must search for hosts in colonies which occur less frequently, are smaller and vary less in size than those of the parasitoid's hosts. Iwasa et al. (1981) predicted that the optimal foraging strategy which should be adopted by a parasitoid depended on the distribution of hosts. When all patches are of equal size the parasitoid should attack a fixed number of hosts in each patch and then leave. Clearly, this would not be an optimal strategy for either D. rapae or A. fuscicornis as both species search for hosts which occur in colonies of varying sizes (Figure 7). If there is a large variance in the number of hosts per patch, Iwasa et al. predicted that a 'fixed

giving-up time' strategy should be adopted. When the host distribution is Poisson, however, the optimal strategy would be to leave each patch after a fixed time. In most cases, therefore, it seems likely that the optimal strategy which should be adopted by both species is that of fixed giving-up time. When the densities of parasitised aphids are low, however, and their distribution becomes Poisson, A. fuscicornis might be more efficient if it foraged by a fixed time rule.

The hosts of D. rapae become increasingly more numerous towards the end of October, both in terms of number of aphid colonies and of colony size, corresponding to the increase in the aphid population. Similarly, the hosts of A. fuscicornis also increased during the sampling period in terms of the numbers of groups of parasitised aphids. This is probably due to both an increase in the parasitoid population and the increased availability of their hosts. The number of parasitised aphids per colony does not appear to increase with increasing colony size. This may be because of a refuge effect which prevents aphids in the centre of a large colony from being attacked. It must, therefore, become increasingly easier for the parasitoid and increasingly more difficult for the hyperparasitoid to locate their respective hosts as the season progresses. This is likely to be a major contributing factor to the decline of hyperparasitoid populations at the end of October.

Aphid colonies were most numerous and largest on the undersurfaces of leaves, in these positions they are likely to be protected from heavy rain which has a detrimental effect on aphid populations (Hughes 1963).

Colonies on the middle and lower leaves may be larger than elsewhere due to the mode of growth of the Brussels sprouts plant, with youngest leaves at the top and the oldest leaves at the bottom of the stem. Young colonies which are started by alatae alighting on the top of the plant would increase with size and age as the leaves matured and 'moved' down the stem (van Endem 1961). On wild Cruciferae, however, the distribution of B. brassicae is different with aphids occurring mainly on the inflorescences at the top of the plant, which are the preferred feeding site (Hughes 1963, Ayal 1987).

The distribution of colonies which have been attacked by D. rapae is a product of both the amount of searching time spent by the parasitoid on different parts of the plant and the original distribution of the aphids. It is the resulting distribution of parasitism, however, which influences the searching strategy of the hyperparasitoid. Ayal (1987) observed that D. rapae spends more time on the upper parts of the plant, probably because it has evolved on wild crucifers where aphids are most common on the flower heads. It seems likely, therefore, that more aphids will be attacked on the crown and upper leaves of Brussels sprouts. Significantly ($p<0.05$) more colonies were attacked by the parasitoid on the crown and undersurfaces of the middle and lower leaves than elsewhere on the plant. This is probably because colonies are most common on the middle and lower leaves and the parasitoid allocates more searching time to the crown. There were no differences in the number of aphids attacked per colony at different positions probably because

aphids in the centre of large colonies are inaccessible to parasitoids, due to honeydew and wax secretions and the defence reactions of aphids on the colony edge (George 1957, Akinlosotu 1973). This distribution could also be caused by egg limitation of D. rapae females attacking large colonies. Not surprisingly, groups of parasitised aphids within aphid colonies have a similar distribution to aphid colonies (i.e. they are most common on the undersurfaces of middle and lower leaves). Groups of parasitised aphids on the undersurfaces of middle leaves were larger and included more hyperparasitised aphids than groups elsewhere on the plant. The latter was probably a function of aphid distribution and parasitoid behaviour rather than the allocation of more searching time by hyperparasitoids. There was no significant difference between the number of groups of parasitised aphids which had been attacked by A. fuscicornis at different positions, despite the fact that the hosts were more frequent at some positions than at others. The distribution of host colonies and parasitism is summarised in Table 14. The difference between the searching patterns of D. rapae and A. fuscicornis is discussed further in the next chapter.

For both species in this study, the distribution of parasitism was not necessarily related to the spatial distribution of searching adults as, although both showed aggregative behaviour, there was no evidence of a density dependent relationship between the resulting distribution of parasitism and host density. Smith and Maelzer (1986) carried out a similar field experiment with various

densities of red scale and observations of the distribution of searching adults of A. melinus and the resulting pattern of parasitism. They also found that, although the parasitoid had a weak aggregative response, there was no evidence of density dependent parasitism. Similarly, Waage (1983) observed a field population of Diadegma sp. foraging for a range of densities of Plutella xylostella caterpillars and concluded that, although the parasitoid population spent more total time on higher density host patches, there was no positive density dependent parasitism.

Although at first only direct, and later inverse, density dependence were considered to promote stability, more recent authors (Hassell and May 1988) have shown that even when there is no pattern of density dependence between patches, the spatial distribution of parasitism can affect stability. Akinlosotu (1973) demonstrated in the laboratory that D. rapae spends increasing amounts of time on leaves with higher host densities. He attributed this to the change in behaviour of a searching female parasitoid which is elicited after encountering an aphid. The wasp shows increased turning which decays unless another host is encountered. Despite this behaviour, the percentage parasitism of aphids decreased at a decreasing rate as their density increased. A similar result was recorded by Hafez (1961) for D. rapae. This phenomenon was attributed to egg limitation and/or handling time (Akinlosotu 1973). Also, periods of inactivity increase with patch size, so that the rate of oviposition of a female parasitoid per unit time does not increase in proportion to increases in host density (Hafez 1961).

Generally, a number of hypotheses have been proposed to explain differences between the distribution of searching parasitoids and the resulting relative distribution of parasitism. The distance between patches may be a critical factor in determining the distribution of parasitism (Hassell 1982). For example, when Morrison et al. (1980) varied the distances between leaves bearing the hosts of Trichogramma spp., the relationship between percent parasitism and host density varied from inverse density dependence to density independence. This relationship may also depend on the overall density of hosts in the habitat (Hassell 1982).

Morrison and Strong (1981) considered spatial variations in egg density and the intensity of parasitism in the chrysomelid Cephaloleia consanguinea. They found an inverse relationship between overall probability of parasitism and egg density per leaf, despite apparent aggregation of adult parasitoids. They suggested that this may be because of increasing costs, in terms of energy and searching time, of finding each additional host egg on a leaf. The costs of achieving a given proportion of parasitised hosts is, therefore, greatest on leaves with high host densities. Alternatively, parasitoids which discover leaves with high host densities may suffer egg depletion which leads to a decrease in searching activity. Or, parasitoid egg supplies may be adequate but the rate of encounter with unparasitised hosts may decrease as the patch is exploited, causing the parasitoid to leave the leaf before a large proportion of the available hosts have been attacked.

Lastly, the exploitation of high host density patches may be limited by 'handling time'.

Hassell (1982) proposed a model, based on a negative binomial distribution of hosts, to explain this phenomenon. The number of hosts parasitised in a patch was given by a 'Type II' functional response, described by an attack equation (Rogers 1972) which arises from the Holling disc equation. On this basis, parasitism within a patch was shown to depend on host density, the number of parasitoids present (each spending a fixed time on the patch), the parasitoids' searching efficiency (the proportion of hosts encountered per parasitoid per unit searching time) and handling time. The maximum rate of parasitism per parasitoid within the patch was defined by time spent within the patch divided by handling time. In some cases, however, egg limitation rather than handling time will determine the maximum attack rate. In the absence of any aggregative response, the effect of handling time will be to reduce per cent parasitism as host density increases. With a weak aggregative response, as in the case of D. rapae and A. fuscicornis, and a low maximum attack rate, due to a large handling time or egg limitation, the percent parasitism will tend to be density independent. When the aggregative response is strong parasitism per patch will become density dependent as the aggregative response 'outweighs' the factors limiting the rate of parasitism within a patch (Hassell 1982).

D. rapae shows a weak aggregative response whose effects may be overcome by egg limitation at high host densities (Hafez 1961). Similarly, A. fuscicornis also has a weak aggregative response which probably does not result in density dependent

parasitism because of the limiting effects of handling time on the maximum rate of parasitism. The handling time of this species is comparatively large, firstly because females waste time probing both unparasitised and parasitised aphids and secondly, because on finding a parasitised aphid the wasp must locate parasitoid larvae within the haemocoel before oviposition can occur. Weseloh (1986) observed that percent hyperparasitism of Cotesia melanoscelus cocoons in different sized clumps, in the field, was density independent. He attributed this to the limitation of hyperparasitism by long host handling time and / or low reproductive capacities of the hyperparasitoids.

A. fuscicornis showed aggregative behaviour both to patches with varying numbers of unparasitised aphids and with constant overall numbers of aphids but varying numbers of parasitised aphids. This aggregative response will result in wastage of searching time and energy in the field when many aphid colonies contain no or only a few parasitised aphids. This behaviour is probably caused by the hyperparasitoid probing each aphid in order to detect parasitoid larvae, but it seems odd that the wasp does not appear to abandon the patch after a certain number of encounters with unparasitised aphids or after a certain length of time without ovipositing.

7. HOST SELECTION

The efficiency of parasitoid and hyperparasitoid foraging is directly linked to the success of reproduction and it seems likely, therefore, that foraging strategies are the subject of rigorous natural selection (Cook and Hubbard 1977, Hassell and Southwood 1978, van Alphen and Vet 1986). Parasitoids will tend to optimise the number of offspring produced per unit of foraging time. Many authors have considered the theoretical implications of optimal foraging and have developed mathematical models to describe the optimal strategy (eg. Cook and Hubbard 1971, Charnov 1976, Hubbard and Cook 1978, Comins and Hassell 1979, McNair 1986). The most adaptive solution in the field may differ from the one predicted by an optimisation model because of additional biological constraints not included in the model (van Alphen and Vet 1986).

Host species are often absent from the immediate vicinity in which adult female parasitoids emerge. In order to locate their hosts and oviposit they proceed through a hierachical process, which has been arbitarily divided into five steps; host habitat location, host location, host acceptance, host suitability and host reception (Doutt 1959, Mackauer 1973, Vinson 1976, Vinson and Iwanstch 1980, Vinson 1981). In many parasitoids these steps are overlapping and not clearly divisible (Arthur 1981).

