Ann. appl. Biol. (1982). **101**, 143–203
Printed in Great Britain

Proceedings

A meeting of the Entomology Group of the Association of Applied Biologists was held at the Department of Experimental Psychology, University of Oxford on 27–28 July 1981 entitled:

NATURAL ENEMIES AND INSECT PEST DYNAMICS

The meeting developed from an Entomology Group workshop held in Cambridge in the autumn of 1980 entitled:

Methods used to assess the role of natural enemies

The workshop was concerned with the extent to which different approaches to the quantification of natural enemies' effects could be integrated. These approaches seemed to fall into four overlapping areas:

1. Laboratory-based experiments assessing the components of a predator's performance in relation to changes in prey density (attack rate, handling time, prey preference, time spent in prey 'patches' etc.). These often lead to deterministic analytical models of changes in the numbers of predators and prey.
2. Field observation of individual enemies' performance to give realistic information on searching behaviour.
3. Experimental manipulation of natural enemy numbers in the field, using barriers, cages etc.
4. Wholly field-based work assessing predator/prey numbers, often over a wide spatial and temporal range and depending heavily on correlative analyses to explain observed differences in prey density. This may sometimes include smaller-scale manipulative work.

All the approaches have inherent weaknesses: laboratory models are often precise and analyse clearly some components of predation but may not be sufficiently realistic or general to attract the interest of a field-based worker. A field approach may be more realistic but even if striking results are obtained, the mechanisms involved may be poorly understood. The choice of which method a research worker uses is often based on a combination of chance, background, pragmatism and, sometimes, degree of confidence in the use of numerical techniques.

As the goal of the applied ecologist working on natural enemies is to analyse and improve the contribution to pest control made by natural antagonists, some kind of integration of the above approaches must be the ideal. Whether such an integration of approach is occurring can perhaps be judged from these Proceedings of the Oxford meeting. The reader may conclude that the main stumbling blocks are still:

(a) insufficient communication between theoreticians and field workers so that few of the ideas of the former group are adopted by the latter;
(b) too few attempts at simulation by field workers. Such simulations could identify the realistic constraints to make the theoreticians' ideas more applicable to the field.

The details of most analytical models, however, with their concepts of inter-generation stability, may be of doubtful applicability to predator–prey interactions in short-duration arable crops. Broader conclusions from the models, such as the importance of spatial and temporal heterogeneity, are of more direct use in practical studies and since the Cambridge and Oxford meetings, one or two new projects have begun which are using the stimuli of these meetings in attempts to integrate theory, manipulation and observation. The next few years will be of great interest in this important area of applied biology.

S. D. Wratten
Entomology Group Convener & Proceedings Editor

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Contents of Proceedings

Session I

Chairman: M. P. HASSELL

Session II

Chairman: J. H. LAWTON

Voracity, cannibalism and coccinellid predation

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INTRODUCTION

There have been many successes in the use of coccinellids as biological control agents, particularly against coccid prey (Bartlett, 1978). While there have been introductions of coccinellids against aphid prey, there are no classic examples of control. Despite this, there is still a considerable amount of interest in the use of aphidophagous coccinellids in control programmes for pest species both in the field (Hagen, 1974; Hodek, 1970), and under glass (Hamalainen, 1977; Gurney & Hussey, 1970). The impact of coccinellid predation on the prey population is dependent on the voracity and abundance of predators in relation to the density of prey. In the present discussion the response of *Adalia bipunctata* (L.) to the density of its principal prey *Eucallipterus tiliae* (L.) will be considered, as an example of aphidophagous coccinellid predation.

RESULTS

Voracity and the numerical response

Coccinellid adults and eggs were sampled by leaf counts on a range of lime trees in Norwich in 1977 and in Oxford in 1980, at the peak of the egg-laying period in June. In Fig. 1 the fecundity of the coccinellids in both years is related to aphid density. This reproductive numerical response is comparable for both years, rising from a threshold for reproduction at 0·5 aphids per 100 cm^2 to a maximum of 31·5 eggs per adult above nine aphids per 100 cm^2. A series of point observations of the activity of adult coccinellids throughout the day at these higher aphid densities showed that 49% of the available time was spent inactive, 29% searching, 10% eating and 12% in copulation or ovipositing. This suggests that at densities above nine aphids per 100 cm^2, prey are sufficiently abundant to satiate the adult coccinellids, allowing them to spend most of the day in digestive pause and to produce a maximum number of eggs.

The aggregative numerical response in Fig. 2 shows the distribution of adult coccinellids in relation to aphid density. The number of *A. bipunctata* that emerged from hibernation in 1980 was probably typical for most years, while the overwintering population in 1977 was abnormally large (Heathcote, 1978) due to the favourable seasons of 1975 and 1976. In 1980 the aggregative response reached an asymptote of 0·015 adults per 100 cm^2, above a density of 10 aphids per 100 cm^2, just beyond the level at which satiation was apparent in the reproductive numerical response (Fig. 1). Satiation limits the aggregative response since the higher aphid densities are all equally favourable to the foraging coccinellids. The abundance of coccinellids in 1977 resulted in a more variable response, with many coccinellids present at low aphid densities. However, since satiation occurred in the reproductive response (Fig. 1) it is probable that the aggregative response in 1977 also has an asymptote. The variability about a mean level of 0·053 adults per 100 cm^2 may be due to additional factors such as tree size, exposure and proximity to overwintering sites.

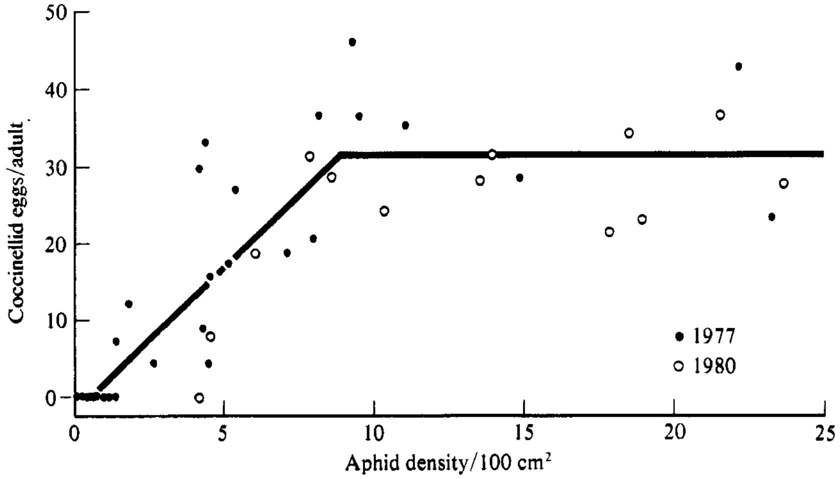

Fig. 1. The reproductive numerical response. Lines fitted by linear regression and mean.

The product of the reproductive and aggregative responses results in the combined numerical response of eggs laid in relation to aphid density (Fig. 3). For both years an asymptote is reached above a density of 9–10 aphids per 100 cm^2, at 1·67 eggs per 100 cm^2 and 0·40 eggs per 100 cm^2 in 1977 and 1980 respectively. The variability of points about the combined response is largely attributable to variation in adult abundance rather than adult fecundity. The numerical response of the coccinellid to aphid density is therefore confined to the range 0–10 aphids per 100 cm^2, beyond which the voracity of the coccinellids is curtailed due to satiation.

Cannibalism

Field observations suggest that while there is no predation of coccinellid eggs, their survival over the incubation period is dependent on the extent of cannibalism by adults and young larvae. Of 42

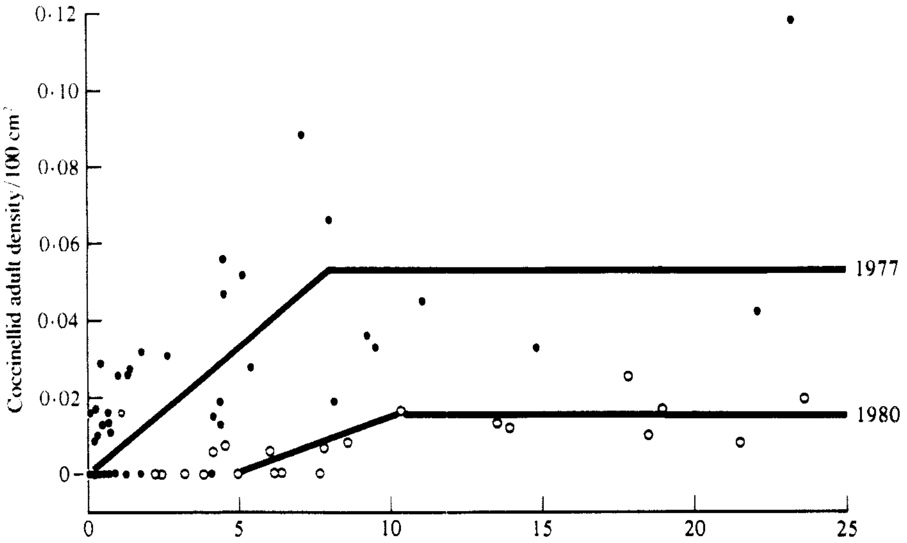

Fig. 2. The aggregative numerical response. Lines fitted by linear regression and mean.

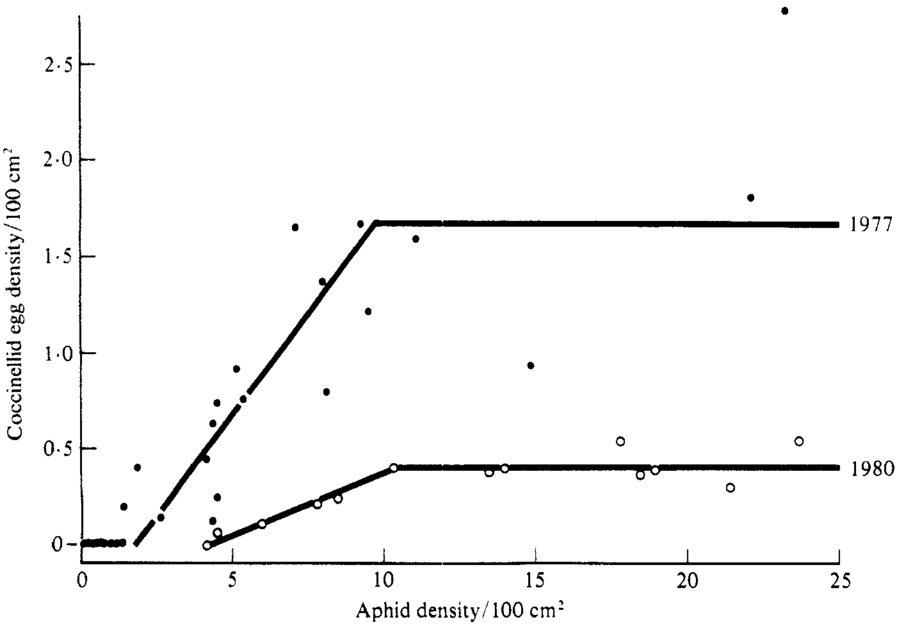

Fig. 3. The combined numerical response. Lines fitted by linear regression and mean.

observations of egg cannibalism in the field, 22%, 19%, 33% and 26% were due to adult, 1st, 2nd and 3rd instar larvae respectively. Contrary to laboratory findings (Dixon, 1959; Brown, 1972), little cannibalism resulted from the first larvae to hatch consuming the rest of the batch. The field observations of first instar cannibalism were of dispersed larvae consuming eggs of other batches. The laboratory phenomenon probably results from the infertility common in eggs laid by adults under artificial conditions.

Cannibalised eggs are identifiable by the yellow-stained egg base that remains, in contrast to the white egg base of successfully hatched larvae. The cannibalism estimated during sampling is expressed as a k-value (log initial number – log final number) in relation to the logarithm of the egg density in Fig. 4. The

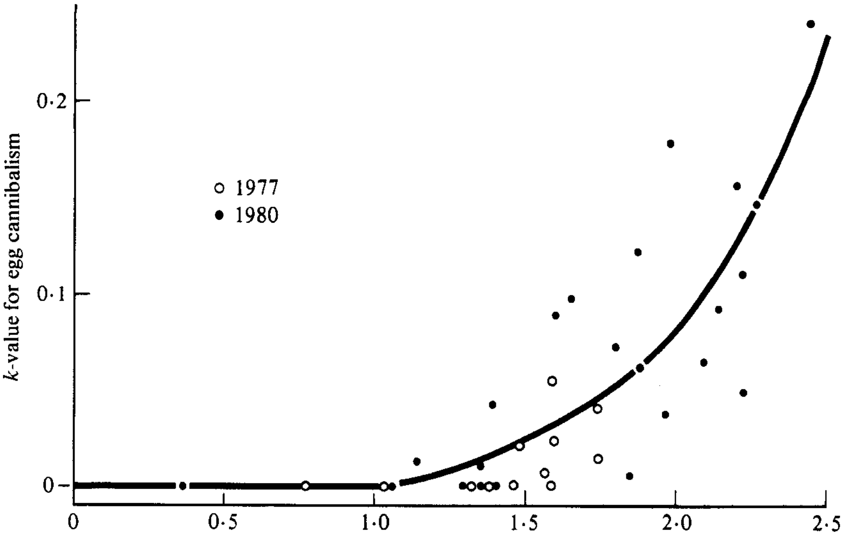

Fig. 4. Density-dependent egg cannibalism. Curve fitted by non-linear regression.

results are similar for both years of sampling and indicate a density-dependent relationship of the type suggested by Bellows (1981):

$$k \text{ (egg cannibalism)} = 0{\cdot}002\ (E - 10{\cdot}930)^{0{\cdot}862} \quad \text{with } k \geqslant 0,\ r^2 = 0{\cdot}67,\ P < 0{\cdot}001$$

where E is the egg density, 10·930 is a threshold density for cannibalism, 0·862 is a density-dependent moderator and 0·002 is a constant.

Cannibalism is therefore a significant self-regulatory mechanism that increases in intensity as egg density rises. The resultant decrease in the density of larvae consequently reduces the impact of coccinellid predation on the prey population. Larval densities were reduced by 30% in 1977 and 8% in 1980 through egg cannibalism.

DISCUSSION

The impact of aphidophagous predators on prey populations is largely a result of predation by the juvenile stages. Adult coccinellids feed in a variety of habitats before oviposition begins, after which for example *A. bipunctata* requires only one quarter the consumption of a single larva during development to produce a batch of 13 eggs at 20 °C (Mills, 1981*a*). The numerical response of the adult coccinellids to the density of aphid prey is therefore important in determining the effectiveness of these natural enemies. The sampling data from the field show that *A. bipunctata* can only respond to the lower range of lime aphid densities through its aggregative and reproductive numerical responses. A similar lack of response by aphidophagous coccinellids at higher aphid densities has been documented by Sakuratani (1977) and Wright & Laing (1980). This response is then further reduced by density-dependent egg cannibalism.

The aphidophagous coccinellids largely belong to the sub-family Coccinellinae and are characterised by laying eggs in batches exposed on the surface of the host plant of their aphid prey. The coccidophagous coccinellids, which have been so successfully used in biological control, belong to other sub-families and lay their eggs singly, or in small groups of 2–3, often concealed beneath the prey. These coccinellids therefore avoid the levels of egg cannibalism found in their aphidophagous counterparts.

The batch egg-laying strategy provides enhanced aposematic protection for eggs that cannot be concealed by a mobile prey and may at times aid survival when feeding on aphid prey. The host-alternation and aestivation by which aphids overcome periods of food shortage (e.g. Dixon, 1977) can result in a rapid decline in their abundance soon after the coccinellid egg laying period. Under these conditions the ability to cannibalise eggs would enhance the likelihood of at least some larvae surviving to maturity.

Aphidophagous coccinellids belonging to the Coccinellinae, such as *A. bipunctata*, are therefore unlikely to be effective natural enemies of aphids, due to inherent disadvantages. The rapid development rate of aphids exceeds that of the coccinellids and in addition many aphidophagous coccinellids, such as *A. bipunctata*, show little specificity (e.g. Mills, 1981*b*) and probably experience satiation at moderate densities of their favoured prey. Lastly, the potential for density-dependent cannibalism must further reduce the impact of coccinellid predation below that set by the numerical response.

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Host-finding behaviour of some hymenopterous parasitoids of *Musca domestica*

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INTRODUCTION

In many regions of the world the common housefly, *Musca domestica* L., is still a serious pest species (Busvine, 1951). Not only is it an important vector of such diseases as typhoid or cholera but it is also a nuisance due to its abundance in areas where large accumulations of animal manure occur (Legner, 1966).

Many attempts have been made to control *Musca* by introducing hymenopterous pupal parasitoids (Bay, Berg, Chapman & Legner, 1976) and some of these projects have been successful (e.g. Morgan, Patterson & Labreque, 1976). The species most commonly used in such projects belong to the genera *Muscidifurax* and *Spalangia* (Pteromalidae) as these are frequently found attacking synanthropic Diptera in natural situations (Ables & Shepard, 1976*a*; Legner, 1977). Several studies (e.g. Legner, 1967: 1977;

Gerling & Legner, 1968; Ables & Shepard, 1976*b*) have been conducted to determine the behavioural and ecological characteristics of these parasitoids, so that control programmes have a basis for choosing a suitable species.

This study attempts to contribute to this basis by considering the problem of how four of these parasitoids, *Muscidifurax raptor*, *M. zaraptor*, *Spalangia cameroni* and *S. endius* find *Musca* in its habitat. These four species form part of the natural enemy complex that attacks *Musca* and other noxious Diptera in Southern California (Legner, 1966; Legner & Olton, 1971). However, strains of *M. raptor* and the two *Spalangia* species are found in other regions of the world (Legner, Bay & White, 1967).

Salt (1938), followed by Flanders (1953), divided the process of host-finding by parasitoids into two general steps: host habitat location and then host location. The behaviour of many parasitoid species has now been studied and several stimuli involved have been identified (Vinson, 1976). Chemical stimuli have been found to be particularly important at all levels of the host-finding process.

This study was conducted to investigate the response of the four pupal parasitoids to various fractions of *Musca* breeding medium. Particular attention was paid to chemical stimuli present in these fractions.

Musca females usually lay their eggs in four types of medium (Busvine, 1951): faeces of animals, rotting vegetation, decaying animal remains and general garbage. After hatching, the larvae bury themselves in the breeding material and when the last larval stage ceases to feed it crawls away to pupate. This may occur either in the cooler drier parts of the breeding material, which consists mostly of frass, or in the surrounding substrate. Any of these natural media would have been extremely impractical to use in the laboratory, so an artificial medium was used that closely resembled rotting vegetation.

MATERIALS AND METHODS

The basic method of culturing *Musca* was taken from Spiller (1966) except that the larvae were reared on a medium consisting of wheat bran, grass meal, yeast, malt extract and water (ratio by weight = 45:20:1·5:1:100). The larvae were reared at a constant density by incubating 0·2 ml of eggs in 837 g of medium. All culturing and experimental work was conducted in rooms held at 25 ± 1 °C, 70 ± 10% r.h. with a 16/8 h light/dark cycle.

Preliminary observations on host-finding behaviour

Observations were made on the responses of female parasitoids to unused, 4-day-old *Musca* medium (Treatment 1) and 8-day-old medium in which larvae had fed and pupated (Treatment 2). Puparia were removed from this such that the medium consisted only of frass. A small dish containing 10 g of one of these media was attached to the underside of a small square clear plastic arena. This arena had a hole cut in the centre of the floor to expose the rim of the top of the dish to the inside of the arena. Five females (mated and up to 24 h old) of each species were then released into this arena in turn and their behaviour was observed. None of the species responded to unused medium but they all responded in the same manner to 8-day-old medium. They either flew or walked onto the medium and then restricted their movements to it. All the species exhibited frequent turning behaviour on, and at the edge of the medium.

These preliminary observations suggest that the observed host-finding behaviour of the parasitoids can be divided into two phases: orientation to areas containing host frass and arrestant (i.e. localised) searching behaviour in these areas.

Response to chemical stimuli in Musca *medium*

Chemical stimuli were assayed in the above two treatments and also in a treatment consisting of 6-day-old medium in which larvae had fed, pupated and then been removed (Treatment 3). Two other treatments were tested to see if chemical stimuli originated from larvae, puparia or both. Thus tests were made on 8-day-old medium from which larvae had been removed in their last instar (this was to prevent the medium from becoming contaminated with puparial stimuli) (Treatment 4) and on puparia 2–3 days old (Treatment 5). The larvae, from which these puparia had formed, were removed in their last instar to prevent the puparia from becoming contaminated with frass.

The response of the parasitoids to the above treatments was measured with a choice-chamber olfactometer (Fig. 1). The bottom half of the chamber consisted of a platform onto which two containers were fastened, one for the treatment and one for a control (an empty container). The top half of the chamber formed an arena with a removable top to enable parasitoids to be introduced. The floor of this

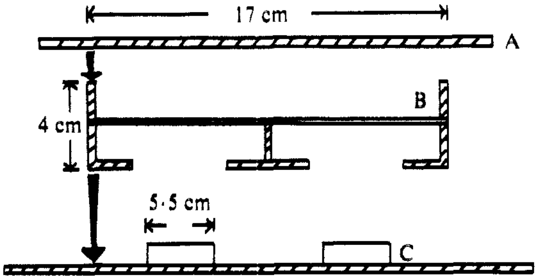

Fig. 1. Choice-chamber used to measure the response of female parasitoids to chemical stimuli in *Musca* medium. The diagram has been drawn in exploded form and shows a cross-section through the chamber. A = glass top; B = arena; C = containers for treatment and control.

arena was made of fine muslin so that volatile chemical components from the treatment could permeate upwards into one side of the arena. Humidity on each side of the arena was measured in a preliminary run with each treatment using cobalt thiocyanate paper. If found to be unequal, this was corrected by placing a dish of water next to the appropriate container.

Each treatment was tested by introducing 10 females (mated and up to 48 h old) into the arena of the chamber and observing the numbers on each side of the arena 10 min after the start of the experiment. This procedure was repeated six times.

RESULTS AND DISCUSSION

The total number of female parasitoids occurring on each side of the chamber arena for each of the treatments is shown in Table 1. None of the species shows a significant response to medium 4 days old (Treatment 1). The two *Muscidifurax* species clearly respond to (one or more) chemical stimuli present in 8-day-old medium (Treatment 2) whereas the two *Spalangia* species respond to stimuli present in 6- and 8-day-old medium (Treatments 2 and 3). The fact that the two *Muscidifurax* species and *S. endius* respond to Treatment 4 but not to Treatment 5 shows that they respond to stimuli related to larvae but not to those related to puparia. However, results from the same two treatments show that *S. cameroni* responds to both pupa- and larva-related stimuli.

The chemical stimuli present in Treatment 4 could be due to one or a combination of factors. For

Table 1. *The number of female parasitoids occurring on each side of the choice-chamber (data for all six replicates pooled together).* * *indicates* P < *0·01; chi-squared test with 1* D.F.

Treatment no.	Treatment / Control	Total no. recorded on each side of chamber			
		M. raptor	*M. zaraptor*	*S. cameroni*	*S. endius*
1	Medium 4 days old (uninfested)	27	33	26	21
	Blank	33	27	34	39
2	Medium 8 days old	43*	45*	47*	48*
	Blank	17	15	13	12
3	Medium 6 days old	38	31	42*	42*
	Blank	22	29	18	18
4	Medium 8 days old (final instar larvae removed)	40*	41*	46*	48*
	Blank	20	19	14	12
5	Puparia 2–3 days old	23	24	43*	33
	Blank	37	36	17	27

example, they could originate either directly from the larvae, or from larval by-products, or from the action of bacteria and fungi which attack the medium after the larvae have fed on it.

The type of locomotory behaviour (i.e. taxes and kineses) elicited by the chemical stimuli in the above treatments cannot be identified by using a choice-chamber (Kennedy, 1977). Therefore, the degree to which these stimuli elicit the attraction and arrestment behaviours identified in the preliminary observations has yet to be determined.

In conclusion, the four pteromalid parasitoids are attracted and arrested by *Musca* medium in which larvae have fed and pupated. Therefore, this type of medium probably forms an important cue for host habitat location in the natural environment. The stimuli eliciting this behaviour are probably varied, but chemical stimuli seem to be involved. Differences in the behaviour of the four species are small although, compared with the *Muscidifurax* species, the *Spalangia* species respond to a wider range of the treatments tested.

I would like to thank Dr J. K. Waage and Ms R. J. Stitt for comments on the manuscript, and the Natural Environment Research Council for financial support.

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The carabid *Agonum dorsale* as a predator in cereals

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INTRODUCTION

Polyphagous predators may be important in reducing the numbers of cereal aphids because they can persist in crops during periods when aphids are at low density or absent. This means that they could have an effect during the period of aphid immigration and increase when specialist predators or parasites are often in low numbers. Many of the polyphagous predators identified as feeding on cereal aphids have been carabids. Of the Carabidae, *Agonum dorsale* (Pont.) has shown promise on three counts; it can feed on aphids even when the aphids are at low field density (Sunderland, 1975), aphids can form a high percentage of the beetle's diet (Vickerman & Sunderland, 1975) and strong inverse correlations have been shown between the numbers of cereal aphids and those of *A. dorsale* (Edwards, Parsons, George & Heilbroon, 1978).

The aim of this project has been to study the underlying mechanism by which the polyphagous predator *A. dorsale* selects its prey. Laboratory arena experiments have shown many of the important factors but cannot re-create entirely the field situation. Accordingly, field work in 1981 concentrated on observation of the foraging behaviour of *A. dorsale* when placed in field arenas. Of particular interest were the general time budget of the beetle in the field and its behaviour in areas of high and low aphid density. Previous laboratory work had suggested that *A. dorsale* spends little time climbing and previous field work implied that prey availability is normally higher per unit area on the ground than on the plant. The 1981 field season provided a real test of the link between these laboratory and field observations.

In addition, a short experiment to assess the fate of aphids on the ground in the absence of *A. dorsale* was also carried out. This has relevance to all aphid predators whose foraging activity is at least partly at ground level.

METHODS

The area of winter wheat (cv. Hobbit) used was a 5 m × 5 m plot in the University's experimental grounds. Although this plot had no natural population of *A. dorsale*, it was used in preference to an actual farm site because of the equipment needed to observe the beetles.

Laboratory work had earlier established that the nocturnal *A. dorsale* could be observed at night with the use of red lights. Previous field experience showed that the maximum size of arena in which individual beetles could easily be followed under such conditions was 0·5 m × 0·5 m. Twenty-four such arenas were dug into the plot with the minimum of disturbance. Twelve arenas were covered with 1·5 m high, Terylene mesh cages so that large aphid populations could be built up. The other 12 arenas were left uncovered to ensure that they contained low aphid populations.

From each set of 12 arenas *A. dorsale* was introduced into two of them, one being used for observation, the other for removal of beetles for gut dissection. The remainder were left unaltered for prey sampling. Dissection of *A. dorsale* was necessary because identification of prey taken was not possible by direct observation. Numbers of *A. dorsale* were released into the sample arena and collected after 3 days when most had fed; these were then dissected. Sampling for prey was not possible in the two types of *A. dorsale* arena because of potential disturbance. Instead prey samples were taken from the 10 other arenas which contained no *A. dorsale*. Sampling involved taking soil surface samples (to a depth of 2–3 cm) and wheat tillers from each arena.

Observation of beetles was carried out three nights a week over the beetles' field-active period; sampling of prey was carried out weekly while sampling of *A. dorsale* for gut analysis was once every 2 wk.

The components of the beetles' behaviour were recorded using a stopwatch and tape recorder. Gut analysis was by visual identification under a microscope. For the prey samples, wheat tillers were searched with the naked eye and soil samples had organic matter removed by flotation and this was then sorted using a microscope.

Observation of *A. dorsale* finished at the end of the beetle's field active period. The caged sampling arenas were then used to assess the fate of aphids moving or falling onto the ground. Aphids were knocked off wheat plants by tapping tillers, any remaining aphids being removed carefully with a soft paint brush. The numbers of aphids returning to tillers were then recorded after 24 and 48 h.

RESULTS

Early laboratory work had shown that *A. dorsale* had distinct recognisable postures associated with its various activities and this was also so in the field arenas. The four main activities were: still (no activity), running (rapid locomotion not including predation), searching (slow locomotion, beetle receptive to prey), eating. Only a very small proportion of time was spent in other activities such as grooming and egg laying. Initial trials showed that at densities greater than 10 individuals per arena the behaviour of *A. dorsale* became altered from that shown at low density (three per arena). At a density of three per arena individuals rarely came into contact with one another or with the arena walls so it was assumed that their behaviour would be close to the natural situation.

Such interference between *A. dorsale* individuals as did occur was limited; interactions lasted 1 to 2 s and appeared to be non-aggressive. This probably allowed higher densities of individuals per arena than would be possible with some carabid species.

The diel activity cycle of *A. dorsale* was found to be a similar to that reported by Luff (1978) except that peak activity was at 02.00 rather than 24.00. The few individuals active during the day rarely showed predatory behaviour, so daytime predation by *A. dorsale* is probably negligible.

Individuals spent most of the night searching for prey; no other activity occupied a significant amount of time. This was the case in the plots of high and low aphid density.

Climbing of wheat plants occurred only rarely in areas of both high and low aphid density. Climbs were similar in both areas being short in duration (1 to 2 min) and not higher than about 30 cm. Stem and leaf surfaces were searched equally and no obvious discrimination occurred between green and senesced leaves.

Gut analysis showed that only a small proportion of individuals in the low density area had fed on aphids; the reverse was true in the high aphid density area.

The aphids removed from tillers in the caged sample arenas did not return in detectable numbers after 24 or 48 h.

DISCUSSION

Continuous observation of invertebrate predators in the field is time-consuming for the information gathered and with small, difficult-to-follow, invertebrates it is essential that they are at a sufficiently high density to ensure that most of the time in the field is spent observing the animal. *A. dorsale* overwinters as an adult in large aggregations at field boundaries; this 'social' part of the life cycle may have allowed higher densities of individuals per arena in these experiments than would have been possible with other invertebrate predators.

A. dorsale was found to be distinctly nocturnal with little activity outside the hours of full darkness, peak activity being around the middle of this period (02.00 h). Most of this period was spent searching for prey but only rarely were the catching and eating of prey items observed. This was not due to an improverished prey fauna as prey densities in the arenas were similar to natural field prey densities. It may be because prey handling times are short or that *A. dorsale* does not catch many prey items during the course of one night.

A. dorsale searched for prey almost entirely on the ground. Tiller climbing was rare and generally not high enough for the predator to encounter aphids. Despite this, a much higher proportion of beetles contained aphids in the high aphid density area.

These results imply strongly that *A. dorsale* eats more aphids with increasing aphid density but that these aphids are caught and eaten on the ground. This may be true of many Carabidae in cereals. Unquantified observations of predatory arthropods seen climbing wheat during the night suggested that Dermaptera and Araneae were the most active with the Staphylinidae next. The majority of Carabidae seen were active on the ground only.

Earlier work suggested that the fate of aphids on the ground may determine the potential of *A. dorsale* to control aphid numbers. The caged sample arena results show that, even in the absence of *A. dorsale*, no aphids managed to climb back on to tillers. This result is subject to at least two criticisms; predators other than *A. dorsale* were present in the sampling arenas and aphids may have moved to feeding sites outside the arenas after being disturbed. Even so this work has important implications for biological control.

It is essential to discover the fate of aphids which fall or move off wheat plants onto the ground. If such aphids are lost to the populations on the plants through causes other than predation, the effect of ground predators will be minimal. If, however, these aphids would normally climb back up wheat stems the implications for ground predators are clear. The development of integrated control of cereal aphids will need to quantify not only which species feed on aphids but where and when they do so.

I thank the Natural Environment Research Council for support and Drs G. P. Vickerman and S. D. Wratten for supervision.

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The role of predator searching efficiency in carrot fly egg loss

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INTRODUCTION

Although there have been many surveys of the occurrence of parasitism in the carrot fly (*Psila rosae* (Fab.)) (Wright, Geering & Ashby, 1947, van't Sant, 1961, Naton, 1968) there have been no previous studies of the role of predation as a mortality factor. Polyphagous predators play a significant part in the population dynamics of several dipteran pests, for example *Delia brassicae* (Coaker & Finch, 1971), *Leptohylemia coarctata* (Jones, 1975; Ryan, 1975) and *Oscinella frit* (Allen & Pienkowski, 1975), and the exposed position of *P. rosae* eggs, at or near the soil surface, probably makes this stage particularly vulnerable to predation.

During the period of this study, which included the drought years of 1975 and 1976, the population of *P. rosae* at the study site underwent a severe decline, and field egg densities during the oviposition periods were very low (mean densities of two to 10 eggs per 0·5 m row length). Consequently an indirect method was used as a measure of egg predation throughout this study, and the fate of high densities of artifically-placed eggs was followed during oviposition periods. A range of techniques indicated some of the predator groups responsible for the observed egg loss, whilst the potential importance of individual predator species was investigated in the laboratory.

MATERIALS AND METHODS

Measurement of predation using artificially-placed eggs

Prior to placing in the field, eggs collected from laboratory-reared *P. rosae* were stained with Bengal Rose using a procedure similar to that described by Wishart, Doane & Maybee (1956). Eggs were stained in a solution of 16 mg ml^{-1} Bengal Rose in 50% ethanol for 30 min, and all excess stain and alcohol then removed. In a range of potential predators tested, staining did not affect the readiness to eat treated eggs (Burn, 1980).