Information on location of macrohabitats, such as forests or grassland, by parasitoids is limited, but it has been shown that plant volatiles are important at this and other stages

of host selection (Vinson 1976, 1981). Several species of the parasitic Hymenoptera are attracted to odours from their host's food plants. This relationship may be due to the evolution of insect parasitoids from plant parasitic species (Malyshev 1968). The alteration of the food plant by the hosts may cause the release of odours which are attractive to parasitoids, but several species are attracted by certain plants irrespective of whether their hosts are present (Doutt 1959). Other species respond directly to odours such as pheromones which are released by the host (Vinson 1976, 1981). The selection of a particular habitat in this way has the effect of restricting the range of hosts which are available to the parasitoid and is, therefore, of significance in determining host specificity (Stary 1964, van Alphen and Vet 1986).

After locating the microhabitat of the host, parasitoids may search areas in which the hosts are most likely to occur (Doutt 1959). For example, seven species of hyperparasitoids of C. melanoscelus were shown to attack unexposed host cocoons more readily than exposed cocoons, suggesting that hyperparasitoids tended to search unexposed areas of the habitat (Sickle and Weseloh 1974). Plant volatiles may be important in host location, but host-related chemicals frequently also have a role, especially over short distances.

Non-volatile compounds with high molecular weights are often important in the final stages of host location. Parasitoids do not perceive such chemicals until they are in contact with them (Vinson 1976) and typically respond by a change in

walking speed and an increase in the rate of turning (van Alphen and Vet 1986). 'Contact' chemicals include host traces near eggs, frass and host mandibular and labial gland secretions (Weseloh 1981). The function of contact chemicals in the process of host selection and location is unclear, but they appear to elicit an intense, directed search of the contaminated and surrounding areas (Vinson 1976).

On finding a host, a parasitoid may reject it if the correct stimuli are lacking. Host acceptance involves four steps; examination of the host, thrusting with the ovipositor, insertion of the ovipositor and oviposition. (Arthur 1981). This process is often mediated by physical criteria, such as size, shape, surface texture and movement. For example, Trichogramma females will probe objects of a certain size, regardless of their shape or texture (Salt 1935). Chemical stimuli are generally less important than in the previous steps, but some species are stimulated to accept a host by chemotactile stimuli on the cuticle or within the host (Arthur 1981). It is difficult, however, to separate the effects of contact chemicals and physical properties of the host (Vinson 1976). Host odours may result in a reflex action of the ovipositor, such as probing, but a host must be present before egg release will occur.

(After a host has been accepted it may be immune or otherwise unsuitable for the development of the parasitoid progeny (Doutt 1959, Vinson and Iwanstch 1980)).

This chapter aims to consider the first three steps in the foraging process (i.e. habitat location, host location and host acceptance, which together are known as host selection (Mackauer 1973)). Few studies have considered the foraging strategies of hyperparasitoids (but see Gutierrez and van den Bosch 1970 a and b, Gutierrez 1970 a, b and c, Weseloh 1968, 1971a, 1971b, 1972). It seems likely that their process of host selection will be similar to that of parasitoids. Hyperparasitoids must, however, include an additional step in the foraging process as they must find, not only the phytophagous host, but also parasitised individuals within the host population. The loss of efficiency in host detection due to this extra step might be compensated by changes in the overall foraging strategy.

7.1 Host location.

Once within the host habitat, which in this case is likely to be a brassica crop such as Brussels sprouts, the parasitoids and hyperparasitoids must locate aphid colonies. Females of both species tend to remain on the crop and show less dispersive activity than males (Vater 1971). Until recently it had been assumed that female parasitoids locate their hosts by random searching on plants (Hafez 1961, Read et al. 1970). Ayal (1987) carried out detailed observations on the movement of D. rapae females on uninfested Brussels sprouts plants. These studies revealed a non-random search pattern which corresponded with the distribution of aphids on wild crucifer plants. Parasitoids move between plant parts by walking while palpating the plant surface with

their antennae. They tend to move upwards on the stem and the upper sections of the plant, in particular the heart, were visited most frequently. After foraging unsuccessfully for some time the parasitoids flew off the top of the plant. This foraging behaviour was modified when the plants were contaminated with honeydew. On encountering a contaminated area on a leaf surface the parasitoids moved rapidly on the contaminated surface, turning when they reached its borders (klinotaxis). The behaviour on a contaminated plant involved three basic responses;

(a) a klinotactic response to a contaminated horizontal surface. This was followed by upward flight if no hosts were encountered.

(b) upward movement on a contaminated section of vertical stem.

(c) downward movement on an uncontaminated vertical surface and a contaminated surface.

D. rapae, therefore, has a basic directional searching pattern on cruciferous plants which is modified in the presence of aphid honeydew. This behaviour increases the time spent searching areas which are likely to be infested by aphids and so increases the chances of oviposition. As the hosts of A. fuscicornis have a similar distribution in the field (see Chapter 5), it seems likely that female hyperparasitoids will adopt a similar searching pattern. The following experiment was carried out to compare the searching behaviour of A. fuscicornis with that of D. rapae.

Method.

A small uninfested Brussels sprouts plant was placed in a Perspex cage (dimensions 450 mm x 470 mm x 500 mm). The plants used had approximately nine leaves (4 lower leaves and 4 to 5 upper leaves), plus a group of tightly curled leaves at the top of the stem, the 'heart'. One hyperparasitoid female at a time was introduced to the cage. The following were recorded using an eight channel 'Rustrak' event recorder; time from introduction to landing on the plant, time on stem, heart, upper and lower leaves, time on upper and lower leaf surfaces, time spent searching or resting and direction of movement on the plant stem. These observations were continued until the hyperparasitoid left the plant.

They were repeated on a similar plant on which half the upper surface of one of the four lower leaves and the petiole and stem beneath it had been contaminated with honeydew solution. Honeydew was collected from aphid cultures and diluted with water, it was then applied to the plants with a fine brush and allowed to dry. Treated surfaces were shiny and easily distinguished from untreated surfaces.

Ten replicates were carried out for both uncontaminated and contaminated plants using a different hyperparasitoid female for each replicate.

Results.

Generally, the pattern of foraging employed by A. fuscicornis females on uninfested plants was similar to that of D. rapae, as recorded by Ayal. Hyperparasitoids tended to alight on the upper surfaces of lower leaves and, having searched them, they walked along the petiole, often returning to the leaf a few times before reaching the stem. Overall their movement was upward (i.e. negative geotaxis) as they alighted on lower leaves and flew off upper leaves at the end of a foraging bout. On the stem, however, they frequently walked upwards for a short distance then turned and walked down, checking leaf nodes on their way. Occasionally they searched up and down a leaf petiole without visiting the leaf surface.

As with D. rapae equal amounts of time were allocated to searching upper and lower leaf surfaces (Table 18), irrespective of the presence of honeydew. Searching was concentrated on the upper leaves of the plant, which received a significantly ($p < 0.001$) higher proportion of the total time than any other area (Table 19). This is also similar to the allocation of foraging time by D. rapae, but the hyperparasitoids spent a much lower percentage of total time on the heart (approximately 4% in comparison to 25% observed for D. rapae by Ayal). Significantly ($p<0.05$) longer was spent on the first leaf to be visited than on any of the other leaves (Table 20).

The mean length of time spent on plants treated with honeydew did not differ significantly from that spent on untreated plants (1467.61 and 1324.85 seconds, respectively).

Table 18: Time spent on upper and lower leaf surfaces (seconds ± S.E.)

	upper	lower
no honeydew	412.31 ± 190.92	428.93 ± 147.95
with honeydew	414.25 ± 103.31	408.69 ± 129.02

Table 19: Proportion of time spent on different parts of the plant (without honeydew).

	upper leaves	lower leaves	heart	stem
mean	0.68	0.19	0.04	0.08
S.E.	± 0.07	± 0.06	± 0.03	± 0.05

Table 20: Time spent on first and subsequent leaves (seconds).

	First leaf	Subsequent leaves	
mean	94.03	48.93	$p<0.05$
S.E.	± 28.07	± 17.46	

Table 21: Proportion of time spent on different parts of the plant (with honeydew).

	upper leaves	lower leaves	heart	stem
mean	0.69	0.25	0.05	0.01
S.E.	± 0.07	± 0.08	± 0.02	± 0.006

On encountering a treated area the wasp became excited, the speed of walking increased and it turned back on reaching the edges of the treated area. The searching behaviour of hyperparasitoids on treated plants appeared to be only slightly modified; a higher proportion of time was spent on the lower leaves than previously (Table 21).
The foraging pattern of A. fuscicornis on uninfested plants is, therefore, directed and non-random, with certain areas being visited for longer periods than others. This is similar to that of D. rapae and is likely to increase the success of the hyperparasitoid in locating parasitised aphids.

7.2 Response of A. fuscicornis to D. rapae females.

A. fuscicornis females are attracted to D. rapae females in an olfactometer (Read et al. 1970) and sex pheromones are known to play a part in the courtship behaviour of the primary parasitoid (Askari and Akishah 1979). It seems likely that hyperparasitoid females respond to the sex pheromones of their hosts during the 'habitat location' phase of host selection. This behaviour is not unique and several parasitoids are attracted by the sex or aggregation pheromones of their hosts (Hassell and Southwood 1978, Vinson 1981, Weseloh 1981, van Alphen and Vet 1986). The egg parasitoid, Trichogramma, for example, responds to the pheromones of its adult hosts and so is attracted to areas in which the hosts are ovipositing (Lewis et al. 1982). Similarly, parasitoids such as Aphytis melinus De Bach and A. coheni De Bach are attracted by the sex pheromones of

their coccid hosts (Sternlicht 1973). In a hyperparasitoid, such an attraction might be less beneficial, as females oviposit in parasitoid larvae which are several days old and not in newly deposited eggs (Broussal 1966, Chapter 3). It is not known, however, whether A. fuscicornis responds to host pheromones only over long distances. The following experiment was carried out to examine the responses of A. fuscicornis females to their adult hosts over short distances.

Method.

A small Brussels sprouts plant (with 4 upper and 4 lower leaves) was placed in a Perspex cage (450 x 470 x 500 mm). Any aphids present were removed and the plant was washed with water to remove any traces of honeydew or wax. Clip cages were attached to each of the four upper leaves. One D. rapae female was placed in each of two of the clip cages on opposing leaves, the other clip cages were left empty. A hyperparasitoid female was placed gently on one of the upper leaves and allowed to forage. Time spent resting and searching on the leaf was recorded. The hyperparasitoid was removed from the cage when it had been off the leaf for more than three minutes.