Eggs were placed among five or six soil crumbs scattered over a layer of sand in a Petri dish (7 cm diam) with a fine mesh bottom, the dish partially buried in the soil to present no obstruction to surface-moving predators. After a period of exposure to predation in the field (less than the time to eclosion at mean field temperatures) the dishes were recovered and remaining eggs extracted using brine flotation. The efficiency of recovery was high, 90% ± 2·9 for three samples of 50 treated eggs not exposed to predation.

Densities of 20 eggs per dish (area 38·5 cm^2) were used in 1975, and 30 eggs in 1976 and 1977 (compared with a maximum localised egg density measured during the study of 28.5 eggs 100 cm^{-2}). During each sampling interval of 6 or 7 days, 20 dishes were placed in the field (area *c.* 0·25 ha) in 1975, 9 in 1976 and 21 in 1977.

Identification of predators of P. rosae *eggs*

Pitfall traps were used to determine the relative abundance and activity of surface active predators during all 3 years of the study. In 1976 and 1977 these were also used to monitor the effect of partial exclusion on predator numbers. Exclusion barriers (described in Burn, 1980) were used in spring 1976 and throughout 1977 around three plots of 9 m^2 each; the effect of exclusion on levels of predation was again measured using artificially-placed, stained, eggs.

The damaged remains of marked eggs after exposure to predation in the field were compared with the characteristic damage patterns made by selected predators in the laboratory. Samples frequently contained remains characteristic of damage by *Trechus quadristriatus* (Schrank) and the clearly distinct remains left by small Aleocharinae (Burn, 1980). Although other predators (especially small beetle larvae) may have caused damage similar to either category, all damaged marked eggs were classified as either '*Trechus*-type' or '*Aleochara*-type'.

Laboratory comparisons of predator efficiency

All laboratory feeding experiments were performed on predators collected from the field and given free access to food, then starved for 24 h prior to an experiment, usually within 10 days of their collection.

The predatory effectiveness of two abundant carabids (*T. quadristriatus* and *Bembidion quadrimaculatum* (Linn.)) and one staphylinid (a member of the genus *Metaxya* (Reg.)) was compared using the functional responses to a range of prey densities. The experimental arena was a circular plastic dish, 15 cm diameter, with walls coated with fluon (P.T.F.E.) and a moist black filter paper substrate. Six prey densities, from 2·8 to 90·5 eggs 100 cm^{-2}, were used, spanning the range of densities found in the field and used in field experiments. All experiments were carried out over 24 h at 18 °C, using a 16-h light : 8-h dark régime and 100% r.h.

Preliminary observations (Burn, 1980) had suggested that against a particulate substrate in the field, eggs might be less easily detected by predators. The effect of this environmental complexity on the functional response was examined in the laboratory by covering the filter paper in the experimental arena (a Petri dish, 9 cm diameter) with a continuous single layer of sand. The effective total surface area of exposed sand over which a predator could move was estimated as 123 cm^2. Eggs were placed on the surface of the sand at six densities of from four to 130 eggs per 100 cm^2 effective surface. From six to 20 trials were performed at each prey density.

RESULTS

Egg predation measured by losses of marked eggs was variable (Fig. 1) but over 3 years showed regularly higher losses during spring (23% to 42%) and again in autumn (27% to 60%) and little loss during midsummer (13% to 18%). The collapse of stocks of cultured *P. rosae* in summer 1976 prevented estimates of predation then.

The range of predators trapped was very similar to that of a number of other studies made in agricultural habitats (Jones, 1976; Ryan, 1975; Speight, 1977) and they have been grouped in Fig. 2 into three classes: large carabids (greater than 8·5 mm long) small carabids (less than 8·5 mm long) and predatory Aleocharinae of which the numerically most important species were Myrmedoniini, especially the genus *Metaxya* in spring. The lowest levels of egg loss occurred during periods of peak activity of the larger carabids (Fig. 2*a*) which probably play little part in egg predation. There is broad agreement between egg removal and the peaks of activity of smaller carabids and Aleocharinae in spring, and again with smaller carabids – comprising almost entirely one species, *T. quadristriatus* – in autumn.

The larger carabids were almost completely eliminated from exclusion plots (Fig. 2*b*); however this had no effect on losses of marked eggs within the plots, again suggesting that this group is not responsible for predation. The Aleocharinae and *T. quadristriatus* are active fliers however, and reduction of these groups was only partial, so that there was a significant reduction in egg loss within exclusion plots in only two samples, during the June peak in predation. *T. quadristriatus* was probably present in sufficient numbers to have caused similiar losses in both exclusion and control plots in autumn, although the lower

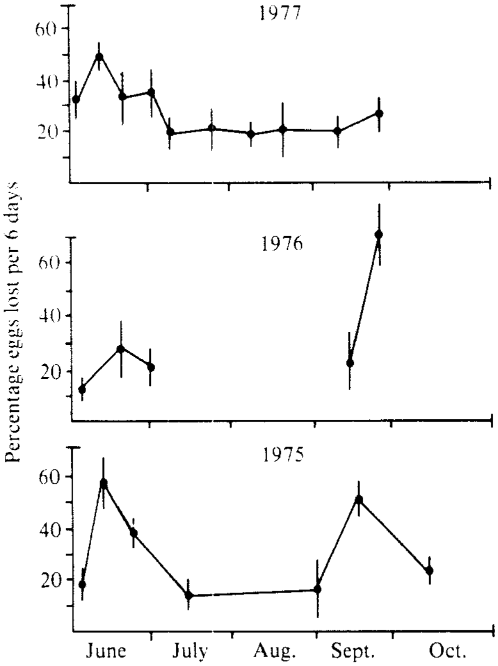

Fig. 1. Percentage loss of marked eggs (±95% C.L.) per 6-day interval, over 3 yr.

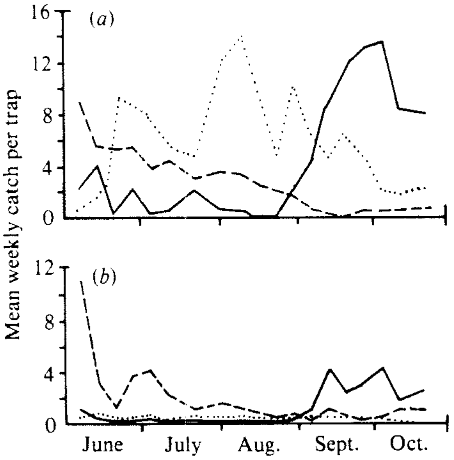

Fig. 2. Combined mean weekly pitfall trap catches: (*a*) Control plots (1975, 1976 and 1977); (*b*) Exclusion plots (1976 and 1977). (····) Large carabids (>8·5 mm), (——) small carabids (<8·5 mm), (– – – –) Aleocharinae.

recovery of eggs showing '*Trechus*-type' damage within exclusion plots (Fig. 3) suggests that other species may also be contributing to the autumn peak in predation.

Peaks in losses of marked eggs were associated with increases in the recovery of damaged eggs (Fig. 3). The predominant types of damaged egg recovered were clearly different during the two peaks of egg loss in 1977, corresponding to peaks in activity of the two predator groups. Although restricted to only two categories of damage, this does offer further evidence for the involvement of different components of the predator complex at different times of the year, and that the early peak in loss is partly attributable to the activity of the Aleocharinae, the later peak to predation by *T. quadristriatus*.

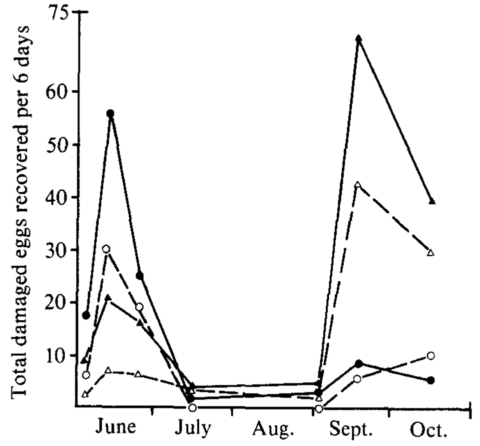

Fig. 3. Damaged eggs recovered per 6-day interval (1977). Control plots (● '*Aleochara* type', ▲ '*Trechus* type'). Exclusion plots (○ '*Aleochara* type', △ '*Trechus* type').

Initial laboratory tests showed that only the smaller carabid and staphylinid species took eggs readily; carabids larger than 8·5 mm took few or none. The functional responses of three readily-feeding species, on a filter paper substrate, are shown in Fig. 4*a*. The curves are similar to a Type II response (Holling, 1959) although that for *Metaxya* could also fit a sigmoid (Type III) curve. Differences between the

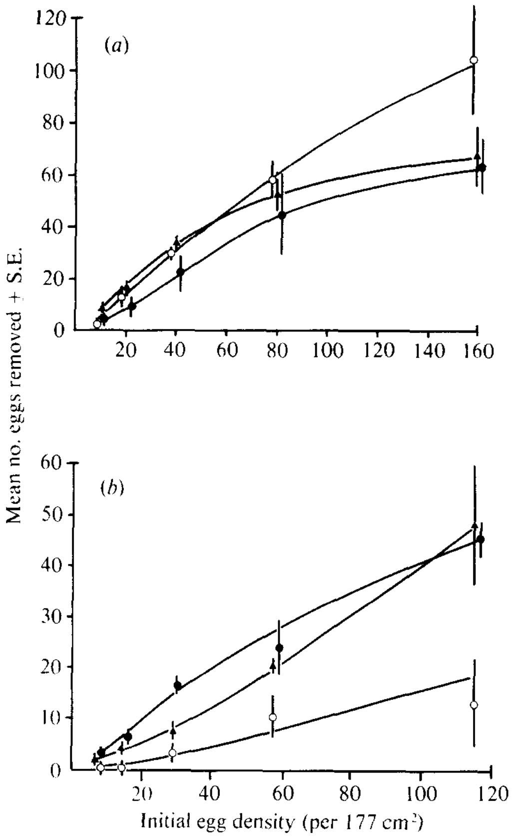

Fig. 4. Functional responses of three predators to *P. rosae* eggs: (*a*) on filter paper surface; (*b*) on sand surface. ▲ *B. quadrimaculatum*, ○ *T. quadristriatus*, ● *Metaxya* sp.

species are slight, although at high egg densities *T. quadristriatus* is apparently the most effective predator, whilst *Metaxya* is the least effective over a wide range of densities. Increasing the complexity of the experimental arena by adding a layer of sand altered not only the sequence of effectiveness of different predators, but also the shape of their functional response (Fig. 4*b*). Over all prey densities *Metaxya* and *B. quadrimaculatum* were more efficient than *T. quadristriatus* on the uneven substrate, and the shape of the response curve for the two carabids becomes a shallow exponential. Other factors, such as satiation, must limit the increase in predation rate at higher prey densities, and the form of the curve over a wider range of egg densities would be sigmoid (Type III response).

DISCUSSION

The observed peaks in *P. rosae* egg predation coincide roughly with first and second generation adult oviposition activity. The larger carabids are probably not involved in egg-predation; possibly these very small eggs lie outside the acceptable size range of prey, whilst different predator guilds (including the smaller Aleocharinae and *T. quadristriatus*) are probably responsible for the two peaks in spring and autumn.

Laboratory feeding tests in simple arenas also show these groups as potential predators. At all prey densities tested, increasing the substrate roughness reduced the predatory efficiency of the two small carabids. In contrast, the staphylinids apparently encountered an initial prey item equally readily, and showed a similar response curve, on both substrates. Factors responsible for this difference may lie in the methods of prey detection; in differences in body shape–the slender elongate staphylinid may search more effectively over a rough surface; or in circadian activity patterns–different species may spend a different proportion of the available searching time in hunting activities.

The change in shape of the functional response curves of *B. quadrimaculatum* and *T. quadristriatus* on an uneven surface results from the aggregative response of individual predators to clumped prey items (Hassell, Lawton & Beddington, 1977). At high prey densities, an encounter with an initial prey item results in a large proportion of the remainder of the eggs being found, following increased turning activity locally. At low densities, on the sand surface, there is greater difficulty in making an initial encounter with an egg, even though the effective surface area available for search is similar in both smooth and rough arenas. Thus a potentially important autumn predator, *T. quadristriatus*, may readily take artificially placed eggs at locally high densities, but its poorer ability to locate eggs at low densities, especially on an uneven (soil) surface, may reduce its effectiveness as a predator of naturally oviposited eggs.

Prey size and patch size, in this case the distribution of eggs among host plants, affect the probability of predation by polyphagous predators. Such predators have an important effect on the survival of eggs of *D. brassicae* for example (Coaker & Finch, 1971), the relatively larger eggs of which are distributed typically among fewer, widely-spaced hosts. In contrast, the small eggs of *P. rosae* are widely dispersed among a very large number of host plants, and lower predator searching efficiency under such conditions may limit the role of predation in this species.

I thank the Perry Foundation for financial support and Dr T. H. Coaker for supervision of this research, which was carried out at the Department of Applied Biology, University of Cambridge.

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Sex ratio and population dynamics of natural enemies – some possible interactions

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INTRODUCTION

One of the earliest models in insect population dynamics was Chapman's (1931) simple formula for the *biotic potential* of a population. This was a representation of population growth rate calculated from three parameters; female fecundity, generation time and sex ratio. Since these humble beginnings, population models have grown increasingly elaborate, but in the process the interesting parameter of sex ratio has more or less disappeared. Perhaps this has left us today less aware than our predecessors of the importance of sex ratio in population dynamics. My goal in this brief paper is to reinstate that awareness and explore some of the possible interactions between sex ratio and population dynamics in natural enemies, as a preliminary to more formal, mathematical studies.

As for all insects, populations of natural enimies will increase at a rate proportional to the frequency of females in the population, and thus proportional to the sex ratio. The rate at which the prey population is killed may also depend upon the sex ratio. This is true for parasitoid/host systems, where only females kill prey, but not for predator/prey systems where both sexes kill prey, unless they kill them at different rates (e.g. some coccinellids; Gawande, 1966).

Having acknowledged that parasitoid and predator systems exhibit these fundamental differences in the effect of sex ratio on their dynamics, we can treat the sex ratio itself as a constant in models of many natural enemy populations. Insect predators and dipteran parasitoids, for instance, generally exhibit stable primary sex ratios of 0·5 (proportion males). The proximate cause of this sex ratio is the simple process of Mendelian assortment in heterogametic diploids. Its ultimate cause is thought to be a form of stabilising selection. Fisher (1930) has shown that, in a population with unrestricted competition for mates and an equal cost to the production of males and females, variations from a sex ratio of 0·5 will favour mutant genotypes producing more of the rarer sex, and the spread of these genotypes will return the population sex ratio to 0·5. It is not certain how much this stability in diploid sex ratios is the result of active selection, and how much it is simply the consequence of the system of Mendelian assortment (Williams, 1979).

In contrast to diploid natural enemies, the haplodiploid parasitic Hymenoptera exhibit great intra- and interspecific variability in sex ratio. In such species, males usually arise from unfertilised eggs (arrhenotoky). Fertilisation is largely controlled by the female's 'decision' to release sperm stored in a spermatheca. Intraspecific variation in sex ratio, therefore, reflects the effect of external and internal stimuli on this decision, while interspecific variability may reflect as well differences in the decision process itself, which is probably more easily modified by natural selection than the Mendelian mechanism of sex ratio determination in diploids.

INTERSPECIFIC VARIABILITY

Hamilton (1967) has shown that deviation of evolutionarily stable sex ratios from 0·5 can occur if one relaxes Fisher's assumption that competition for mates is unlimited. This assumption will not be true for many parasitoids which mate in small local groups emerging from a host or patch of hosts. If a patch of hosts is attacked by n females, whose offspring mate randomly amongst themselves after emergence, Hamilton has shown that the stable sex ratio will be $(n - 1)/2n$. Thus as n increases and competition for mates becomes less restricted, the sex ratio will approach the expected 0·5, while a decrease in n will lead to higher local mate competition and a lower sex ratio. Ultimately, at $n = 1$, sibmating is complete, and the realistic interpretation of the stable sex ratio of zero is that a female will produce only enough sons to mate all her daughters. Subsequent modifications of Hamilton's model (Maynard Smith, 1978; Green, 1980; Taylor & Bulmer, 1980) all make the similar prediction that sex ratio will decrease with decreasing n and consequent increasing levels of sibmating.

Hamilton's model may be used to make predictions of species' sex ratios from a knowledge of their reproductive ecology. A crude but broadly accurate prediction is that gregarious parasitoids, which often exhibit high levels of sibmating on the host, have lower sex ratios than solitary parasitoids which must disperse before mating. In a more precise test of the model's predictions, I have found sex ratios of different species of solitary scelionid wasps to be strongly correlated with levels of sibmating inferred from their reproductive ecology (Waage, 1982).