This was repeated, with a different wasp being placed on each leaf, until all four leaves had been visited and then the plant was replaced. Ten replicates were carried out for each leaf type (i.e. with or without a parasitoid).

Table 22: Time spent on a leaf in relation to the presence of a parasitoid (± S.E.)

	searching time	total time
with parasitoid	240.79 ± 53.27	760.87 ± 239.68
without parasitoid	503.07 ± 189.65	1413.14 ± 361.94

Results.

It can seen from Table 22 that there was no significant difference between the total time spent searching on leaves with or without parasitoids. Hyperparasitoid females do not, therefore, appear to modify their searching behaviour in the presence of primary parasitoid females. Kairomones produced by female parasitoids do not appear to be important in short range host detection by A. fuscicornis. It is possible that the presence of clip cages and the restriction of the experiment to a cage interfered with the development of suitable odour plumes. This experiment was, therefore, repeated in the field.

If female hyperparasitoids respond to kairomones produced by the primary parasitoid it seems likely that they would visit plants were D. rapae females are present more frequently than plants without D. rapae females. Also A. fuscicornis females should visit plants infested with parasitised aphids more frequently and spend longer on them than on plants infested only with healthy aphids.

The following experiment was carried out at Silwood Park in September and October 1986.

Method.

The experiment was carried out in a plot of Brussels sprouts (roughly 1200 plants) which had been planted the previous spring and which were now at the 20 to 30 leaf stage. Sixteen plants from the plot were placed in large polythene pots. All the aphids were removed from each plant and they were reinfested using insects from laboratory cultures as

follows, according to a 4 x 4 Latin square design: four plants had unparasitised aphids, four had parasitised aphids, four had two D. rapae females in clip cages and four plants were not reinfested (controls). Plants with aphids were infested the day before the experiment, and the leaves with aphids were covered with muslin to prevent access by parasitoids or predators. The aphids were allowed to settle overnight and the muslin was removed the following morning. The numbers of parasitoids and hyperparasitoids present on each plant was recorded at ten minute intervals throughout the day until both species had stopped searching. The observations were continued for a second day when weather permitted.

This experiment was repeated three times, but due to adverse weather conditions only four days of observations were recorded.

Results.

The results and parameters calculated using GLIM analysis are shown in tables 23 to 26. Primary parasitoids were observed more frequently on the plant with parasitised aphids than on the control plants. As can be seen from Table 25 significantly more hyperparasitoids were observed on plants with parasitised aphids than on any of the other treatments. There was no significant difference between the numbers of hyperparasitoids observed on plants with D. rapae females and the controls. There were also no significant differences between the numbers of wasps observed per plant for both species between different days.

7.3 Responses of *D. rapae* and *A. fuscicornis* to aphid honeydew.

In many parasitoid species contact chemicals are important cues in the process of host selection (Vinson 1976, 1981, Weseloh 1981). On making physical contact with such chemicals parasitoids undergo a behavioural change and typically begin an intense examination of the contaminated substrate due to a reduction in walking speed and an increase in turning (klinokinesis) (Weseloh 1981, van Alphen and Vet 1986). Contact chemicals have been recorded from a variety of host-related substances including frass, mandibular and labial gland secretions, silk, webbing and moth scales (Weseloh 1981, Chiri and Legner 1982). Some species of predators and parasitoids are known to respond to a contact chemical in host honeydew (Vinson *et al.* 1978, Bouchard and Cloutier 1984, Carter and Dixon 1984). *D. rapae* and *A. fuscicornis* may also respond to honeydew as a source of contact chemicals and the following experiment was conducted to test their response to host secretions.

Method.

Honeydew was collected from aphid colonies and dissolved in an equal volume of water. One drop was added to the centre of a piece of filter paper in a Petri dish. After allowing a few minutes for the honeydew to dry, a parasitoid female which had been experienced two to three hours previously for 30 minutes with 10 to 20 aphids, was introduced to the dish. The movements of the parasitoid were traced on a piece of acetate paper which was fixed to the lid of the Petri dish.

Table 23: Mean numbers of *D. rapae* observed.

Treatment	parasitoids/plant	S.E.
unparasitised aphids	13.00	7.23
parasitised aphids	32.75	10.23
D. rapae females	16.75	10.23
control	3.56	10.23

Table 24: Mean numbers of *D. rapae* observed on different days

Day	parasitoids/plant	S.E.
1	9.06	10.34
2	19.00	10.34
3	16.00	10.34
4	3.24	10.34

Table 25: Mean numbers of A. fuscicornis observed.

Treatment	parasitoids/plant	S.E.
unparasitised aphids	6.25[a]	2.00
parasitised aphids	12.50[b]	2.83
D. rapae females	1.44[b]	2.83
control	0.75[b]	2.83

Table 26: Mean numbers of A. fuscicornis observed on different days

Day	parasitoids/plant	S.E.
1	4.12	2.88
2	4.312	2.88
3	6.25	2.88
4	6.25	2.88

This was repeated with a hyperparasitoid female and six replicates were carried out for each species.

Results.

The responses of the parasitoid and hyperparasitoid are shown in Figures 22 and 23, respectively. On contacting the area contaminated with honeydew individuals of both species showed a reduction in walking speed and, as can be seen from the traces, an increase in the rate of turning. This type of behaviour should tend to concentrate the searching time of the parasitoid in the vicinity of the host and is advantageous to parasitoids such as D. rapae and A. fuscicornis whose hosts occur in colonies.

7.4 Patch exploitation.

Once she has encountered an aphid colony a parasitoid must make two decisions, whether to accept or reject individuals for oviposition and, secondly, how much time to allocate to that colony or patch.

Host acceptance by insect parasitoids is generally based on a number of criteria. Many parasitoids are stimulated to accept or reject a host by chemotactile stimuli on the cuticle or in the body. Kairomones that stimulate host acceptance have also been found in host frass, haemolymph, labial and mandibular gland secretions (Arthur 1981). Physical factors are also important at this stage of host selection. Acceptance is limited to hosts of a certain size in several parasitoid species (Arthur 1981). In other species shape, sound, surface texture and presence or

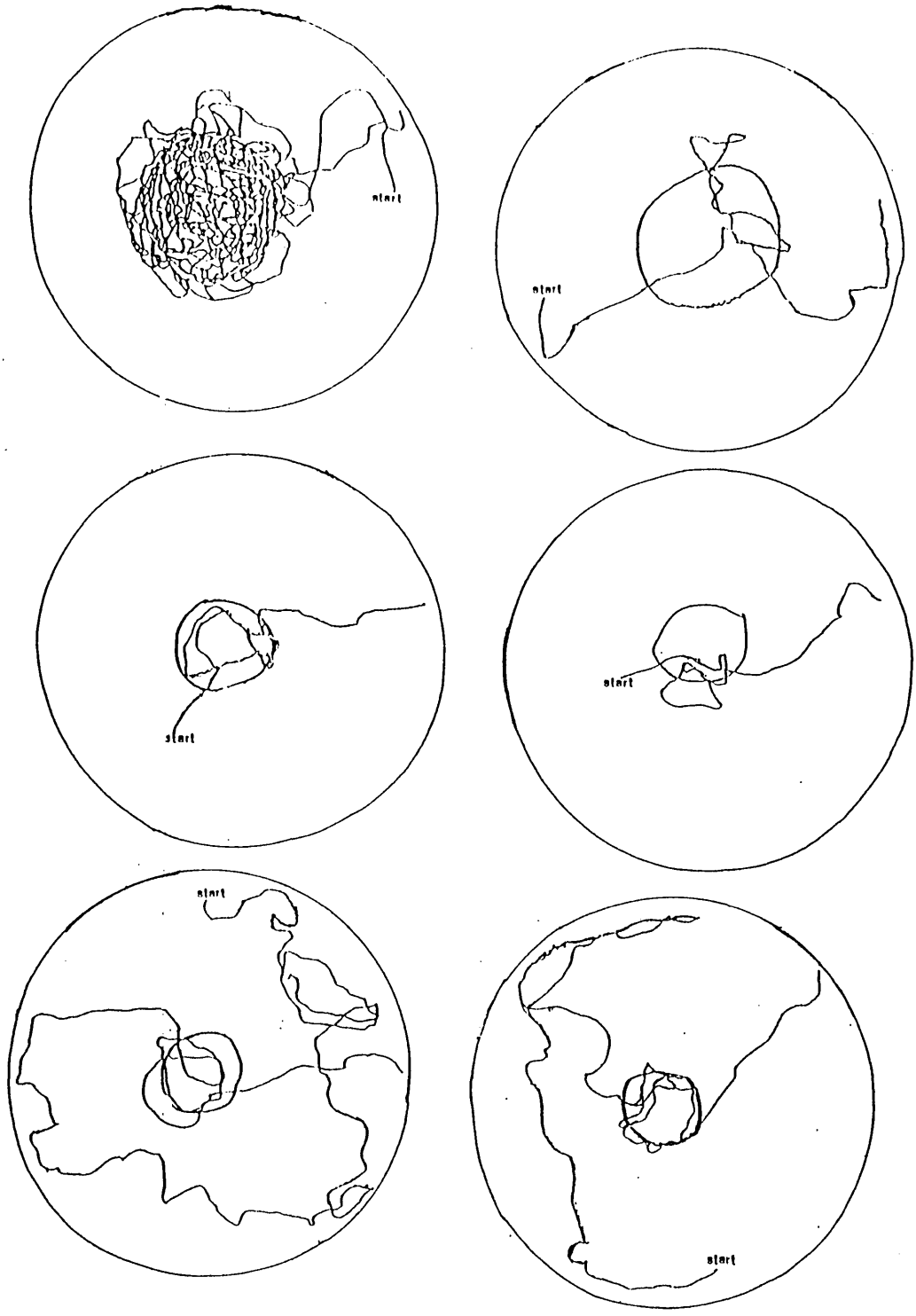


Figure 22 Response of D. rapae to aphid honeydew

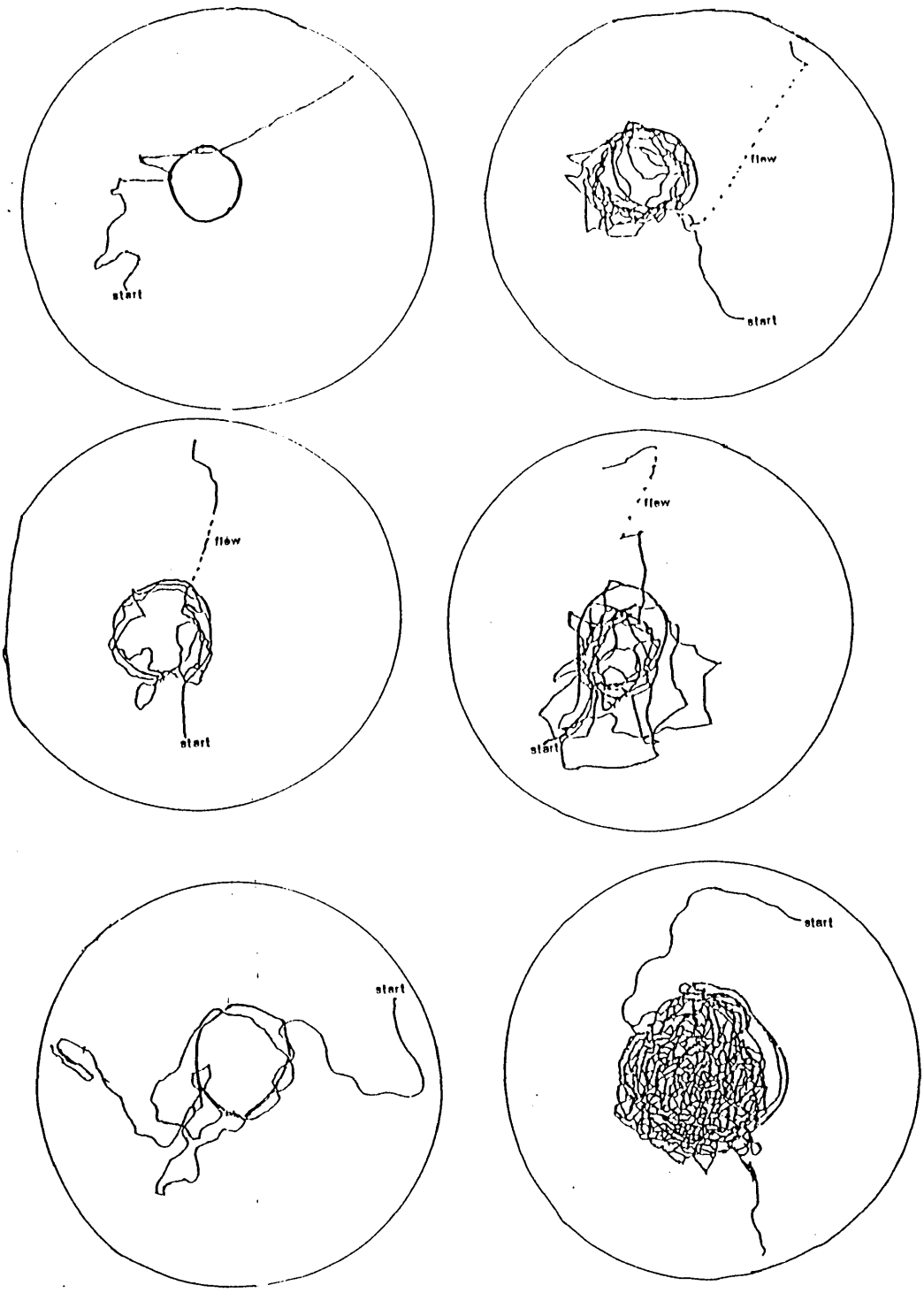


Figure 23 Response of A.fuscicornis to aphid honeydew

absence of movement are important mediating factors (Vinson 1975, Arthur 1981).

Host acceptance or rejection by D. rapae and A. fuscicornis could be determined either prior to encountering a host, during examination with the antennae or during the probing stage.

Parasitoids which could reject hosts at the first or second stages would waste less time on unsuitable hosts than those which must probe a host in order to determine its suitability for oviposition.

A parasitoid which is foraging in a habitat containing a number of host patches of varying densities should base its foraging pattern on two decisions; which patches to visit and how long to remain in each patch. (A patch is considered to be a limited area whose boundaries are defined by the searching behaviour of the parasitoid i.e. the area within which the parasitoid perceives the host (Waage 1977, van Alphen and Vet 1986)). Changes in behaviour frequently occur in response to contact chemicals produced by the host (Waage 1977, Carter and Dixon 1984). It seems reasonable to assume that, within this system, both D. rapae and A. fuscicornis females perceive aphid colonies as patches.

A number of simple mechanisms have been suggested by which a parasitoid or predator might decide when to leave a patch:

(a) Number expectation rule; the parasitoid leaves the patch after it has encountered a fixed number of hosts (Krebs 1973).

(b) Time expectation rule; the parasitoid leaves the patch after a fixed length of searching time (Gibbs 1962).

(c) Fixed giving-up time rule; the parasitoid leaves the patch if it does not encounter a host within a threshold time. After a host has been encountered the parasitoid's 'clock' is reset to zero and it continues to search until another host is found or the 'giving-up' time has elapsed (Hassell and May 1974, Murdoch and Oaten 1975).

These rules do not, however, strictly apply to decision making in hyperparasitoids. These may respond either to encounters with all phytophagous insects in a colony or only to parasitised individuals (which are not yet hyperparasitised). Assuming that the primary parasitoid leaves the patch before encountering all the hosts present, it would be inefficient for a hyperparasitoid to leave a patch after encountering only one unparasitised individual. It would be also be undesirable for the hyperparasitoid to continue searching a patch were only a small proportion of phytophagous insects are parasitised. Decisions about patch leaving in hyperparasitoids must, therefore, be related to both encounter rates with healthy and with parasitised individuals. The three basic rules of patch leaving may be rewritten as follows:

(a) Number expectation (i) leave after encountering a fixed number of phytophagous insects (regardless of the number parasitised) (ii) leave after encountering a fixed number of parasitised aphids (ignoring encounters with unparasitised individuals).

(b) Time expectation; leave after a fixed time.

(c) Fixed giving-up time (i) leave when a fixed amount of time has elapsed without encountering any aphids.

(ii) leave when a fixed amount of time has elapsed without encountering any parasitised aphids.

The following experiment was designed to test the ability of the parasitoid and hyperparasitoid to distinguish between hosts and non-hosts and to allocate their searching time according to the quality of the patch. In the field, many aphid colonies escape parasitism by D. rapae and, to maximise the number of ovipositions in her lifetime, a hyperparasitoid female should not waste time searching for hosts in a healthy colony. Also D. rapae females tend not to parasitise all the aphids in a colony. Patch quality for hyperparasitoids will, therefore, depend on three factors; proportion of aphids which are parasitised, number of parasitised aphids and the number of aphids which are already hyperparasitised. For primary parasitoids, however, only two factors will be important; number of aphids present and number which are already parasitised. Although the avoidance of parasitised aphids by D. rapae is not strictly analogous to avoidance of unparasitised aphids by A. fuscicornis, it is most closely related to the situation in the field. An analogous comparison might be the avoidance of unsuitable aphid species by D. rapae, but this does not arise frequently and on brassicas in the field.

Method.

A disc (diameter 4 cm) was cut out of a Brussels sprouts leaf and placed, underside uppermost, in the centre of a Petri dish. Thirty-two unparasitised aphids (second to third instar, five days old) were placed on the disc and allowed

to settle for 30 minutes. A female hyperparasitoid which had been exposed to six parasitised aphids for four hours, two days previously, was introduced to the dish. The wasp was observed as it foraged on the 'patch' and the following were recorded using an eight channel 'Rustrak' event recorder: total time on leaf, time spent searching, resting and probing aphids, number of antennal contacts and number of aphids probed. The wasp was removed from the Petri dish when it had been off the leaf disc, engaged in any activity, for two minutes, this was replicated ten times, using a different wasp and fresh aphids for each replicate.

The above procedure was repeated using similarly experienced A. fuscicornis females and 32 aphids which had been parasitised by exposing them individually to a D. rapae female, three days previously. This was repeated with a mixed group of 16 parasitised and 16 unparasitised aphids on the disc. The parasitised and unparasitised aphids were distinguished by marking the hind legs of one group with a water soluble felt marker. The marked group was alternated when half the replicates had been completed. Sixteen parasitised aphids alone were then placed on the patch and the same observations were recorded.

Newly emerged D. rapae females were experienced by exposing them to ten unparasitised aphids for four hours. After two days they were placed in a Petri dish, as above, with a leaf disc with one of four patch types: 32 unparasitised aphids, 32 parasitised aphids, 16 parasitised plus 16 unparasitised aphids and 16 unparasitised aphids. The same observations were recorded as for the hyperparasitoid, except that time spent attacking each aphid replaced probing time and number

of ovipositor stabs per aphid were also recorded. Ten replicates were again completed for each treatment.

Results.

D. rapae and A. fuscicornis females have striking differences in their methods of oviposition. D. rapae, on contacting a host with its antennae, doubles its abdomen over and shoots it out from beneath the thorax to stab the host with the ovipositor. The aphid under attack frequently reacts by kicking out with its hind legs and moving away from the parasitoid. Several stabs are often necessary before oviposition is achieved and hosts are occasionally abandoned without successful oviposition.

In contrast, on finding an aphid an A. fuscicornis female will examine it with her antennae before climbing onto its back. The aphid may react by kicking but the hyperparasitoid is rarely dislodged. The wasp positions herself over the dorsal surface and inserts her ovipositor. During this phase of oviposition the wasp appears motionless with her antennae pointing backwards and her abdomen slightly lowered. If no parasitoid larvae are found in the haemocoel the hyperparasitoid may alter her position and probe again or abandon the aphid. If the aphid is parasitised oviposition occurs and the wasp dismounts and begins the search for a new host.

It seems reasonable to assume that D. rapae and A. fuscicornis will distinguish between aphids which are suitable or unsuitable for oviposition during one or more of three steps in host acceptance; before antennal contact,

during antennal contact or during probing. If the first statement were true, only parasitised aphids would be examined with the antennae by A. fuscicornis and only unparasitised aphids by D. rapae. As can be seen from Table 27, there is no significant difference between the total number of unparasitised or parasitised aphids contacted for either parasitoid. If discrimination occurred as a result of antennal contact more 'non-hosts' than hosts would be rejected after antennal contact. The ratio (R) of the number of 'non-hosts' rejected after antennal contact to the total number of antennal contacts was calculated. In this case primary parasitoid females can distinguish between parasitised and unparasitised aphids (Table 28, $p<0.05$) when they occur separately. When this parasitoid encounters both aphid types together, however, there is no significant difference between rejection of parasitised and unparasitised aphids following antennal contact.

The hyperparasitoid cannot determine whether an aphid is suitable for oviposition using the antennae.