By an analogous argument, useful predictions of reproductive ecology can be made from a knowledge of a species' sex ratio. One of the consequences of the laboratory rearing of parasitoids from small initial inocula is a high level of inbreeding. The model predicts that species with extremely low field sex ratios will probably be naturally inbred and therefore less affected by laboratory inbreeding than species with field sex ratios nearer to 0·5. The effect of inbreeding on these latter outbred species can be disastrous: inbred lines of the solitary icheumonid, *Diadegma eucerophaga* Horst. undergo shifts in sex ratio from 0·32 to 0·76 in the course of four generations (Waage, unpublished data). A similar change has been observed in the solitary ichneumonid, *Mastra carpocapsae* (Cush.) under inbreeding conditions (Simmonds, 1947). By contrast, inbreeding appears to have little effect on the highly-sibmated gregarious parasitoids, *Trichogramma* spp., which can be mass reared from small inocula for many generations in the laboratory without substantial changes in the sex ratio. However, inbreeding has been shown to increase sex ratio in at least some parasitoids with highly female biased sex ratios (Wilkes, 1947; Biemont & Bouletreau, 1980). Thus, the predicted relationship between natural sex ratio and susceptibility to inbreeding depression in the laboratory (as measured here by sex ratio changes) is not always indicated.

INTRASPECIFIC VARIABILITY

Simple population models will treat the average sex ratio of a parasitoid population as a constant whose value is closely dependent on the reproductive ecology of the species. This average sex ratio, however, obscures considerable intraspecific variability which results from a number of factors, both abiotic and biotic (Viktorov, 1976). Amongst the latter, three are of particular relevance to population dynamics: host quality, host distribution and parasitoid density.

Host quality

Host acceptance by parasitoids is influenced by a variety of factors, particularly size and age of the host. A number of parasitoids are known to discriminate amongst acceptable hosts in the allocation of sexes, laying mostly male eggs in smaller hosts and mostly female eggs in larger hosts (Viktorov, 1976). Charnov (1979) has proposed an explanation for this strategy. He suggests that parasitoid fitness should increase with parasitoid size, which in turn should increase with host size. If the fitness of females (fecundity and longevity) increases more rapidly with host size than the fitness of males (mating success and longevity), then a female maximises fitness by allocating her female offspring to relatively larger hosts and her male offspring to relatively smaller hosts. Several studies have supported this hypothesis (Charnov *et al.*, 1981), although interpretation is complicated by difficulties in estimating parasitoid fitness.

Variation in sex ratio as a function of host size, or host age, has interesting consequences for population dynamics. Factors which influence the size structure of hosts' populations, such as changes in age structure or scramble competition, will directly influence population sex ratio, and thereby change population growth rate without changing the overall level of parasitism for a particular generation.

Size-dependent sex ratios are to be anticipated in parasitoids which attack a non-growing host stage (i.e. egg or pupa) or which paralyse their hosts (many larval ecto-parasitoids), but not in parasitoids which develop in a growing stage (egg-larval or larval endoparasitoids), for which host size is not a good predictor of larval resources. A more general expression of this strategy, however, may be found in the effect of superparasitism on sex ratio. Sex ratio is often seen to increase with increasing levels of superparasitism. In some cases, this has been attributed to superparasitising parasitoids laying a more male-biased sex ratio than their predecessors on the host (Holmes, 1972). Insofar as larval resources are much reduced for these second comers, Charnov's model predicts that they should deposit proportionately more male eggs than the first wasp, which has responded to a relatively larger host resource.

Host distribution

The hosts of parasitoids are often distributed patchily in their environment. For at least some parasitoids, the size of the host patch may influence the sex ratio produced. Parasitoids with female-biased

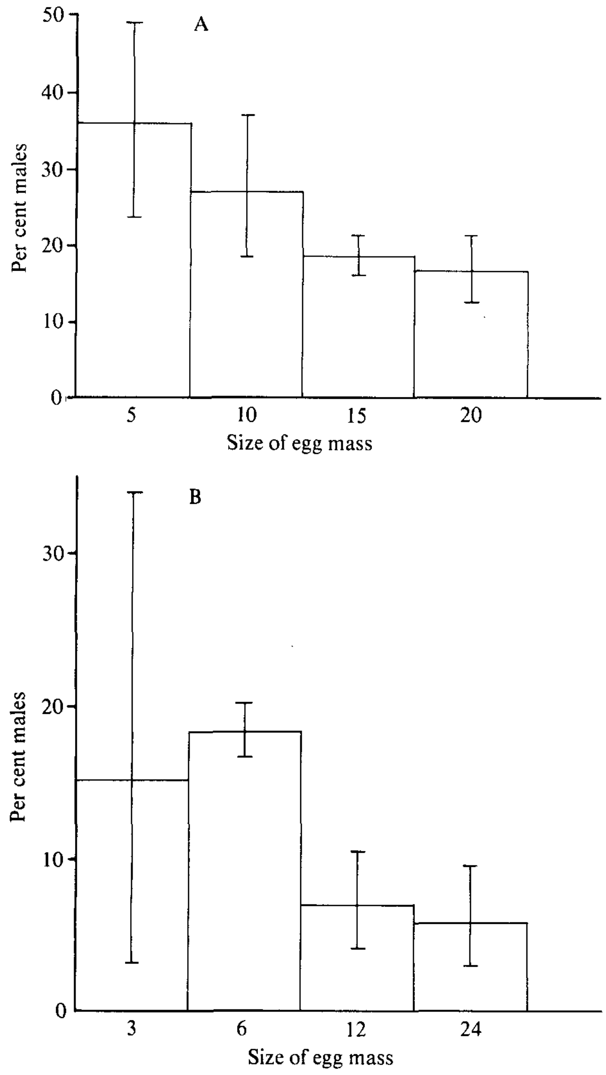

Fig. 1. The relationship between sex ratio and density of hosts per patch for two species of egg parasitoids. (*a*) *Trichogramma evanescens* (Trichogrammatidae) attacking the noctuid, *Mamestra brassicae*. (*b*) *Gryon atriscapus* (Scelionidae) attacking the coreid *Leptoglossus phyllopus*. Histograms represent (square-root arcsine) detransformed means with 95% confidence limits.

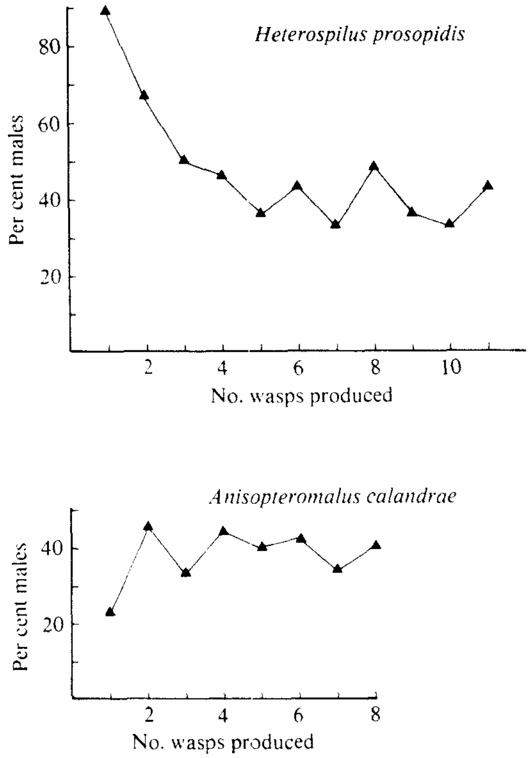

Fig. 2. Cumulative sex ratios during an oviposition bout for two larval parasitoids of the bruchid *Callosobruchus maculatus*, *Heterospilus prosopidis* (Braconidae) and *Anisopteromalus calandrae* (Pteromalidae). Individual wasps were exposed to an excess of hosts at 30 °C and 70% r.h., and oviposition was terminated at varying intervals to obtain different brood sizes. While the ultimate sex ratio of both species stabilises at about 0·4, *Heterospilus* lays a preponderance of males early in a bout, while *Anisopteromalus* lays a preponderance of females. Each point represents a minimum of three replicates.

sex ratios often lay male eggs first in an oviposition bout, followed by a long sequence of female eggs (Waage, 1982). As patch size decreases for such a parasitoid, so will the number of eggs laid, and sex ratio will consequently increase. Fig. 1 shows this phenomenon for two egg parasitoids.

For parasitoids with variable sex ratio sequences, dynamical factors which influence the size of hosts' patches can directly affect population sex ratio and thereby affect the rate of increase. Different patterns of sex ratio sequencing are found in parasitoids (Fig. 2), which will of course have quite different effects on the relationship between host distribution and population sex ratio.

Parasitoid density

Local increases in the ratio of parasitoids to hosts can produce a rise of sex ratio in both field populations (Zelinskaya, 1981) and laboratory populations (Wylie, 1979) of Hymenoptera. A number of factors may cause this density dependent shift in sex ratio, including increased superparasitism (see above), a decrease in the number of hosts parasitised per wasp (with a consequent shift in sex ratio, as indicated Fig. 1) or a direct change in the sex ratio allocated to unparasitised hosts in response to the perception of competitors. This latter phenomenon has been demonstrated for some parasitoids in response to contact with (Wylie, 1976) or traces of (Viktorov & Kochetova, 1973) other individuals at the oviposition site. It is not immediately clear why female parasitoids should reduce their production of female offspring in the presence of high densities of other wasps. One hypothesis (Viktorov, 1968) is that parasitoids are regulating population size and stability by reducing reproductive rate at high parasitoid/host ratios, where there is a risk of eliminating the host. An alternative to this group selection hypothesis has been proposed by Hamilton (1967) and elaborated by Werren (1980) and Suzuki & Iwasa (1980). These authors propose a sex ratio game, wherein the first female to find a group of hosts will bias her sex ratio towards females, thereby maximising her fitness in the anticipation of no subsequent visitors. A second female, however, will maximise fitness by producing a higher proportion of males, who are the rarer sex in the progeny to emerge from the hosts (the first female having laid mostly female eggs). The precise sex ratios produced will depend crucially on the frequency of second visits and the number of eggs laid by each wasp. The optimisation model itself has not yet been extended beyond the case of a first and second visitor. Nonetheless, it is clear that this stable strategy will produce an increase in sex ratio with an increase in parasitoid density as the frequency of second visits increases from zero to one.

Density-dependent increases in sex ratio should act as a form of stabilising interference in parasitoid population dynamics (Hassell, 1978), although it may be difficult to separate this effect from other consequences of crowding on hosts, such as increased mortality and egg retention (*cf.* Walker, 1967).

CONCLUSIONS

Parasitoid systems have provided much material for the recent development of sex ratio theory. These theories in turn elucidate a number of sex ratio processes which will clearly influence population dynamics. To date, the importance of these processes in parasitoid/host dynamics has received little investigation, although there is strong evidence that sex ratio may be an important factor in some biological control programmes (Wilkes, 1963; Kfir & Luck, 1979).

The incorporation of sex ratio parameters into population models might take a variety of forms. Average species sex ratios can be used as constants in simple equations. Their value has been shown to be closely related to the reproductive ecology of the species examined, and modelling may indicate which species' sex ratios provide the lowest and most stable parasitoid/host equilibria.

More realistic considerations of sex ratio in population dynamics must treat sex ratio as a variable, the value of which will be influenced by such factors as the size and age structure of host populations, the spatial distribution of hosts, and the relative density of parasitoids. The complexity of these interacting factors points clearly to a practical role for population modelling in exploring the dynamical consequences of sex ratio changes in parasitoid populations.

I would like to thank Ms T. Waring for assistance with the experiments on bruchid parasitoids, and Ms. J. Burford for preparation of the figures.

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Population dynamics of Carabidae

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INTRODUCTION

Several species of Carabidae are now being studied as potential general predators in agricultural crops. Much of this work is concerned with feeding studies (e.g. the paper by Griffiths in these Proceedings) and there have been few long-term studies of carabid abundance and changes in numbers within and between years in one particular field except by Jones (1979) who studied carabid populations in winter wheat for 7 years. Den Boer (1977) trapped Carabidae in various habitats for 9 years, but gives only totals caught per year. This paper presents interim results of a further long-term study of carabid numbers pitfall-trapped in N.E. England, and discusses the possible mechanisms contributing to their population stability.

POPULATION STUDIES

Pitfall-trapping

Carabidae were sampled by pitfall-trapping at the University of Newcastle field station at Close House, Northumberland, in a walled garden from 1966 to 1972, and in an arable field by the River Tyne from 1973 to 1981. Traps used were either 5 × 5 grids of plastic pots, 6·5 cm diameter × 7·5 cm deep, or 2-m lengths of plastic guttering (details in Luff, 1975). Numbers caught were standardised to mean catch per gutter trap per wk, ('catching rate'). The only abundant species in the garden was *Pterostichus madidus* (F.) and details of its biology and annual activity pattern are given in Luff (1973). In the field *Harpalus* *rufipes* (Degeer) was most numerous, and its biology is outlined in Luff (1980). Also abundant were *H. aeneus* (F.), *Pterostichus melanarius* (Illiger) and *Nebria brevicollis* (F.). Data on all these five moderately large species are given here.

Pitfall-catch is determined by both population size and activity, and is a measure of 'effective abundance' (den Boer, 1977). The relationship between pitfall catch and population density of *H. rufipes* was studied from 1973 to 1978 by using multiple mark and recapture analysis (Jolly, 1965) to estimate numbers present in June, July and August each month. There was a significant ($P < 0{\cdot}05$) relationship each month (Fig. 1) between l_n catching rate and l_n-estimated population; the slopes each month did not differ significantly from one another. For *H. rufipes* at least, therefore, pitfall-catch is closely related to population density. As much variation in activity is likely to be caused by temperature changes, the effect of this factor on activity of *H. rufipes* was assessed in the laboratory. 100 *H. rufipes* were introduced into a soil-filled propagating chamber, 117 cm x 71 cm x 10 cm deep, with a glass cover 55 cm high: both soil and air temperature could be altered by thermostatically-controlled heaters. Activity was monitored by pitfall traps set in the soil and by a light-beam actograph which recorded the numbers of beetles crossing the long axis of the chamber. The apparatus was run for a week at each of a range of temperatures from 10 to 17 °C, in both increasing and decreasing order, under 18 h photoperiod. The activity at each

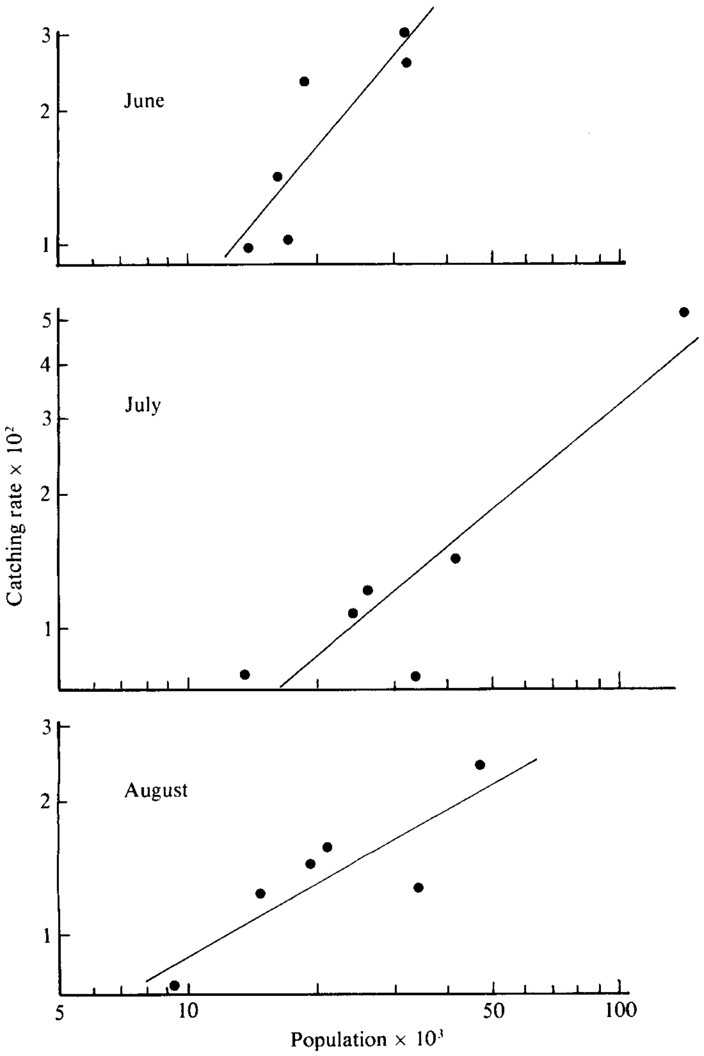

Fig. 1. The relationship between 'catching rate' (*H. rufipes* per trap per week) ($\log_e$ scale) and estimated population size ($\log_e$ scale) for June, July and August, 1973–1978.

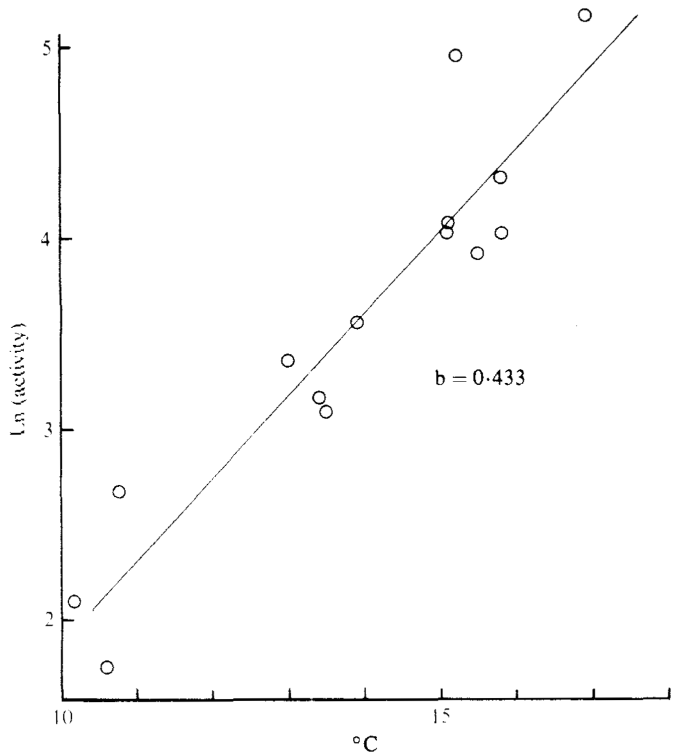

Fig. 2. The relationship between the activity of *H. rufipes* in the laboratory and temperature.

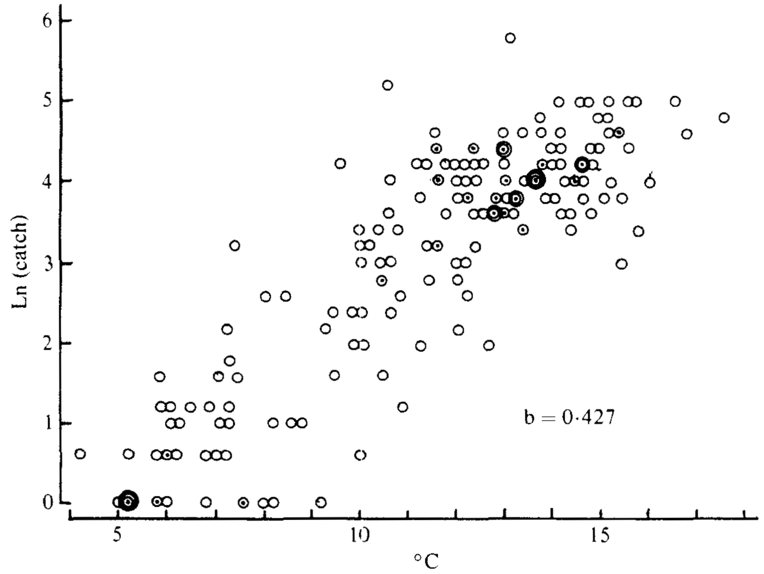

Fig. 3. The relationship between $\log_e$ daily pitfall-catch of *H. rufipes* and weighted hourly mean temperature. Concentric circles indicate more than one point at the same co-ordinates.

temperature was calculated by correcting the pitfall-catch and actograph count for mortality rate during the experiment, and then standardising the log-transformed values of each to units of standard deviations away from their appropriate mean. The mean of the two measures of activity at each temperature was then calculated (Fig. 2), showing a significant ($P < 0{\cdot}001$) linear relationship between log activity and temperature, with a slope of 0·433 per °C.

The extent to which temperature influenced pitfall-catch of *H. rufipes* in the field was studied in 1974 by emptying pitfall traps daily from 26 April to 25 October, whilst monitoring soil surface temperatures hourly using a 'Grant' thermistor recorder in the field. Daily log catching rate was compared with various measures of temperature including daily minimum, maximum, mean of these two, hourly mean and a weighted hourly mean in which the weight given to each hourly temperature was the proportion of *H. rufipes* activity occurring in that hour (determined by a time-sorting pitfall trap, in Luff, 1978). This weighted hourly mean was the temperature measure most closely associated with log catching rate (Fig. 3), accounting for 75·7% of the variation in catch. The significant ($P < 0{\cdot}001$) slope of 0·427 per °C agrees closely with that previously presented from the laboratory experiment and an average value of a change in log catch of 0·430 per °C is therefore used later to correct catch of *H. rufipes* for variation in temperature.

Annual fluctuations

The changes in numbers of each species trapped during each year follow a regular pattern termed the 'annual activity pattern' (Luff, 1973). This is characterised by the period of abundance, time of peak catch, changes in sex ratio of the catch and in the physiological condition of the beetles trapped. *H. rufipes* has a long period of abundance from May to September, females predominating except at the beginning of this period (Luff, 1980), whereas *P. madidus* is most abundant from June or July to September, with more males being caught at this time (Luff, 1973). *P. melanarius* has a similar pattern to *P. madidus*: peak catch occurred between mid-July and late August each year. *H. aeneus* was always most abundant between mid-May and mid-June, when females were gravid and subsequently laid eggs. *N. brevicollis* has two activity peaks each season, before and after summer diapause (Greenslade, 1965; Penney, 1966) but highest numbers were always trapped during September. Thus each annual activity pattern is characterised by an annual peak at a time of year characteristic of that species. This peak catching rate shows relatively little change from year to year in any of the species studied (Fig. 4). *H. rufipes* tended to alternate between high and low numbers in successive years because of its biennial life cycle (Luff, 1980), until a more marked decline from 1979, when there was an increase in the other species studied. This corresponded with a change in cultivation of the study field, much previously cultivated ground being allowed to develop into a grass and weed sward which was then mown instead of being ploughed. Williamson (1972) used the standard deviation of $\log_e$ population size as a measure of the amount of variation in animal populations. The values obtained in this work (Table 1) are at the lower end of the range given by Williamson (1972) for insect populations, and suggest that these carabid populations are relatively stable. The peak log catch of *H. rufipes* each year was corrected for variation in temperature by averaging the daily minimum screen temperatures during the appropriate trapping period, and then calculating the corrected catching rate at 10 °C (using the previously determined mean slope of 0·43 per °C). The standard deviation of corrected log catch was 1·48, so that taking temperature into account showed the active population to be slightly more variable than indicated by pitfall catch alone.

Table 1. *Standard deviations of yearly maximum* $\log_e$ *(catching rate)*

Species	Years	*n*	S.D.
H. rufipes	1973–81	9	1·029
H. aeneus	1975–81	7	1·026
P. madidus	1966–72	7	1·084
P. madidus	1973–79	7	0·959
P. melanarius	1973–79	7	0·316
N. brevicollis	1973–79	7	0·436

Roughly comparable values of population variability can be obtained from Jones (1979) by using monthly (rather than weekly) totals caught. Standard deviations of $\log_e$ catch calculated from Jones' data range from 0·47 (*P. madidus*) to 1·47 (*N. brevicollis*) for the five species studied here; the range of variation is thus very similar to that found over the same time period at Newcastle.

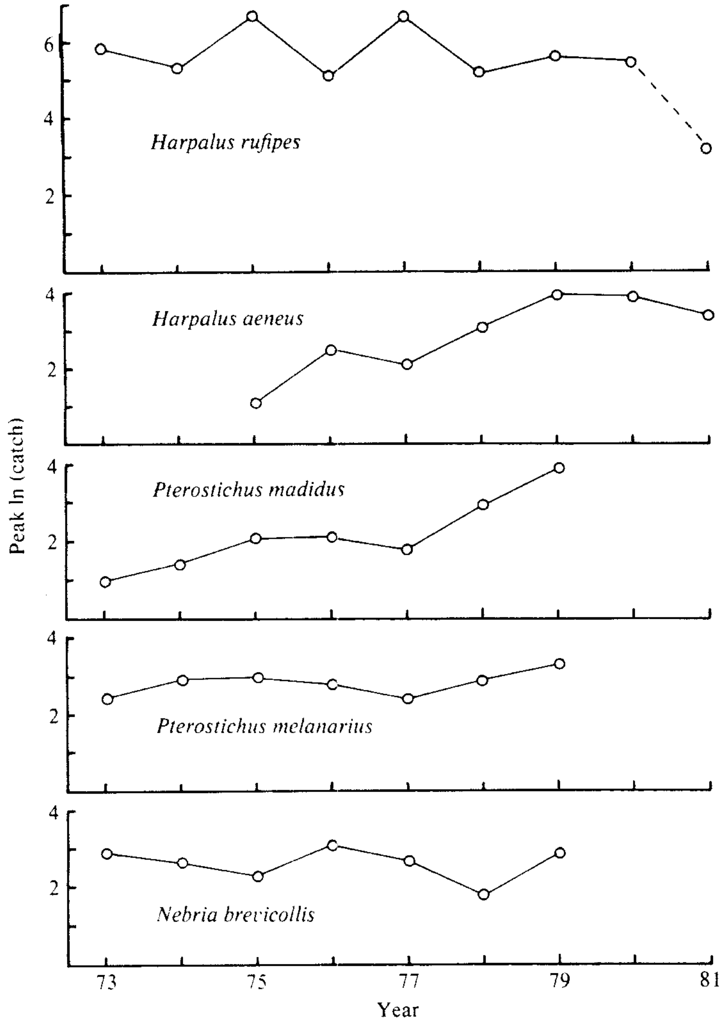

Fig. 4. Annual peak $\log_e$ catching rate of five species of Carabidae from 1973 to 1981. No data are available from mid-July onwards in 1980 and 1981.

STABILISING FACTORS

This relative stability of these carabid populations may result simply from a low rate of population change, from density related feedback or a combination of these. The factors contributing to population increase are the individual longevity, fecundity and rate of development. *H. rufipes* is relatively long-lived, with a slow development, taking nearly 2 yr from oviposition to adult breeding, with about one-third of the population then surviving to breed again in the following year (Luff, 1980). Adults of other species of *Harpalus* may live for up to 3 yr (Schjøtz-Christensen, 1965). *P. madidus* has an annual life cycle, with 1 yr from oviposition to breeding (Luff, 1973), but about one-quarter of the population survive to breed again in a second season. Briggs (1965) found that *H. aeneus*, and some individuals of *P. madidus* and *P. melanarius* bred in more than one season, as does *P. versicolor* (Sturm) and some autumn breeders such as *Calathus melanocephalus* (L.) (van Dijk, 1979). This overlapping of breeding cohorts will reduce population fluctuations (van Dijk, 1979; Macdonald, 1976). Fecundity is also low, especially in *Harpalus* species. The peak number of eggs found by dissection of female *H. rufipes* each year ranged from 10 to 15 (Luff, 1980), although actual fecundity could not be determined because very few eggs were laid in the laboratory. However, 25 female *H. aeneus* (with 25 males) laid a total of 276 eggs from 15 May to 20 July 1981, a mean fecundity of 11·04 eggs per female, which agrees well with the dissected maximum of

12 eggs. In *P. madidus* also, the mean laboratory fecundity of apparently healthy females (26·5, S.E. 3·01) agrees with the mean monthly maximum of eggs found by dissection, which was 23·5: only occasional females produced more than one batch of eggs in a season (Luff, 1973). Mean annual fecundity was not related to peak pitfall-catch that year ($r = -0{\cdot}04, P > 0{\cdot}05$). The number of eggs found in female *P. melanarius* was found to be similar to *P. madidus* (max. 26 eggs), although Hurka (1975) found that one field-caught female laid many more eggs (158) than laboratory-reared specimens (17 to 77). However, *P. versicolor* females lay eggs at a constant rate throughout their breeding season (van Dijk, 1979). *Nebria brevicollis* also lays its eggs over a longer period and the mean fecundity ranges from 31 to 40 eggs per female (Penney, 1966; Luff, 1976*a*). The exceptionally low fecundity of the *Harpalus* species is related to the relatively larger size of harpaline eggs in comparison to other groups of Carabidae (Luff, 1981). Estimation of fecundity by assuming a constant oviposition rate throughout the period of female maturity (Grüm, 1973) is certainly inappropriate for *Harpalus* and some *Pterostichus* females.

Mortality rate of adult *H. rufipes* was more or less constant at 10% in each of 3 months (Luff, 1980) but in *P. madidus* rose markedly in September each year after breeding. Grum (1975) found that adult mortality of several species was highest when breeding. In all cases, however, mortality was hardly catastrophic, killing less than 10% of the population in any one month. Parasitism of adult Carabidae is seldom extensive, although the proportion of *P. madidus* infested by *Mermis nigrescens* Dujardin (Nematoda) rose from 1% to 61% between 1966 and 1972 in the Close House garden (Luff, 1973), as *P. madidus* numbers declined: there was a significant ($r = -0{\cdot}787, P < 0{\cdot}05$) negative association between peak log catching rate and % parasitism, so that nematode parasitism was either delayed or inverse density dependent in this species, and did not contribute to population stability. *H. rufipes* adults are parasitised by the braconid *Microtonus caudatus* (Thomson) (Luff, 1976*b*) which has two generations per year: the peak % parasitism by the summer generation of 1973, 1974 and 1975 was 16·7%, 27·2% and 21·9% respectively, with no obvious relationship between catching rate and percentage parasitised. The importance of larval parasites needs to be studied further: 20·3% of 69 *H. rufipes* larvae collected by soil sampling in May and June 1975 were parasitised by *Proctotrupes gladiator* Hal., a species previously recorded from *H. rufipes* by Briggs (1965). Less than 1% of *N. brevicollis* larvae, however, were parasitised by *Phaenoserphus* species (Luff, 1976*a*). The few pathogens recorded from Carabidae tend to kill mainly old, post-reproductive beetles, such as *H. rufipes* killed by richettsiae (Carter & Luff, 1977).

In conclusion, therefore, the Carabidae studied fluctuate relatively little in abundance, as measured by pitfall trapping, from year to year. This probably also reflects similar changes in actual numbers present. Population growth and mortality rates are low, which contributes to the lack of fluctuations in numbers. There is little evidence of density-dependent adult mortality but larval mortality needs to be studied. Changes in relative abundance of different species may be associated with habitat changes, and the importance of adult dispersal (emphasised by den Boer, 1977) may then be very important to enable location and colonisation of new suitable habitats. The stability of carabid numbers implies that they are unlikely to respond rapidly in a numerical way to changes in prey density but conversely they will remain as a potentially useful component of environmental resistance to pest outbreaks even during periods when pests are absent from the crop.

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What is searching efficiency?

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INTRODUCTION

The term 'searching efficiency' has been used by both applied and theoretical ecologists in roughly the same sense–a more efficient predator* attacks a larger proportion of the prey over a given period of time than does a less efficient one. A universal, rigorous definition, however, of use both in population models and in assessing the performance of natural populations in the field, is still lacking. In this paper, I shall show how the theoretical ecologist's view of searching efficiency can be applied in studies of natural populations. The paper is in three parts. In the first part, searching efficiency is defined within the context of population models. I shall then turn to some problems arising from a patchily distributed prey population, and finally discuss a measure of overall efficiency that allows for incomplete predator survival.

SEARCHING EFFICIENCY IN POPULATION MODELS

Simple, analytical population models for predator–prey interactions normally contain some term the magnitude of which reflects the ability of an unsatiated predator to attack prey per unit time. This value, for real predators, will depend on their foraging behaviour which in turn depends on their efficiency at finding the habitat of the prey and, once there, of locating and successfully attacking prey individuals.

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* For convenience I shall for the most part refer to predators and their prey to include insect parasitoids and their hosts.

A convenient step towards a rigorous definition of such 'searching efficiency' is given by the simplest of equations for the functional response to prey density (Holling, 1959):

$$N_e/P = a'T_sN \tag{1}$$

where N is the number of prey, N_e is the number of prey encountered by P predators, T_s is the time spent searching (in the disc equation (Holling 1959), $T_s = T - (T_hN_e/P)$, where T is the total time of the interaction and T_h is the handling time per prey item eaten), and a' is the instantaneous measure of searching efficiency. This model assumes that prey are replenished as eaten or, alternatively, that exploitation during the interaction time T is minimal. Rearranging (1) now gives:

$$a' = \frac{N_e}{NPT_s} \tag{2}$$

from which a' emerges as the proportion of prey encountered per predator per unit of searching time. It is dimensionless if N and P are total populations, but otherwise has the same units of area as used to define the population densities.

This definition of the instantaneous searching efficiency is common to most difference equation models of predator–prey or parasitoid–host interactions (see Hassell (1978) for a review). Three immediate difficulties arise in its use: (1) exploitation of the prey by the predators may not be negligible, (2) to evaluate properly the searching time, T_s, behavioural observations are needed on the predator's distribution of time between different activities and (3) the number of searching predators at any one time, P, is an elusive measurement in the field.