At the final stage of host acceptance, i.e. probing with the ovipositor, both species show at least partial discrimination. This is evident from a reduction in probing time in suitable aphids (Table 29). D. rapae can again discriminate only when parasitised and unparasitised aphids occur separately, A. fuscicornis, however, shows a significantly longer probing time in parasitised aphids, both in mixed and unmixed patches. D. rapae attacked significantly ($p=0.004$) more aphids on high quality patches (i.e. patches with 32 unparasitised aphids) than on low quality patches (i.e. 32 parasitised aphids or 16 unparasitised aphids) (Table 30).

It is, therefore, unlikely that D. rapae uses a fixed number rule to decide when to leave a patch. Also significantly more total time and more searching time were spent on profitable patches than on low quality patches, suggesting that D. rapae does not use a fixed time mechanism (Table 31).

There was no significant difference between the giving-up times on different patches (Table 31).

Similarly, A. fuscicornis females attacked more hosts and spent significantly longer on high quality patches (32 parasitised aphids) than on low quality patches (32 unparasitised aphids or 16 parasitised aphids) (Tables 32 and 33). Again, although giving-up times were longer on high quality patches, there were no significant differences between different patches (Table 34).

Hyperparasitoid females were shown to have a significantly longer mean probing time per host than primary parasitoid females (Table 30). This is probably due to the extra step in the searching process of the hyperparasitoid, i.e. drilling through the aphid cuticle and location of parasitoid larvae in the haemocoel. 'Mean probing time' is probably related to overall handling time although it does not account for time spent cleaning and resting after oviposition. Hassell (1978) noted that estimates of handling time obtained by observation tend to differ from those predicted by mathematical models, as the former only consider actual oviposition time.

Table 27: Number of antennal contacts with parasitised and unparasitised aphids, on a mixed patch (± S.E.)

	D. rapae	A. fuscicornis
unparasitised aphids	18.3 ± 3.53	18.4 ± 3.73
parasitised aphids	20.1 ± 3.73	18.3 ± 4.18

Table 28: Ratio of aphids rejected after antennal contacts to total number of contacts (± S.E.).

		D. rapae	A. fuscicornis
separate patch			
32	unparasitised	0.16 ± 0.04	0.29 ± 0.04
		p<0.05	N.S.
32	parasitised	0.36 ± 0.03	0.20 ± 0.03
mixed patch			
	unparastised	0.22 ± 0.04	0.32 ± 0.06
		N.S.	N.S.
	parasitised	0.21 ± 0.03	0.39 ± 0.08

Table 29: Probing times per patch (seconds ± S.E.)

	D. rapae	A. fuscicornis
seperate patch		
32 unparasitised	1746.30 ± 381.05	191.09 ± 35.42
	p<0.005	p<0.004
32 parasitised	228.24 ± 43.96	3445.50 ± 977.78
mixed patch		
unparasitised	150.48 ± 35.10	778.47 ± 412.67
	N.S.	p<0.01
parasitised	157.20 ± 25.99	1273.40 ± 241.28

Table 30: Number of aphids attacked by D. rapae (± S.E.)

	32 unparasitised	32 parasitised	16 unparasitised
No. attacked	51.80 ± 6.23	21.30 ± 3.45	20.30 ± 3.86

Table 31: Time spent on patches by D. rapae (seconds ± S.E.)

	total time	searching time	giving-up time
32 unparasitised	4757.10 ± 687.16	1422.50 ± 248.87	188.87 ± 69.57
32 parasitised	541.04 ± 96.45	284.11 ± 53.13	44.60 ± 12.55
mixed	709.65 ± 121.43	358.98 ± 76.84	58.23 ± 21.16
16 unparasitised	1071.10 ± 288.39	352.82 ± 85.06	83.44 ± 28.00

Table 32: Number of aphids attacked by A. fuscicornis

(± S.E.)

32 unparasitised	32 parasitised	16 parasitised
10.6 ± 1.61	48.2 ± 12.20	16.4 ± 1.94

Table 33: Time spent on patches by A. fuscicornis (± S.E.)

	total time	searching time	giving-up time
32 parasitised	5629.60 ± 1259.85	1074.1 ± 174.56	214.92 ± 131.23
32 unparasitised	689.78 ± 111.63	302.90 ± 56.60	92.97 ± 43.32
mixed	3626.50 ± 644.78	804.80 ± 163.80	208.64 ± 95.18
16 parasitised	3483.40 ± 577.43	608.74 ± 103.09	175.74 ± 60.08

Although A. fuscicornis females spend significantly longer on a patch of 32 hosts than D. rapae females on an equivalent patch, they parasitise the same number of hosts (Tables 30 and 32). This also suggests a greater handling time for A. fuscicornis. The ratio of handling time to longevity is, however, thought to be more meaningful than just handling time. (Hassell 1978). The longevity of A. fuscicornis is considerably greater than that of D. rapae (Hafez 1961, Vater 1971, Chapter 3) thus perhaps compensating for the longer handling time of the hyperparasitoid.

It appears, therefore, that both species can distinguish aphids which are suitable or unsuitable for oviposition. In D. rapae this discrimination may be partial as it appears to operate only when the two aphid types are presented separately. This agrees with the results found both experimentally and in the field sampling programme (see Chapters 4 and 5, respectively) where D. rapae was shown to have low avoidance of superparasitism.

7.5 Effect of unparasitised aphids on the time spent by A. fuscicornis on a patch.

A. fuscicornis females can detect unparasitised aphids and allocate their searching time so that patches with unparasitised aphids receive less time than those on which all aphids are parasitised. Van Lenteren (1981), referring to parasitoids, stated that 'discrimination initiates migration after a number of probes at or in parasitised hosts'.

It is likely that this will be true for hyperparasitoids encountering unparasitised hosts.

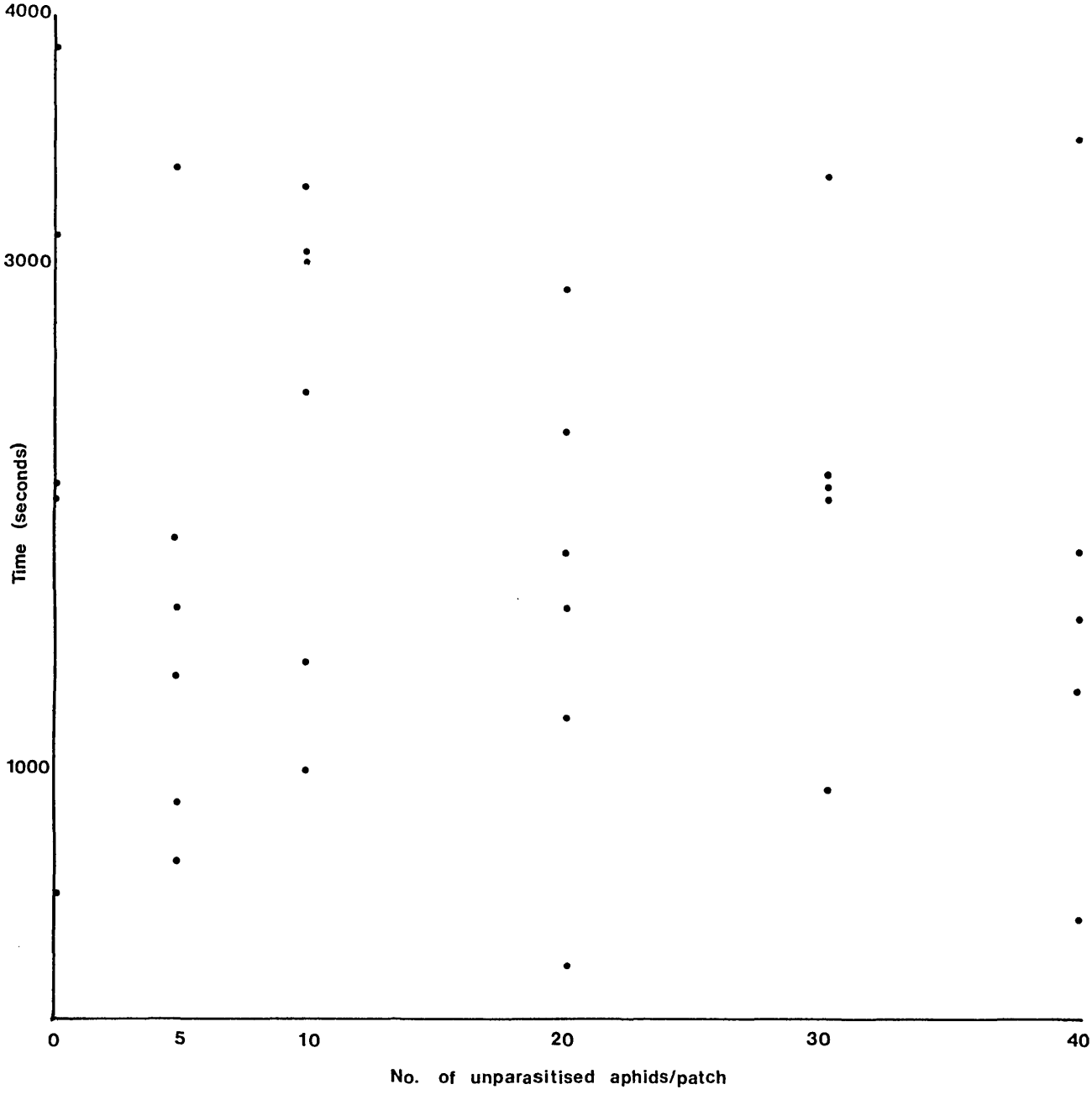
Method.

An experiment similar to that described above was carried out. A leaf disc was placed in a Petri dish and one of six aphid densities were placed on the disc. The densities used were; five second to third instar, parasitised aphids alone or five parasitised aphids plus 5, 10, 20, 30 or 40 unparasitised aphids of the same instar. (Parasitised aphids were marked as before). An experienced A. fuscicornis female was introduced to the Petri dish and the following were recorded: time spent on the patch, antennal contacts with aphids of both types and number of aphids of each type probed. Six replicates were carried out at each density.

Results.

Time spent on a patch is not related to the number of unparasitised aphids present (Figure 24). When the number of unparasitised aphids is increased there is a significant ($p<0.01$) decrease in the number of antennal contacts and the number of parasitised aphids probed by the hyperparasitoid on the patch (Figures 25 and 26). There is no significant relationship between the giving-up time and the number of unparasitised aphids on a patch.

Figure 24 Time spent on patches in relation to density of unparasitised aphids



r = −0·07 N.S.