Prey exploitation

Nicholson (1933), Nicholson & Bailey (1935), Royama (1971), Rogers (1972), Frazer & Gilbert (1976) and many others have allowed for prey depletion in predator–prey equations simply by assuming that prey individuals are encountered at random. The number of prey attacked N_a is then based on the Poisson distribution of potential encounters as follows:

$$N_a = N[1\text{-exp}\,(-a'T_sP)] \tag{3}$$

which, on rearranging, gives

$$a' = \frac{1}{PT_s}\log_e\frac{N}{N - N_a} \tag{4}$$

The term $\log_e (N/(N - N_a))$ is the k-value of Haldane (1949) – a proportionate mortality on a logarithmic scale. This definition of a' is thus very similar to that from eqn. (2), becoming identical as exploitation vanishes.

Searching time

The searching time T_s has figured explicitly in all the equations above. As a consequence, all factors affecting T_s should be considered in evaluating a'. For example, Beddington (1975) in a largely theoretical study defined T_s as:

$$T_s = T - T_h\frac{N_e}{P} - T_w \tag{5}$$

This allows for a 'handling time-limited' functional response and for mutual interference between predators, T_w representing the total time lost per predator due to interference. Satiation (or egg-limitation for parasitoids) can also be viewed as a factor limiting the functional response in much the same way as T_h in eqn. (5). This point has been made forcibly by Frazer & Gilbert (1976) who explicitly include the predators' average hunger level, as well as a searching efficiency term (a in eqn. (6) below) in their general predation model (see also Gutierrez *et al.* (1979, 1980)).

To assess the actual searching time in a field situation will always present problems in addition to those of constructing general models, simply because less predictable factors such as climate as well as prey and predator density will also affect T_s. An example of this is given by Klomp (1959) who compared over 6 years the searching efficiency (a in eqn (6)) of the tachinid *Carcelia gnava* (Meig.) parasitising caterpillars of *Bupalus pinarius* (L.) with the amount of sunshine during the period available for search. His data are given in Fig. 1. If the relationship is real ($0{\cdot}10 > P > 0{\cdot}05$), it is presumably largely mediated through increasing time devoted to active search in sunny conditions. Under such conditions direct observations on predators and parasitoids while foraging will be needed to build up a time budget from which actual searching time can be abstracted for use in eqn. (4).

Alternatively, the problem of estimating searching time can be side-stepped if T_s in eqn. (4) is replaced by the predator's searching lifetime, T. Searching efficiency then becomes the 'area of discovery' a of Nicholson (1933), where

$$a = a'\,T = \frac{1}{P}\log_e\left[\frac{N}{N - N_a}\right] \tag{6}$$

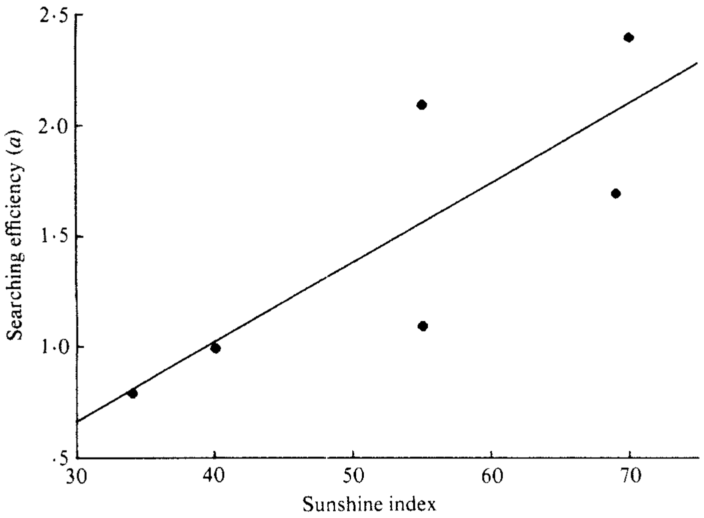

Fig. 1. The relationship between the searching efficiency of *Carcelia gnava* (expressed as a from eqn. (6)) and the amount of sunshine during the searching period (expressed as a percent of the maximum recorded) over a 6-year period. The data are described by the regression line: $Y = -0{\cdot}41 + 0{\cdot}036X$ ($r = 0{\cdot}81$; $0{\cdot}10 > P > 0{\cdot}05$). (Data from Klomp, 1959.)

With T now included in the definition of a, searching efficiency becomes affected by all factors influencing the proportion T_s/T; in particular, by those factors causing a plateau in the functional response, such as handling time or satiation, by those leading to mutual interference between predators, and by environmental vagaries as illustrated in Fig. 1. This need be no bad thing if one seeks a measure of overall predator efficiency, rather than some measure per unit of time spent actually searching.

Predator density

Without estimates of predator density, no proper measure of searching efficiency is possible. This is not the place for a discourse on sampling techniques; suffice it to say that one alternative is to sample the predators at some convenient point of time and assume that these are the subsequent searchers, as done by Varley & Gradwell (1968) for the parasitoids of the winter moth (*Operophtera brumata* (L.)). Alternatively, one can make direct observations of the searching predators and so develop some index of predator abundance over time (e.g. parasitoid-hours per plant (J. K. Waage, personal communication)).

SEARCHING EFFICIENCY IN A PATCHY ENVIRONMENT

The definitions so far have been in the context of a homogeneous prey population, randomly exploited by P predators. We now take the necessary step of assuming the prey to be patchily distributed, which has important implications for the measurement of searching efficiency. Let us consider the example where 155 prey are divided between five patches each of N_i prey as follows

$$\{N_i\} = 5, 10, 20, 40, 80 \tag{7}$$

The predator distribution is given by the simple expression of Hassell & May (1973) where the fraction of the total predators per patch β_i is given by

$$\beta_i = c\, a_i^{\mu} \tag{8}$$

a_i being the fraction of prey per patch, c a normalisation constant and μ the 'aggregation index'. This is a convenient, albeit rather naive, means of generating different predator distributions: the predators tend to aggregate in low density patches when $\mu < 0$, are evenly distributed when $\mu = 0$ and tend to aggregate in high density patches when $\mu > 0$.

In such a heterogeneous situation, we must distinguish between two types of searching efficiency: that within a single patch and that over all patches. Assuming that exploitation within a patch i is random, the patch specific searching efficiency a'_i is given by

$$a'_i = \frac{1}{P_i T_{si}} \log_e \left[\frac{N_i}{N_i - N_{ai}}\right] \tag{9}$$

This is in contrast to the overall efficiency, neglecting any patchiness, which is given by a' from eqn. (4). The patch specific measure a'_i is, of course, independent of predator distribution, but this is not true of a', which now depends sensitively on the predators' response to the spatial distribution of its prey. This is illustrated by the numerical examples in Fig. 2 in which the a'-values have been calculated for a wide range of predator aggregative responses ($\mu = -4$ to 6) for three different levels of searching efficiency within a patch. Notice that in each case a' rises to a maximum as μ increases, beyond which it declines to some extent. The reason for these apparent changes in overall searching efficiency is simply that any foraging pattern that leads to more prey attacked for a given total prey density must also produce a higher value for a', as illustrated by the rising curves in Fig. 2 as μ increases. The subsequent decline in these curves when $\mu > 1$ is due to 'overaggregation' by the predators in patches of high prey density. This leads to overexploitation of the prey to the point where even random search ($\mu = 0$) would have fared better. This is especially true for high values for a'_i. A predator with a high patch-specific searching efficiency a'_i need

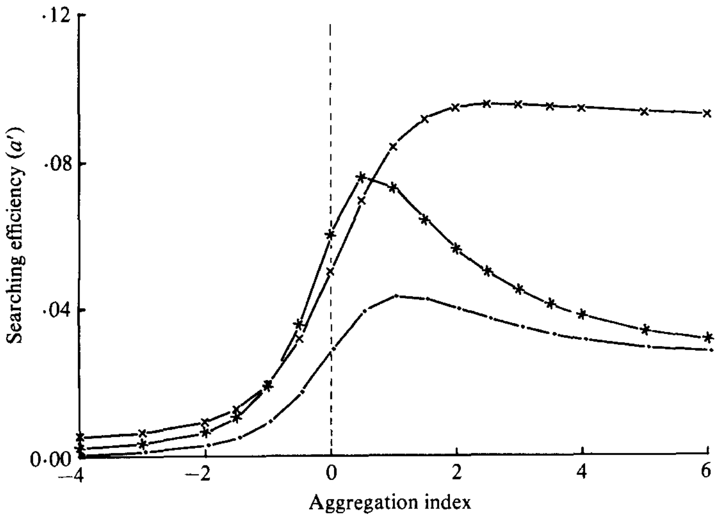

Fig. 2. Numerical examples showing the changes in overall searching efficiency (a' in eqn. (4)) with increases in the aggregation index (μ in eqn. (8)) for three values for the patch-specific searching efficiency (a'_i in eqn. (9)). The prey are divided between five patches as in eqn. (7) (*: $a'_i = 0{\cdot}3$, ×: $a'_i = 0{\cdot}25$, ●: $a'_i = 0{\cdot}15$).

not, therefore, be the most efficient overall, if its distribution is not sensitively attuned to that of its prey. A case in point is shown in Fig. 2 where predator A ($a'_i = 0{\cdot}3$) is less efficient than B ($a'_i = 0{\cdot}25$) for all $\mu \gtrsim 1$. (Such an effect would not be observed by predators tending towards optimal foraging, where the distribution would continually alter in response to the different levels of prey exploitation per patch.)

Searching efficiency as defined in eqn. (4), but in a patchy environment, is thus sensitive to two factors: (1) the patch-specific, intrinsic searching ability of the predators and (2) the extent to which the distribution of the predators relative to the prey is non-random. To some extent this overall searching efficiency is misleading in that it is the value (e.g. in m^2 per unit time, if the populations are expressed in m^{-2}) that would have been necessary to cause the observed mortality *had the searching been at random* (Free *et al.*, 1977). This arises from the structure of eqn. (4) which assumes the total prey N to have been randomly exploited by the P predators. However, for many practical purposes, it remains a useful measure of efficiency that is particularly sensitive to the ability of the predators to match appropriately the prey's distribution.

In other cases, it will be awkward to have a definition so sensitive to predator distribution. Values of a' will fluctuate widely from time to time simply due to factors affecting spatial distributions. A measure of a' that is much less sensitive to this must take the observed distributions into account, and will then depend primarily on the values of a'_i for the different patches sampled. Let us assume that we have information on the distribution of prey, predators, searching time and prey attacked over a number of individual patches. An overall searching efficiency can now be obtained from

$$a' = \frac{1}{n} \sum_{i=1}^{n} \left[\frac{1}{P_i T_{si}} \log_e \left(\frac{N_i}{N_i - N_{ai}} \right) \right] \tag{10}$$

where n is the number of patches. This is merely the average of the a'_i-values from eqn. (9). By taking full account of the actual searching time per patch and the resulting number of prey eaten, eqn. (10) provides the best measure so far of the real searching efficiency in a patchy environment. It is, however, labour intensive!

SURVIVAL OF PREDATOR PROGENY

In seeking natural enemies, and parasitoids in particular, for use in biological control programmes, high searching efficiency is only one ingredient for a successful agent, and could be completely negated if the parasitoid progeny themselves suffer high levels of mortality. A simple means by which such survival can be incorporated into a measure of 'overall performance', A, for parasitoids with discrete generations is given by

$$A = \frac{1}{P_t} \log_e \left[\frac{N}{N - P_{t+1}} \right] \tag{11}$$

(Hassell & Moran 1976) where P_t and P_{t+1} are the densities of searching parasitoids in successive generations t and $t+1$. This expression thus only differs from eqn. (5) when $P_{t+1} \neq N_a$. An example of the extent to which A can differ from searching efficiency alone (a in eqn. (5)) is given by Hassell (1980) for *Cyzenis albicans* (Fall.) parasitising the winter moth in Wytham Wood. The mean value for a is $0{\cdot}167$ m^2 ($\pm 0{\cdot}107$; 95% confidence limits) in contrast to that for A of $0{\cdot}027$ m^2 ($\pm 0{\cdot}018$). This six-fold difference is almost entirely due to the very high puparial mortality suffered by *Cyzenis* during the 10 months or so that it is in the soil. Because eqn. (11) takes into account both searching efficiency *and* the parasitoid progeny that survive to search in the next generation, A is a good measure of the parasitoid's contribution to the depression in the host equilibrium, and hence should appeal to workers directly involved in biological control.

CONCLUDING REMARKS

In this paper a variety of subtly different measures of searching efficiency have been considered, some simple and some requiring rather detailed behavioural observations on searching behaviour. The simplest is the familiar eqn. (6) in which the troublesome T_s can be replaced by the total period available for search ($T = 1$). This will be the most convenient for general life table studies in which the study of predation or parasitism is not the sole aim. With a shift in emphasis to evaluating in some detail the performance of natural enemies in the laboratory or field, estimates of actual searching time become important. Equation (4) requires but a single estimate of T_s per predator so that efficiency can be expressed per unit of searching time, while eqn. (10) demands the same observations as eqn. (4), but for each of many prey patches. This is important for a true assessment of searching efficiency in a patchy environment.

I am grateful to Robert May and Jeff Waage for their helpful comments on the manuscript.

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A survey of cereal aphids and their natural enemies in winter wheat in 1980

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INTRODUCTION

Experiments by the Glasshouse Crops Research Institute in previous years involving caging and barrier exclusion techniques implicated natural enemies as an important factor in determining cereal aphid numbers in winter wheat. In 1980, a survey of fields on North Farm, Worthing, was carried out to look for effects of natural enemies in the absence of experimental manipulations.

Ten fields of winter wheat were selected on the basis of differences in sowing date, type of edge habitat, soil type, altitude and acreage. Five of the fields were early-sown (1.10.79–6.10.79) and five late-sown (24.10.79–1.11.79) and a sampling site was established near the edge (5 m from the field margin) and middle of each. Four pitfall traps for polyphagous predators and three water traps for aerial aphid-specfic predators at each site were emptied at weekly intervals. Larvae and adults of aphid-specific predators were sampled by taking 200 sweeps per site per week. Parasitoids and entomophagous fungi were assessed by counting mummies and dead diseased aphids on the shoots.

PRELIMINARY CONCLUSIONS

Sitobion avenae (F.) was present at all 20 sampling sites and was the most abundant aphid overall. *Metopolophium dirhodum* (Wlk.) was very infrequent, but aphids provisionally identified as *M. festucae* (currently undergoing taxonomic revision) were abundant in two fields and infrequent elsewhere.

The pattern of population development of *S. avenae* was noticeably different from that seen in pest outbreak years on North Farm. Whereas in 1977 populations were initiated by large numbers of immigrant alatae, in 1980 they started from overwintered aphids in the early-sown fields following an autumn migration in 1979 and a mild winter. No aphids were found in late-sown fields until a small immigration of alatae in late May. In 1977, there was a rapid rise to a population peak of about 36 per shoot in July but in 1980 numbers increased approximately exponentially to peaks in June none of which exceeded 3·9 per shoot. All aphids had disappeared by the end of July and no aphicide applications were necessary.

The population peaks of *S. avenae* were both higher and earlier in the early-sown fields than in the late-sown. In addition, populations were significantly ($P < 0·001$) larger during the population growth phase in the middle than at the edge of early-sown fields, but there was no such difference between middle and edge in late-sown fields (Fig. 1). The total catch of polyphagous predators in pitfall traps up to 30

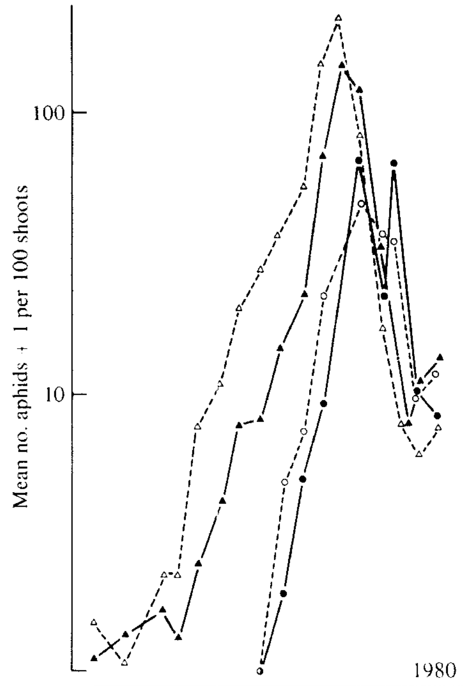

Fig. 1. Aphid populations (*S. avenae* and *M. festucae*) in the edges and middles of early and late-sown fields. △, middle early; ▲, edge early; ○, middle late; ●, edge late.

May was significantly ($P < 0{\cdot}01$) greater in the edge than in the middle of early-sown fields, and these predators may have reduced the overwintered aphid population at the edge to a level below that in the middle. In contrast, by the time aphids had infested the late-sown fields in May, there were approximately equal numbers of predators in edge and middle and no difference in aphid population was produced.

The factors that might have been the cause of the population decline include emigration of aphids from the crop, adverse weather conditions, a change in the nutritional quality of the crop, or the action of pathogens, parasitoids or predators.

Density-related alate production is unlikely to have contributed significantly to the population decline because population density was relatively low at the population peaks and there was no sudden increase in number of potential emigrants (alatiform fourth instars as a percentage of total fourth instars) as would be expected prior to emigration.

There was a cool wet period extending from the third week of May to the middle of July and during this time all populations rose to their peaks and declined, but not in synchrony. On average, the aphid populations in the middles peaked 4 days before the edges and in the early-sown fields 8 days before the late-sown. These peaks, which occurred over a period of about 2 wk in June, were not related to any obvious feature of the weather.

Aphid numbers in the five early-sown fields all peaked at some stage of flowering, while in late-sown fields peak times were more variable (1/4 heading to watery-ripe). These are growth stages when the potential for population increase is known to be high (Watt, 1979). There was no indication that the onset of the population decline was closely linked with a particular growth stage. In three fields the growth stage was more advanced at the middle than the edge, in one the reverse was true, and in the remaining six there was no discernible difference; however the population peak in the middle preceded that in the edge in nine of the 10 fields.

Despite the wet weather, the incidence of fungal disease was low throughout the season and very little mortality of aphids can be attributed to this factor on North Farm in 1980. In general, there were more parasitoid mummies per tiller in the early-sown than in the late-sown fields and more in the middles than the edges; mummy and aphid densities were positively related. Within each field, mummy and aphid densities tended to rise and fall in synchrony and there was no marked increase in numbers of mummies at the start of the population decline as might be expected if parasitoids were the predominant mortality factor. However, it is not known what value the ratio of mummies to aphids on shoot counts needs to reach before a significant effect of parasitoids on the aphid population is indicated.

Eggs of aphid-specific predators were first found in early-sown fields in late April to mid-May and in late-sown fields in late May and early June. In the early-sown fields, the number of aphid-specific predators (as assessed by sweeping) was increasing rapidly at the start of the population decline (e.g. Fig. 2). In most late-sown fields, sweeping did not begin until after the aphid peak and it was not possible to compare the timing of the aphid peak with the predator population.

At the 10 sampling sites in the early-sown fields, syrphid larvae were present at or immediately after the time of the aphid population peak at all 10 sites. Coccinellid adults were present at this time in seven but appeared later in three sites. Larvae of coccinellids were also present about the time of the peak in most sites, but chrysopid larvae were caught at this time in only three of the 10 sites. Sweeping is a selective sampling method which tends to collect the larger predators; therefore, small larvae were probably present in the crop before predators were first caught in the nets. A total of 10 species of predatory syrphids were reared from larvae collected in the fields, including *Syrphus ribesii* (L.), *S. corollae* (F.), *S. nitidicollis* Meigen, *Episyrphus balteatus* (Degeer), *Scaeva pyrastri* L. and five species of *Platycheirus*. Five species of coccinellid were found, the most abundant being *Coccinella 7-punctata* L. and *Propylea 14-punctata* (L.).

In each of the five early-sown fields there were both more aphids and more aphidophagous stages of aphid-specific predators at the middle than the edge ($P = 0{\cdot}031$, binomial test). Rates of aphid increase were negatively related to the number of aphid-specific predators during the aphid increase and decrease phases ($r = -0{\cdot}535$, $P < 0{\cdot}001$). More data have been collected in 1981 to test these relationships further.

From this preliminary analysis of the data it appears that in 1980 aphid numbers were affected early in the season by polyphagous predators and that the aphid-specific predators which appeared later prevented aphid numbers from exceeding 3·9 per shoot. This survey has been repeated in 1981 and a more detailed analysis of the data from both years is being prepared.

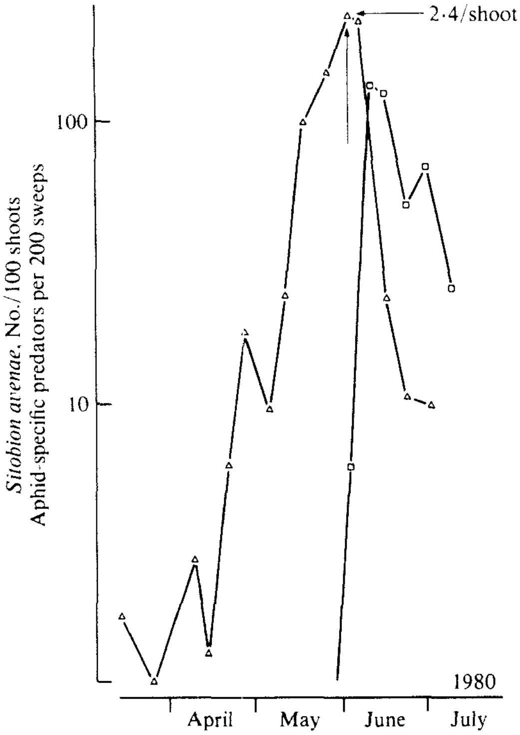

Fig. 2. Aphids and active predatory stages of aphid-specific predators in the field 'Frieslands West'. △, aphids; □, predators; ↑, flowering.

We would like to thank the management of North Farm Ltd for their generous co-operation at all times.

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Predation of sugar beet aphids in New Zealand

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INTRODUCTION AND CHOICE OF METHODS

Beet is one of the most promising potential sources of biomass feedstock for ethanol-based liquid fuel production in Canterbury, South Island, New Zealand. A multidisciplinary study began recently to examine the costs and performance of this crop as an energy source (N.Z. sugar for domestic use is imported from Fiji). For a European entomologist with an interest in the role of the natural enemies of pests, planning a study in such a crop presents a series of methodological problems: 1980 was only the second year in which this crop had been grown on a large scale and only one preliminary survey of the invertebrate fauna had been carried out (Pearson & Goldson, 1980). The relative importance of directly-damaging pests and virus vectors was unknown and the identity and vectors of beet yellowing viruses, which were known to occur, were also not fully known. In view of work on sugar beet pests in the

U.K., the two aphid species commonly occurring on N.Z. sugar beet were chosen as species for further study. These aphids were *Aulacorthum solani* (Kalt.) and *Myzus persicae* (Sulz.). The possible approaches for studying the role of these aphids' natural enemies were:

(1) A large-scale survey of many fields, attempting to correlate aphid numbers with predator abundance. This was not possible in view of the low number of sites where the crop was grown in 1980.
(2) A small or medium-scale autecological study of one or a few natural enemies, assessing searching behaviour, abundance, prey consumption etc. As there was no information on candidate species, such an approach would have been premature.
(3) A plot-based experiment in which the numbers of natural enemies are manipulated and the consequences for pest dynamics studied. This was the approach chosen. Drawbacks of this method are that results may remain correlative rather than explanatory and that details of mechanisms of predator–prey interaction may remain obscure.

The study site was an area of 24 contiguous paddocks, each measuring 52 m × 8 m and separated by levées *c.* 0·5 m high and 1·5 m wide. The paddocks could be irrigated by flooding via dykes running along one of the long boundaries of the site. Such a border-dyke system is typical of central and southern parts of South Island, N.Z. Each paddock was divided lengthwise into two plots as part of a M.A.F. programme investigating the effects of sowing date and insecticide use on sugar yield. The sowing date of the beet used in the predation experiments was 1 September 1980 (cv. Monoire). In the control plots of the above scheme, experimental plots for the predation work were established. Each of these measured 4 m × 4 m. The treatments were: (1) *control*: plot delineated by cord only; (2) *predator numbers increased* (ingress boundaries); (3) *predator numbers reduced* (egress boundaries). The predator manipulation plots were bordered by a 20-cm-wide trench above which rigid bitumenised paper projected horizontally half-way across its width. Depending on whether the paper projected into or out of the plot, the numbers of soil-surface arthropods in the plot would be expected to be increased or decreased. Plots were arranged in a randomised block design incorporating four replicates/treatment. Each week from 14 October, the soil between the plant rows in the predator-reduction plots was sprayed with the insecticide carbaryl at a rate of 0·34 g a.i./litre/plot to supplement the barriers in their reduction of predator numbers (Lowe, 1975). Each week three 8-cm-diameter pitfall traps (with lids supported 10 cm above soil level and containing detergent and 2% formalin) were replaced with identical traps and their contents identified in the laboratory. Weekly counts of aphids, other potential pests and predators were made on beet plants in each plot.

With the above experimental arrangement an attempt was made to answer the following questions, of increasing practical relevance: Do predators:

(1) reduce average population levels (e.g. mean number of aphids/plant)?
(2) impose upper limits on aphid population growth (regulation)?
(3) reduce the proportion of aphid-infected plants?
(4) reduce the proportion of virus-infected plants?
(5) increase sugar yield from the beet?

THE PREDATOR FAUNA

The fauna captured by the pitfall traps comprised mainly the coleopteran families Staphylinidae and Coccinellidae, spiders (mainly Lycosidae), centipedes (Diplopoda) and harvestmen (Opiliones). In marked contrast to the same crop in the U.K. (Jepson, 1982) carabid beetles were rarely captured (three individuals in >300 trap weeks).

Accumulated predator numbers were reduced by *c.* 50% in the reduction plots compared with the control but the plots which were intended to supplement predator numbers were less successful; by the last sample date (12 December 1980), these plots had increased the total catch of predators by only 14% compared with the control. The ingress boundaries were more successful for the larger organisms; total numbers of Opiliones captured for instance were 45% higher in these plots than in the control while number of staphylinids, coccinellids and lycosids were increased by a maximum of 14%.

APHID NUMBERS

Numbers of both aphid species on beet throughout the Canterbury region in 1980 were lower than those in 1979 (J. Pearson, unpublished) and in the control plots in the predation experiments, numbers of *M. persicae* did not exceed 0·3/plant. Peak numbers in the predator-ingress plots were 0·5/plant whereas the peak in the predator-reduction plot was 150 times higher than in the control, at 40/plant on 8 December. Such differences may be of no consequence in terms of virus incidence, however, and a measure of the proportion of plants infested by aphids (one or more aphids/plant) may be more relevant. In this respect, control and predator-ingress treatments differed little, peaking at 26% and 35% infested plants respectively. In the predator-reduction plots, however, the proportion of plants infested was higher than in the other two treatments throughout the season, peaking at 92% infestation on 11 November. The level of infestation declined after this date, coinciding with increasing numbers of third- and fourth-instar coccinellid and chrysopid larvae and of parasitoid mummies observed on the plants during December.

VIRUS INCIDENCE AND SUGAR YIELDS

The virus present in the beet was identified as beet western yellow virus (J. W. Ashby, Department of Scientific and Industrial Research, Lincoln; personal communication) and is transmitted by *M. persicae.* Virus symptoms on the plants were assessed on four dates in April and May 1981; in each case, 50 plants selected randomly in each plot were examined and the number showing virus symptoms was recorded. In the predator-reduction plots there was 31% incidence of symptoms in early April, declining to 17% in late May. Comparable figures for the other treatments were 14% declining to 4% (control) and 11% declining to 5% (ingress plots).

Overall total sugar yields were 17·9% and those for reducing sugar were 0·34% (% dry weight in each case). There were no significant differences between the treatments with respect to either sugar measurement.

CONCLUSIONS AND IMPLICATIONS

In the United Kingdom the main viruses transmitted by *M. persicae* to sugar beet are beet yellowing virus (BYV) and beet mild yellowing virus (BMYV), called jointly 'virus yellows'. When 20% or more of sugar beet plants show symptoms of virus yellows at the end of August, crop yields are appreciably decreased (Hull & Heathcote, 1967). Extrapolation to the southern hemisphere and to another virus is of doubtful use, but the equivalent month to August in New Zealand is February. In 1979, virus symptoms had only just appeared at this time and in 1980, virus incidence was generally lower (J. W. Ashby, personal communication). This, together with the virus incidence data for the predation plots, given above, suggests that the virus levels were too low in all plots in 1980 to reduce sugar yield significantly.

The results suggest that the relatively low numbers of predators in New Zealand sugar beet could have a substantial effect in keeping aphid numbers at low levels (0·27/plant compared with 40·1/plant in predator-reduced plots), with consequent effects on virus incidence. There are two problems with the methods used, however, which leave the explanation incomplete. One problem is that the use of carbaryl on the soil may have killed aphids as well as predators, especially mobile aphid species such as *M. persicae*, thereby underestimating the predators' effects. Such mobility may, however, increase their availability to ground-zone predators which may not all climb plants frequently. This lack of information on where the predation occurs and by which species emphasises the second methodological problem associated with the above barrier work; the results remain correlative because weekly emptying of pitfalls containing preservative precludes immunological or electrophoretic analysis of predators' gut contents. Dissection of the staphylinids was attempted but no aphid remains were found; as the common species in this group were small (*c.* 1 cm in length) it is likely that they were fluid feeders, together with the spiders and Opiliones. The coccinellids were the only group which revealed aphid remains on dissection, but they constituted only 8% of the total predator catch, implicating the more numerous polyphagous predators in the observed reduction in predator numbers.

The questions posed at the beginning of the work can, however, mostly be answered: average population levels of aphids were reduced, a suggestion of regulation was found (with aphid numbers in the control and ingress plots perhaps being held within the 'natural enemy ravine' (Southwood & Comins, 1976) throughout the season. Proportions of plants infested by aphids and showing virus symptoms were also lower when predator numbers were at control levels and only sugar yields were unaffected in what, however, appears to have been a year of low aphid and virus incidence generally.

It remains to be seen whether further work in New Zealand or elsewhere can fill in some of the gaps in the work of 1980. The following changes could be made: regular emptying of dry pitfall traps, followed by immunological or electrophoretic (Murray & Solomon, 1978) analysis of predators' gut contents; the use of information of proportion of a predatory species' individuals containing aphid remains, combined with the predators' abundance, to calculate a 'predation index' (Sunderland & Vickerman, 1980); assessments of virus symptoms earlier than April; increased sample size for beet sugar samples; measurement of spatial variation in natural enemy numbers and its causes.

The fact that relatively low numbers of predators (an average of *c.* three individuals/trap/week) seemed to have the above effects suggests that in sugar beet in the U.K., with higher predator numbers (Jepson, 1982), similar or greater effects may be expected. However, the biological control potential of individual predator species in arable land is still largely unknown (Sunderland & Vickerman, 1980); the extent to which predators regulate the numbers of *M. persicae* in the U.K. can perhaps be judged from the following paper (Jepson, 1982).

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The influence of predators on population development and dispersal of apterous *Myzus persicae* in sugar beet in the United Kingdom

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ABSTRACT

Beet mild yellowing virus and beet yellowing virus are spread in sugar beet crops by apterous *Myzus persicae* dispersing from focal infections initially made by immigrant alatae. The rate and extent of dispersal of these viruses varies greatly from field to field. Although many factors affect aphid and virus dispersal, field resident polyphagous predators, especially carabid beetles, are believed to be an important influence (Jepson & Green, 1982).

The paper described field experiments which investigated the effect of carabid beetles on aphid numbers and dispersal, and observations in separate fields which compared the effectiveness of the resident carabids to the different population densities produced by the experimental treatments. In the field experiment a direct relationship was found between aphid numbers and carabid density; this was not found however when the effects of different carabid densities on separate sites were compared. As the range of foods eaten by beetles trapped on these sites increased, the rate of aphid predation fell. This trend could be expressed by a simple multiple regression model which modified the relationship between aphid population suppression and carabid numbers (derived from the field experiment), with the range of food types

consumed by the three most important carabid species. The fecundity of the carabids increased with the abundance of some of these foods, and it is thought that they play an important role in determining potential beetle density. Future studies must investigate the role of food quantity, quality and range in carabid ecology, and the effects that available foods have on predation of pest species; without these it will be difficult either to predict variation in predation rate between sites, or establish ways of increasing pest predation by these beetles.

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Phenology of aphidophagous predators

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The phenology of insects may be defined as the timing of their occurrence, within or between years. Cereal aphids can cause important crop losses nationally, either by direct damage if enough of them occur at or after flowering, (e.g. *Sitobion avenae* (F.) in 1968 and 1976 and *Metopolophium dirhodum* (Walk.) in 1979), or as vectors of barley yellow dwarf virus (BYDV) in early-autumn sown cereals (George, 1974; Dean, Dewar, Powell & Wilding, 1980). Thus, much research at present is directed towards integrating different farming practices (e.g. undersowing) and application of pesticides with the ecology of the aphids and their natural enemies (parasites, fungal pathogens, aphidophagous and polyphagous predators).