Figure 25 Relationship between number of antennal contacts with hosts and unparasitised aphids/patch (± S.E.)

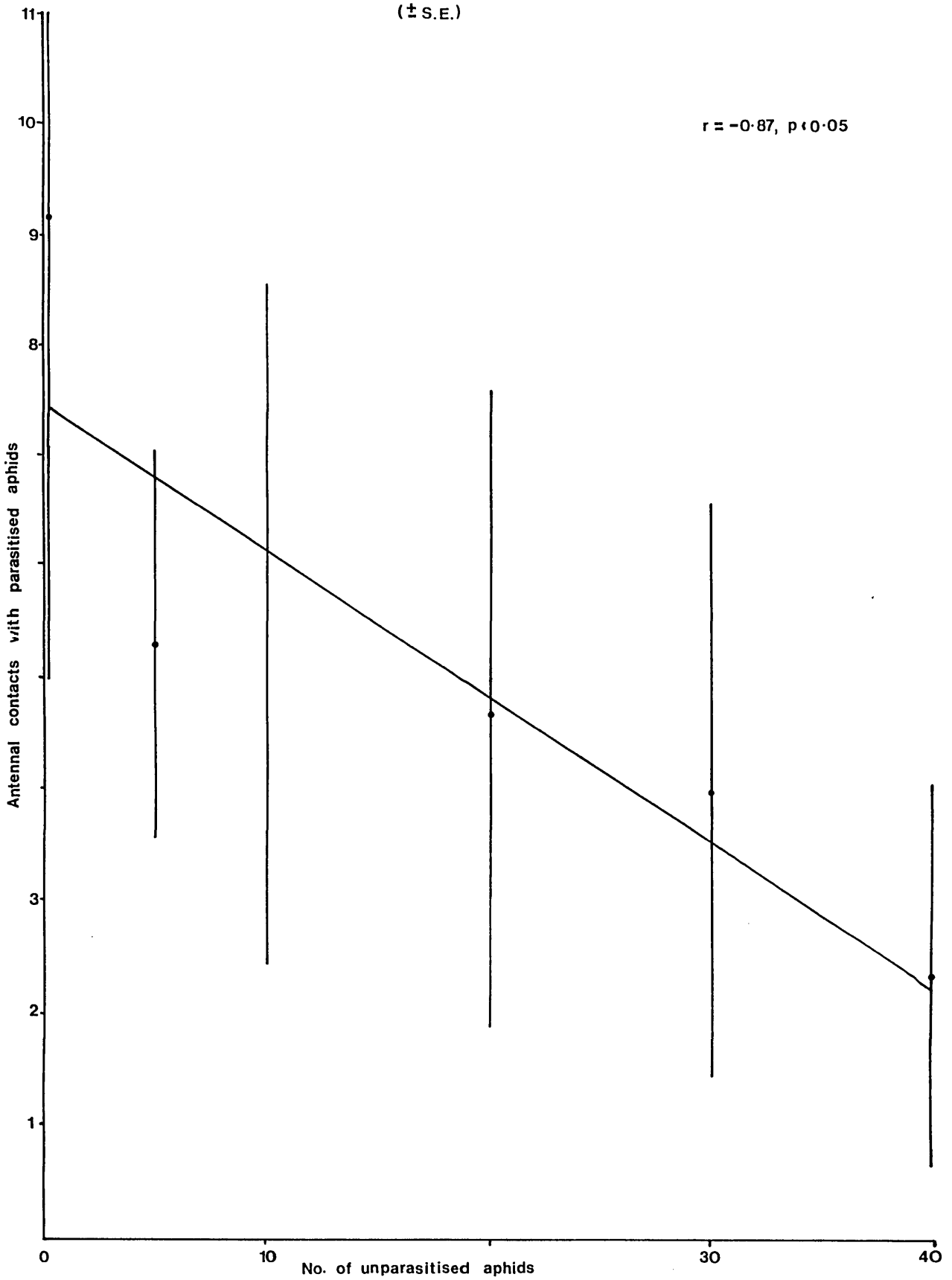
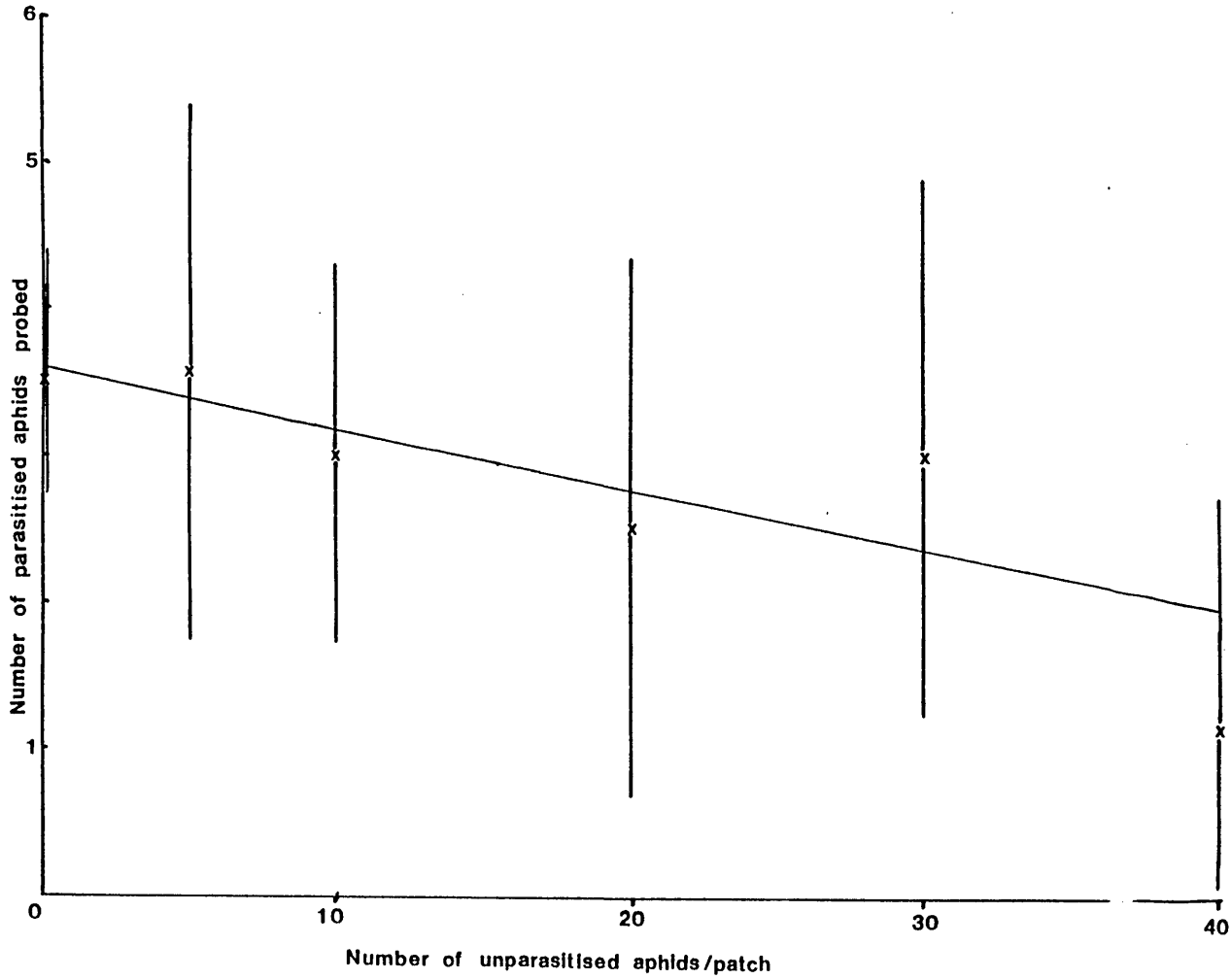


Figure 26 Relationship between number of parasitised aphids probed and unparasitised aphids/patch (S.E.)



r= −0·989
p<0·01

Discussion.

D. rapae is attracted to mustard oils from the cruciferous food plants of the cabbage aphid (Read et al. 1970, Akinlosotu 1973). This suggests that D. rapae females locate the aphid's habitat by an olfactory response to volatile plant odours. It is thought that this response is an aid to habitat selection rather than an essential prerequisite, as D. rapae has been recorded from non-cruciferous plants and will attack aphids on sugar beet and potato (Read et al. 1970). D. rapae is not, however, attracted to cabbage aphids alone. (Read et al. 1970, Akinlosotu 1973). A. fuscicornis does not respond either to odours from crucifers or from aphids (Read et al. 1970, Vater 1971).

Vater (1971) considered the movement of A. fuscicornis and D. rapae within and outside a brassica crop. The females of both species disperse and so are more common than males outside the crop. Vater placed sticky cards with a range of colours in the field. He found that the primary parasitoid occurred most frequently on light green, green and dark green and A. fuscicornis on red, orange, yellow-green and lighter colours; this may be because A. fuscicornis is adapted to search for old aphid colonies, with more parasitised individuals, on older, yellower leaves. D. rapae females must locate younger colonies on young, blue-green leaves. When light was split over a tube containing both species the hyperparasitoids moved closer to the red end of the tube than the primary parasitoids (Vater 1971).

D. rapae, therefore, locates its host habitat by responding to both host plant odours and to certain colours.

A. fuscicornis, however, appears to respond directly to odours emitted by its host, suggesting that it may not be restricted to attacking parasitised aphids on crucifers. Colour is also important in host habitat location by this species.

Orientation to a particular part of a plant has been observed in various other parasitoids (Vinson 1976). For example, Microbracon vestiticida, a parasitoid of the bean weevil, is attracted to the pods of milkweed, irrespective of whether or not they are occupied by weevils (Smith 1943). On the basis of field and laboratory experiments, it seemed unlikely that A. fuscicornis females detect their hosts by first locating D. rapae females as hyperparasitoid females showed no preference for leaves or plants with D. rapae females. Cleptoparasitoids, such as Pseudorhyssa sternata Merill and Temelucha interruptor (Grav.), respond to pheromones left by their hosts previous to and during oviposition (Arthur et al. 1964, Spadberry 1968). P. sternata females can detect the oviposition shafts of the primary parasitoid, Rhyssa persuarsoria (L.), several days after they have been drilled (Spadberry 1968). It is likely that some hyperparasitic species also exploit the host marking pheromones of primary parasitoids. D. rapae has a low avoidance of superparasitism, however, and probably does not use host marking to discriminate between parasitised and healthy hosts (see Chapter 5).

Honeydew elicits a response in D. rapae and A. fuscicornis which is typical of many parasitoids on encountering a contact chemical. Arrestment, a reduction in walking speed (orthokinesis) and increase in turning (klinotaxis) will

tend to retain the parasitoids in the area contaminated with honeydew. This should result in an increase in the time spent searching in the vicinity of their hosts. This type of behaviour is probably especially advantageous to parasitoids such as D. rapae and A. fuscicornis whose hosts occur in colonies. A similar response to honeydew is shown by coccinellid larvae which also attack aphid colonies (Carter and Dixon 1984) and by an aphid parasitoid, Aphidius nigripes Ashmead (Bouchard and Cloutier 1984).

Both males and females of the parasitoid and hyperparasitoid were observed to feed on aphid honeydew. This is typical of many aphid parasitoids (Stary 1964). Ayal (1987) has shown that D. rapae females use honeydew trials to find host colonies, Females searched horizontal contaminated surfaces thoroughly, on contaminated vertical surfaces they moved upwards and if they left the contaminated area they turned and walked back down the plant. On wild crucifers honeydew is washed down the plant from aphid colonies on the inflorescences and by responding to contaminated surfaces in this way, parasitoids would locate their hosts (Ayal 1987). Ayal related this foraging behaviour to the distribution of aphids on wild crucifers, which presumably have been the template for the evolution of the parasitoid's foraging behaviour. On wild crucifers aphids form colonies on the inflorescences and it is therefore beneficial for the parasitoid to spend longer on the upper parts of the plant. On cruciferous crops, however, such a searching pattern would be less efficient as, although aphids occur on the heart and upper leaves of young plants, on older plants the

largest colonies are on the underside of the lower leaves (see Chapter 5).

A. fuscicornis discriminates between parasitised and unparasitised aphids at the probing stage of oviposition. Hyperparasitoids spend significantly ($p<0.01$) longer probing parasitised than unparasitised aphids, probably because there are two stages in oviposition; the first for the detection of parasitoid larvae and the second for depositing an egg. These results disagree with the suggestion by some authors that a hyperparasitoid can determine if an aphid is suitable for oviposition solely by examination with the antennae (Haviland 1921, Askew 1971). Another cynipid hyperparasitoid, A. victrix, has a similar behaviour pattern to that of A. fuscicornis (Gutierrez 1970 e and f). When equal numbers of parasitised and unparasitised pea aphids, Acyrthopisum pisum, were presented to hyperparasitoid females, parasitised and unparasitised aphids were probed approximately the same number of times. Several aphid species were accepted for probing following examination with the antennae and A. victrix females could discriminate between the larvae of various species of aphid parasitoids within aphid haemocoels. Electron micrographs revealed the presence of senosry pits on the ovipositor tip and these were thought to have a chemosensory function.

The encyrtid, Cheiloneurus noxius Compere, is an obligatory hyperparasitoid of scale insect parasitoids. Weseloh (1971a) tested the influence of several physical characteristics of the scale insect on host acceptance by the hyperparasitoid. Host shape was found to be of major and host size of minor importance while surface texture, moisture content and

colour shade did not influence host selection. The hyperparasitoid responded to precise chemotactile stimuli in the scale integument and in its internal contents (Weseloh and Bartlett 1971). Acceptance of the scale was mediated by sensory structures on the antennal tips. Parasitoid larvae were also an important factor in host acceptance and, as in A. fuscicornis, these were detected at the probing stage by sensory structures on the ovipositor tip (Weseloh 1971b). Both D. rapae and A. fuscicornis alter patch time in response to the quality of the patch, spending longer and attacking more hosts on high quality patches. D. rapae does not appear to use either the number or time expectation rules to decide when to leave a patch. Although females are more persistent (i.e. have longer giving-up times) in high quality patches, there are no significant differences between patches. A. fuscicornis does not appear to use either the number or the time expectation rule in its foraging behaviour, either as a response to the total number of aphids per patch or to the number which are parasitised. Obviously such behaviour is adaptive as it (a) saves time, especially for the hyperparasitoid were oviposition takes longer than probing a host and (b) avoids wastage of eggs and hosts (van Lenteren 1981).

It seems likely that there are number of factors which determine the length of time spent by a parasitoid on a patch. The above models are, therefore, probably too simplistic. Waage (1977 and 1979) proposed a model to describe the foraging behaviour of Venturia canescens. In this a certain level of 'responsiveness' was acquired when

the parasitoid entered the patch. This decayed until it reached a threshold level when the parasitoid left the patch. On encountering a host an increment was added to the level of responsiveness so increasing the total time spent on the patch. Van Alphen and Galis (1983) found that the parasitoid, Asorba tabida Nees, increased both its searching time and its giving-up time with increases in host density, thus conforming with Waage's model.

It is likely that the foraging behaviour of A. fuscicornis may be described by a similar model, the initial level of responsiveness being set by contact with honeydew. Subsequent encounters with parasitised aphids would increase the length of time spent on the patch. Encounters with unparasitised aphids might initially also have the effect of increasing responsiveness but this effect would decay with time if no parasitised aphids were encountered, and might even become decremental.

Also, A. fuscicornis females did not leave patches earlier in response to an increase in the number of unsuitable aphids encountered. This disagrees with van Lenteren's hypothesis that migration from a patch should be caused by a high number of encounters with parasitised hosts. This behaviour will result in the hyperparasitoid wasting time on unprofitable patches. Although the hyperparasitoid does not decrease its searching time on a patch in response to encountering increased numbers of unparasitised aphids, neither does it increase searching time in response to increased total numbers of aphids.

It might be expected that the giving-up times will be shorter on low quality patches but no significant trend was found in giving-up times in relation to the number of unparasitised aphids present. Hyperparasitoids must, therefore, allocate searching time to patches on the basis of presence or absence of hosts rather than the rate of encounter with hosts or the total rate of encounter with aphids.

To summarise, A. fuscicornis shows generally similar patterns of foraging to those of D. rapae. Both are attracted to brassica crops by colour, but only the primary parasitoid has been shown to respond to volatile plant odours. Once on the plant, however, both species have a non-random searching pattern featuring negative geotaxis with long periods spent searching the upper parts of the plant and areas contaminated with honeydew. Within patches, A. fuscicornis was found to discriminate between unparasitised and parasitised aphids during the probing stage of oviposition while in D. rapae discrimination between 'suitable' and 'unsuitable' hosts was only partial. Both species, however, spent longer on high quality patches. The foraging behaviour of the hyperparasitoid can be modelled in a similar way to that described by Waage with increments being added to patch time on finding parasitised aphids, but no increments being added for unparasitised aphids.

8. Discussion

This thesis has compared some basic aspects of the biology of an insect parasitoid and hyperparasitoid in order to discover adaptations which are of particular importance or peculiar to the hyperparasitic mode of life. In particular, the factors which determine the host searching strategy were considered as they are of obvious importance to the exploitation of the host and the reproductive success of the parasitoid or hyperparasitoid species.

The biology of A. fuscicornis is generally uncharacteristic of that of most hyperparasitoids, as described in Chapter 2. Firstly, A. fuscicornis is endo- rather than ectoparasitic, and is probably also more host specific than many other species of hyperparasitoids. In common with several other obligate hyperparasitoids (Askew and Shaw 1986) it is a koinobiont, its hosts continue to develop after they have been parasitised. A. fuscicornis benefits from this characteristic as the primary parasitoid forms a mummy which provides protection for the hyperparasitoid larva during the remainder of its development. D. rapae, which is also koinobiotic, benefits as its hosts frequently reproduce before they are killed by the parasitoid larva, providing hosts for adult parasitoids of the subsequent generation. The continuation of aphid feeding also ensures an uninterrupted food supply for most of larval life.

As in many other hyperparasitoids and their parasitoid hosts, the life cycle of A. fuscicornis is closely synchronised with that of D. rapae (Chua 1979).

This results from the later spring emergence of A. fuscicornis and its developmental threshold being similar to that of D. rapae, so that the development of hyperparasitoid and parasitoid larvae occurs over a similar temperature range. The lower thermal constant associated with A. fuscicornis allows the hyperparasitoid larvae to develop more rapidly than those of the primary parasitoid, so that more hyperparasitoid generations should occur each year. (This also results in faster development from the egg to the mummy stage by the hyperparasitoid, so increasing the time spent in a stage which is protected from predation).
Females of A. fuscicornis forage for hosts whose distribution is determined largely by the aggregative behaviour of B. brassicae, the foraging and oviposition behaviour of D. rapae and the hyperparasitoid's own inability to distinguish between entirely healthy aphid colonies and those which contain parasitised aphids. A. fuscicornis, therefore, searches firstly for B. brassicae colonies which have an aggregated distribution, are on average large in size, but which vary greatly in numbers of aphids per colony. Secondly, the hyperparasitoid must locate smaller groups of parasitised aphids within these colonies, which vary less in size and whose variance : mean ratio is smaller, indicative of a less aggregated distribution.
In contrast to A. fuscicornis, D. rapae searches for aggregated hosts in comparatively large colonies. Both species show adaptations to their host distributions in terms of biology and behaviour.

Females of both species locate aphid colonies by responding to colour, but only D. rapae responds to cabbage odours. This suggests that either A. fuscicornis is not restricted to hosts on cruciferous plants or that a more specific chemical cue is important in host location. Although the ability to respond to such a cue would be clearly advantageous to the hyperparasitoid, it does not appear to use the pheromones of either B. brassicae or D. rapae for host detection.

Once on a Brussels sprouts plant, D. rapae and A. fuscicornis females had similar foraging behaviour (i.e. they tended to alight on the upper surface of lower leaves and then had an upward and directional searching pattern which was modified in the presence of honeydew).

In the field, aphid colonies which had been parasitised by D. rapae occurred mainly on the crown, and under-sides of middle and lower leaves, this pattern must result from the upward movement of the parasitoid and its ability to detect aphid colonies by tracing honeydew trials, such behaviour is more effective, however, on wild crucifers where the majority of aphids occur on the upper parts of the plant, rather than on the undersurfaces of middle and lower leaves (Ayal 1987). Most of the parasitised aphids which had been attacked by the hyperparasitoid were found on the undersurface of middle leaves, A. fuscicornis attacked more aphids per colony, on the undersurface of middle leaves although there was a significant difference in the numbers of colonies attacked at different positions on the plant.

This may be because colonies on the middle leaves were smaller than those on the lower leaves, and so had a relatively higher proportion of parasitised aphids which are easier for the hyperparasitoid to detect. Colonies higher up the plant may be younger and so contain mainly unparasitised aphids and aphids which are recently parasitised.

Once a colony of aphids has been located D. rapae and A. fuscicornis females showed markedly different types of behaviour. D. rapae females have larger quantities of eggs available with which they are able to exploit the relatively large and easily located colonies of their hosts. A. fuscicornis females, on the other hand, emerge with a smaller quantity of eggs, which appears to be an adaptation to their less apparent, smaller host colonies. Both species also have the ability to resorb oocytes when hosts are scarce (Broussal 1966), an adaptive mechanism which makes more energy available for host location. It is interesting to note that Eucerus frigidus, an indirect hyperparasitoid, whose planidia attack both parasitised and unparasitised sawfly larvae, is synovogenic and possesses many ovarioles, an adaptation to the high mortality of the planidia rather than to host distribution.

D. rapae also has a short handling time which it enables it to attack a large number of hosts in rapid succession. A. fuscicornis must probe each aphid in order to locate parasitoid larvae, but the longer handling time resulting from this oviposition behaviour may be offset by the comparatively longer adult longevity of the hyperparasitoid.

It seems likely that the greater avoidance of superparasitism by the hyperparasitoid results from the type of oviposition behaviour and also the use of internal and external markers. Superparasitism is less likely to be disadvantageous for D. rapae for a number of reasons.

In the field, both parasitoid species had aggregative behaviour in response to high host densities, but this was not reflected in the resulting pattern of parasitism in either case. It was also shown in laboratory experiments that D. rapae females spend longer in 'higher quality' patches where only unparasitised aphids were present than in 'low quality' patches which contained both unparasitised and parasitised aphids. This was also true for the hyperparasitoid, suggesting that both species can detect high quality patches and adjust their allocation of searching time accordingly.

The comparative approach which formed the basis of this study provided a means of examining the differences in the basic biology and behaviour of D. rapae and A. fuscicornis. This approach was slightly unsatisfactory, as in certain cases it was difficult to make direct comparisons between these two species; for example, in studying the response of the hyperparasitoid to parasitised and unparasitised aphids. It would be interesting to contrast these patterns of parasitism with those of a facultative secondary parasitoid, whose hosts should be more easily accessible than those of a primary parasitoid in the same system, or with facultative secondary/tertiary parasitoids, such as Dendrocerus carpenteri and Asaphes lucens, ectoparasitoids which attack both D. rapae and A. fuscicornis after mummy formation.

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Appendix I: GLIM Analysis for Chapter 5

1. Number of aphid colonies on different days

Day	Estimate of Deviance	S.E.
27.8.85	0.1329	0.04081
1.9.85	0.1591	0.05608
6.9.85	0.05632	0.05723
11.9.85	0.1555	0.05592
16.9.85	0.1058	0.05659
21.9.85	0.1537	0.05584
26.9.85	0.2377	0.05538
1.10.85	0.2925	0.05460
6.10.85	0.2957	0.05409
11.10.85	0.3091	0.05460
16.10.85	0.2809	0.05509
21.10.85	0.3433	0.05409

2. Aphid colony size on different days

Day	Estimate of deviance	S.E.
27.8.85	0.7692	4.003
1.9.85	1.324	5.501
6.9.85	1.515	5.613
11.9.85	2.488	5.485
16.9.85	1.547	5.551
21.9.85	6.536	5.477
26.9.85	6.548	5.432
1.10.85	8.927	5.356
6.10.85	14.86	5.306
11.10.85	21.32	5.356
16.10.85	15.00	5.403
21.10.85	17.34	5.306

3. Number of aphids attacked on different days

Day	Estimate of Deviance	S.E.
27.8.85	0.04895	0.06145
1.9.85	0.04422	0.08444
6.9.85	0.1065	0.08617
11.9.85	0.07375	0.08420
16.9.85	0.03492	0.08521
21.9.85	- 0.006268	0.08408
26.9.85	0.05693	0.08338
1.10.85	0.006298	0.08222
6.10.85	0.1257	0.08145
11.10.85	0.02287	0.08222
16.10.85	0.07174	0.08295
21.10.85	0.2315	0.08145

4. Number of aphid colonies attacked on different days

Day	Estimate of Deviance	S.E.
27.8.85	0.02797	0.01879
1.9.85	0.02172	0.02582
6.9.85	0.01933	0.02634
11.9.85	0.04565	0.02574
16.9.85	- 0.008617	0.02605
21.9.85	0.008613	0.02570
26.9.85	0.01909	0.02549
1.10.85	0.02175	0.02514
6.10.85	0.03552	0.02490
11.10.85	- 0.0003477	0.02514
16.10.85	0.03525	0.02536
21.10.85	0.08314	0.02490

5. Number of groups of parasitised aphids on different days

Day	Estimate of Deviance	S.E.
27.8.85	0.06294	0.03233
1.9.85	0.06750	0.04443
6.9.85	0.01814	0.04534
11.9.85	0.07817	0.04430
16.9.85	0.001579	0.04483
21.9.85	- 0.001961	0.04424
26.9.85	0.01942	0.04387
1.10.85	0.05861	0.04326
6.10.85	0.04288	0.04285
11.10.85	0.1249	0.04326
16.10.85	0.1095	0.04364
21.10.85	0.1275	0.04285

6. Number of parasitised aphids on different days

Day	Estimate of Deviance	S.E.
27.8.85	0.107×10^{-10}	0.5520
1.9.85	0.2500	0.7559
6.9.85	-0.7952×10^{-11}	0.7807
11.9.85	-0.1987×10^{-10}	0.7807
16.9.85	-0.1005×10^{-10}	0.7807
21.9.85	0.1429	0.7807
26.9.85	-0.1061×10^{-10}	0.7198
1.10.85	0.09091	0.7062
6.10.85	0.2381	0.6374
11.10.85	0.1818	0.7062
16.10.85	0.1000	0.7198
21.10.85	0.1250	0.7559

7. Number of hyperparasitised aphids on different days

Day	Estimate of Deviance	S.E.
27.8.85	0.02797	0.01960
1.9.85	0.003084	0.02694
6.9.85	0.01257	0.02749
11.9.85	0.002703	0.02686
16.9.85	- 0.01507	0.02718
21.9.85	- 0.02797	0.02682
26.9.85	- 0.02797	0.02660
1.10.85	- 0.02797	0.02623
6.10.85	0.01965	0.02598
11.10.85	0.02175	0.02623
16.10.85	- 0.02797	0.02646
21.10.85	0.003774	0.02598

8. Number of groups of parasitised aphids containing hyperparasitised aphids on different days

Day	Estimate of deviance	S.E.
27.8.85	0.02098	0.009051
1.9.85	0.003866	0.01244
6.9.85	- 0.007466	0.01269
11.9.85	0.003561	0.01240
16.9.85	- 0.01453	0.01255
21.9.85	- 0.02098	0.01238
26.9.85	- 0.02098	0.01228
1.10.85	- 0.02098	0.01211
6.10.85	- 0.01040	0.01200
11.10.85	0.006645	0.01211
16.10.85	- 0.02098	0.01222
21.10.85	- 0.005106	0.01200

9. Number of aphid colonies at different positions

Position	Estimate of deviance	S.E.
Heart	0.07917	0.02587
Upper leaf upper side	0.02287	0.0364
Middle leaf upper side	0.01026	0.03636
Lower leaf upper side	- 0.00891	0.03651
Upper leaf under side	0.1185	0.03611
Middle leaf under side	0.5291	0.03385
Lower leaf under side	0.6901	0.03197

10. Aphid colony size at different positions

Position	Estimate of deviance	S.E.
Heart	- 4.842	17.89
Upper leaf upper side	- 0.4030	4.249
Middle leaf upper side	3.117	4.246
Lower leaf upper side	5.174	4.261
Upper leaf under side	1.303	4.226
Middle leaf under side	12.30	4.014
Lower leaf under side	12.40	3.857

11. Number of aphids attacked at different positions

Position	Estimate of deviance	S.E.
Heart	0.03538	0.2777
Upper leaf upper side	- 0.0972	0.06595
Middle leaf upper side	- 0.08680	0.06590
Lower leaf upper side	- 0.06659	0.06612
Upper leaf under side	- 0.07083	0.06559
Middle leaf under side	0.08712	0.06229
Lower leaf under side	- 0.01339	0.05986

12. Number of colonies attacked at different positions

Position	Estimate of Deviance	S.E.
Heart	0.02310	0.08333
Upper leaf upper side	- 0.03952	0.01979
Middle leaf upper side	- 0.04745	0.01978
Lower leaf upper side	- 0.04573	0.01984
Upper leaf under side	- 0.03230	0.01968
Middle leaf under side	0.002350	0.01870
Lower leaf under side	0.0009587	0.01797

13. Number of groups of parasitised aphids at different positions

Position	Estimate of Deviance	S.E.
Heart	- 0.01503	0.1417
Upper leaf upper side	- 0.02393	0.03366
Middle leaf upper side	- 0.04505	0.03364
Lower leaf upper side	- 0.04554	0.03375
Upper leaf under side	- 0.02498	0.03348
Middle leaf under side	0.1047	0.03180
Lower leaf under side	0.1400	0.03056

14. Number of parasitised aphids at different positions

Position	Estimate of Deviance	S.E.
Heart	0.05782	0.5550
Upper leaf upper side	- 0.2223	0.1318
Middle leaf upper side	- 0.2218	0.1317
Lower leaf upper side	- 0.1617	0.1322
Upper leaf under side	- 0.1759	0.1311
Middle leaf under side	0.2842	0.1245
Lower leaf under side	0.09269	0.1196

15. Number of hyperparasitised aphids at different positions

Position	Estimate of Deviance	S.E.
Heart	- 0.001351	0.08917
Upper leaf upper side	- 0.01277	0.02118
Middle leaf upper side	- 0.01851	0.02116
Lower leaf upper side	- 0.004069	0.02123
Upper leaf under side	- 0.004391	0.02106
Middle leaf under side	0.04393	0.02000
Lower leaf under side	0.005258	0.01922

16. Number of groups of hyperparasitised aphids at different positions

Position	Estimate of deviance	S.E.
Heart	0.002741	0.04084
Upper leaf upper side	- 0.008499	0.009699
Middle leaf upper side	- 0.01304	0.009693
Lower leaf upper side	- 0.004128	0.009725
Upper leaf under side	- 0.004672	0.009646
Middle leaf under side	0.009059	0.009162
Lower leaf under side	0.002088	0.008804