There is, however, relatively little published information about the effectiveness, ecology and phenology of the aphidophagous predators (Chrysopidae, Coccinellidae, Syrphidae) in England, especially during the main cereal aphid season (May–August). This paper briefly describes the species, techniques and phenological observations made in 1980 in and around a 2-ha field of winter wheat at Rothamsted.

Numerous techniques are available for sampling insect numbers above and within a crop but only five were used to provide different aspects of phenology. Flying adults were sampled with the Rothamsted 40 ft (12·2 m) suction trap and a light trap and sticky traps at crop height; the crop populations were sampled with an insect suction net and by direct visual observations of the wheat stems.

Chrysopa carnea Steph. was the only species of the family identified in 1980 and most were caught in the suction trap (Table 1), 90% of them in August after the wheat had been harvested and the aphids had dispersed. In contrast, 67% of the smaller catch found on the sticky traps, sited about 1 km away from the suction trap, appeared before and during the aphid population increase in June and early July. Very few *C. carnea* were caught by the light trap or the two crop survey methods.

Table 1. *Numbers of adults and species (parentheses) of aphidophagous predators obtained using five different survey methods (April–September 1980)*

	Traps				
	Suction (12·2 m)	Light	Sticky	Suction-net	Visual
Chrysopidae	476 (1)	13 (2)	133 (1)	6 (1)	0
Coccinellidae	1 (1)	0	82 (5)	36 (2)	16 (2)
Syrphidae	7 (2)	0	3973 (21)	18 (6)	0

Considerably more specimens and species of Syrphidae were caught by the sticky traps than by the other methods, although not all were aphidophagous (e.g. *Rhingia campestris* Meig.) or important predators in cereals (e.g. *Platychirus* spp.). *Metasyrphus corollae* (F.) was usually the commonest species 12·2 m above the ground (Bowden & Dean, 1977), while *Platychirus* spp. (mainly *P. manicatus* (Meig.)) were very abundant on the sticky traps at crop height with their larvae attacking the numerous aphids (mainly *Brachycaudus helichrysi* Kalt.) on the lower canopy weeds such as *Veronica* sp. and *Matricaria maritimum* (L.). However, larvae collected and reared from the wheat were identified mainly as *Episyrphus balteatus* (DeGeer) and from adjacent nettle beds as *Syrphus ribessi* (L.) though relatively few adults of these species were caught.

Similarly, more adult Coccinellidae (mainly *Adalia 2-punctata* L. and *Propylea 14-punctata* L.) were caught by the sticky traps than by the other methods, the 12·2 m suction trap and light trap catching fewest. The first species, however, is a rare predator in cereals and is more common in other crops (e.g. beans) and uncultivated areas (e.g. on nettles (*Urtica* spp.) and on trees), while *Coccinella 7-punctata* L., an important predator of cereal aphids in some years (e.g. 1976–77), was not caught in 1980).

The apparent differences in flight times indicated by the suction, light and sticky traps probably were due to most of the adult aphidophagous predators, especially the Syrphidae (G. J. Dean, unpublished), flying at about crop level and so they were rarely caught at 12·2 m except for the migratory generation of *C. carnea* in late summer. The light trap data confirm that, as most of the flight activity of *C. carnea* occurs within the first 3 h after sunset (J. Bowden, personal communication), they are much more likely to be caught using this method than are the Coccinellidae and Syrphidae which fly mainly during the day.

The suction-net and visual assessments were complementary techniques; the former caught adults and larvae, while visual observations of the tillers recorded larvae, eggs and pupae. Both methods seem to give similar estimates of the larval numbers (G. J. Dean, unpublished).

Thus, sticky traps, suction nets and visual surveys are probably the most useful and practical methods for obtaining data about the numbers of aphidophagous predators at crop height and their breeding and occurrence within it, so the observations that follow are based on them in relation to Rothamsted week numbers (Lewis & Taylor 1968).

The sticky traps showed as expected that each of the three predaceous families had approximately similar flight occurrences at the top of the crop. There was an invading immigrant generation of adults which increased and then declined during their breeding period, with a rapid increase in their numbers as the next and usually overwintering generation emerged from the crop and surrounding uncultivated land. For example, the numbers of adult Syrphidae, which were similar at three sticky trap sites within the wheat, increased rapidly during May but decreased steadily thereafter until early July before becoming more numerous again in August (Fig. 1). The crop surveys (suction-net and visual) showed that adult syrphids were found in the wheat about 2 weeks after their first appearance on the sticky traps, while their eggs were found during weeks 23 to 28 (June–July) and larvae from weeks 24 to 29.

Similarly, adult coccinellids (mainly *P. 14-punctata*) were first caught in the wheat during week 21 (May) while their eggs, larvae and pupae were common until week 29 (late July). Adult *C. carnea* were very rarely seen within the crop, although they were relatively common on the sticky traps just above it between weeks 13 and 33, but reproduced abundantly on the tillers during June–July (weeks 23–29).

The aphidophagous 'active' forms of these predators, the larvae of all three families plus the adult coccinellids, occurred on the wheat between weeks 21 and 29 while *S. avenae* were present, their numbers

Table 2. *Relative abundances of 'active' aphid-specific predators* and* Sitobion avenae *on winter wheat*

		Number/100 stems		
	Week No.	'Active' predators	Aphids	Predator–aphid ratio
	19	0	—	—
	20	0	—	—
May	21	0·20	21	1:105
	22	0·25	33	1:132
	23	0·70	63	1:90
June	24	1·60	272	1:170
	25	3·30	327	1:99
	26	0·88	313	1:356
	27	2·18	213	1:98
July	28	2·14	25	1:12
	29	0·40	—	—

* Larvae of Syrphidae and *Chrysopa carnea* plus the larvae and adults of Coccinellidae.

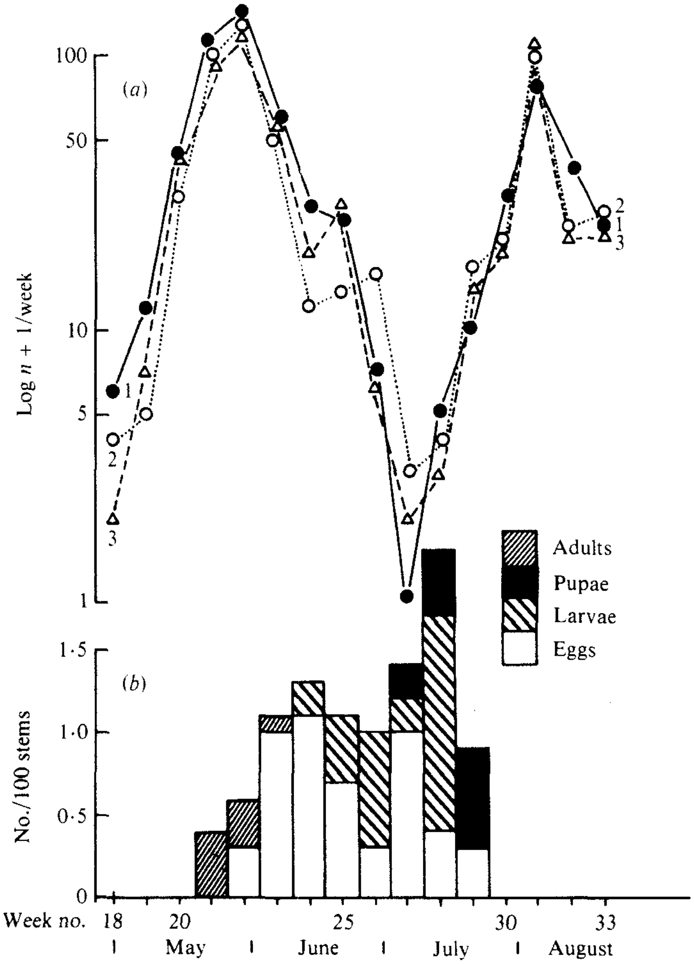

Fig. 1. Numbers of adult Syrphidae caught in 1980 on sticky traps at three sites above winter wheat (*a*) and their occurrence and breeding within the crop (*b*).

increasing to a maximum by week 25 and then decreasing as did those of the aphids (Table 2). The predator–prey ratios were generally similar in most weeks, except for weeks 26 and 28, and it is probable that these predators were important during 1980 in keeping the aphid population below 5 aphids/tiller at the time of flowering (week 23); insecticide application would be recommended (George, 1974) against populations increasing above this level.

Phenological surveys of this type have shown that during the last decade, coccinellids are usually the first and most durable of the aphidophagous predators in cereals but 1980 was an exception for some reason in having such large numbers of larvae of *C. carnea*.

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Distribution and abundance of cereal aphid parasitoids (*Aphidius* spp.) on grassland and winter wheat

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INTRODUCTION

The primary parasitoids of cereal aphids belong to two families of Hymenoptera, the Aphidiidae and Aphelinidae. These may be parasitised by secondary parasitoids, including species of Pteromalidae, Ceraphronidae, Cynipidae and Encyrtidae.

Some of the earliest observations on cereal aphid parasitoids that were made in Britain were recorded by Curtis (1860) in his book *Farm Insects*. He noted that the grain aphid, *Sitobion avenae* (F.), was attacked by two primary parasitoids, *Aphidius avenae* Haliday (now *Aphidius picipes* (Nees)) and *Ephedrus plagiator* (Nees). Arthur (1945*a*, *b*) also observed two *Aphidius* species attacking cereal aphids and even carried out experiments to assess the feasibility of releasing parasitoids for biological control purposes.

Since that time, however, most of the studies carried out in this and other European countries on cereal aphid parasitoids have been concerned with obtaining estimates of percentage parasitism, usually on winter wheat crops between May and August, and the species composition of parasitoids and hyperparasitoids emerging from mummies collected in the field (e.g. Dean, 1974; Jones & Dean, 1975; Rautapää, 1976; Starý, 1976). Apart from some observations by Dransfield (1975) and Vickerman (1977), there is virtually no information on parasitoids, or even aphids, on grassland and no data on the distribution and abundance of the adult parasitoids on either cereals on grasses. In this account, data on the distribution and abundance of primary parasitoids (mainly *Aphidius* spp.) on grassland and winter wheat are considered.

MATERIALS AND METHODS

The work was carried out on a 62 km^2 area of farmland in West Sussex. The study area is situated on the South Downs and consists of 17 farms and 300 fields (Potts & Vickerman, 1974).

Since 1972, samples have been taken with the Dietrick vacuum insect net (D-vac), from cereal and grass fields on three farms on the study area, to provide information on the distribution and abundance of arthropods. The crops were sampled between March and October, at intervals of 7–10 days. Samples consisted of five sub-samples, each of 0·092 m^2, and were taken in a diagonal across each field. Arthropods, including the different cereal aphid species and their parasites, present in the samples were identified and counted. Counts were made of the numbers of unhatched and hatched mummies in the samples and, each year, parasitoids were bred from samples of mummies and live aphids collected from the ears and flag leaves of winter wheat.

COMPOSITION OF PRIMARY PARASITOIDS

The primary parasitoids reared from cereal aphids consisted mainly of *Aphidius* spp.; relatively few *Praon volucre* (Haliday), *Ephedrus plagiator* or *Aphelinus* sp. were usually bred out (e.g. see Table 1) and in this respect the results were similar to those of, for example, Jones & Dean (1975) and Carter, McLean,

Table 1. *Percentage composition of primary parasitoids bred from* Sitobion avenae *collected from ears and flag leaves of winter wheat in 1975, 1976 and 1977*

	1975	1976	1977
Aphidius rhopalosiphi	70·5	72·1	56·9
Aphidius picipes	25·0	10·0	22·5
Aphidius ervi	3·6	10·0	13·7
Praon volucre	0·0	0·7	1·0
Ephedrus plagiator	0·9	3·6	5·9
Aphelinus sp.	0·0	3·6	0·0
Total number	112	140	102

Watt & Dixon (1980). The identification of some species of *Aphidius* presents a number of problems and although it was possible to identify *Aphidius picipes* and *A. ervi* Haliday, for practical purposes it was difficult to distinguish between *Aphidius rhopalosiphi* De Stefani-Perez, *A. uzbekistanicus* Luzhetzki and *A. urticae* Haliday. These species have, therefore, been grouped as *A. rhopalosiphi* until the taxonomic situation is resolved. *Aphidius rhopalosiphi* was usually the most common 'species' of *Aphidius* bred from cereal aphids, followed by *A. picipes* and *A. ervi* (e.g. see Table 1).

DISTRIBUTION AND ABUNDANCE OF *APHIDIUS* SPP. ON GRASSLAND

The mean numbers (/0·5 m^2) of *Aphidius* spp. found on grassland over the period 1972–1979 are shown in Fig. 1. The parasitoids consisted mainly of *A. rhopalosiphi*, *A. picipes* and *A. ervi* and more detailed information on the numbers of these individual species will be considered elsewhere. There was large variation in the numbers of adults found in grass fields in the different years. For example, mean peak numbers (/0·5 m^2) ranged from *c.* 300 in 1974 to <3 in 1978. In general, numbers found on grassland between March and October were relatively high over the period 1972–1975 and low in 1976–1979 (Fig. 1).

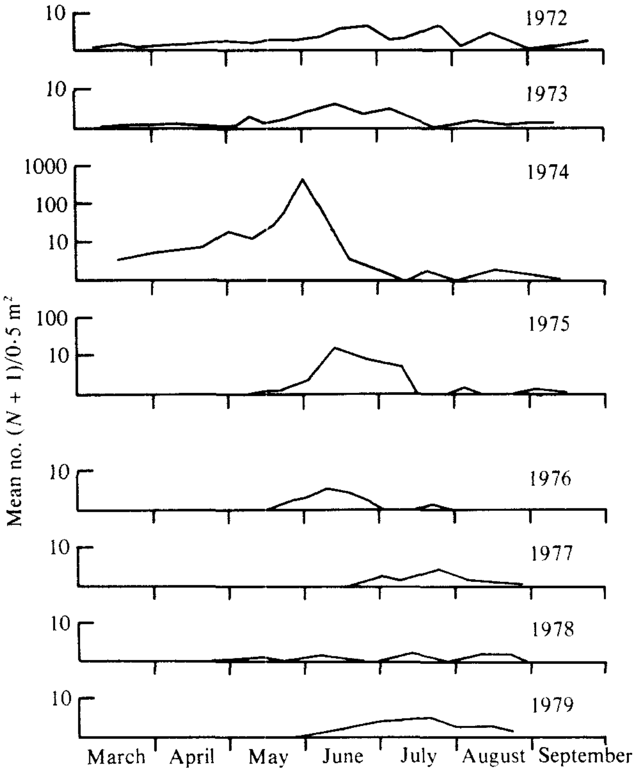

Fig. 1. Mean numbers (/0·5 m^2) of adult *Aphidius* found in vacuum net samples taken from grass fields, 1972–1979.

In some years (e.g. 1972), the adults were present on grassland from the time that samples were first taken, in early March, to the end of September, when sampling ceased, whereas in others (e.g. 1977, 1979) the first adults were not found in the samples until mid to late June (Fig. 1). Peak numbers of adult *Aphidius* were found in June (1972–1976) or July (1977–1979).

In the early spring, numbers of adult *Aphidius* were highest on those grass fields that had not been grazed throughout the winter months and in particular on those that had been established by direct seeding in the previous autumn. Numbers of cereal aphids, in particular of *Sitobion avenae*, were also

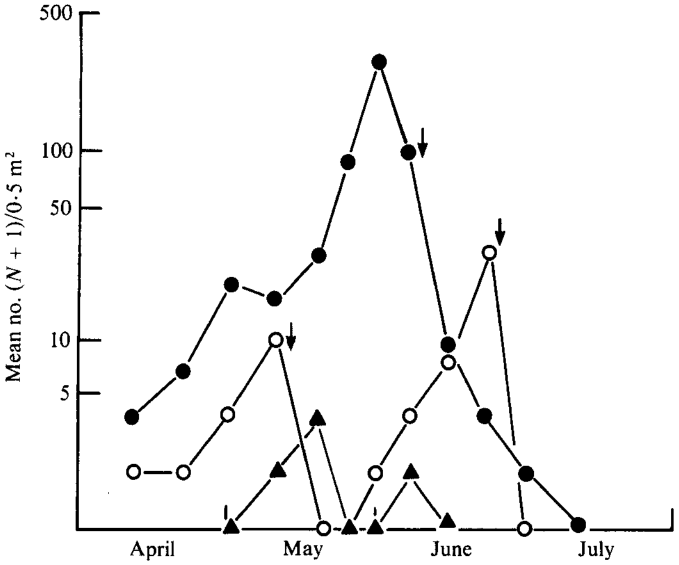

Fig. 2. Mean numbers (/0·5 m²) adult *Aphidius* found in vacuum net samples taken from grass fields cut for hay (●) or silage (○) or grazed by livestock (▲) in 1974. ↓, date of cutting.

usually highest on such fields. Later in the spring and in early summer, the build-up in parasitoid populations was greater in ungrazed grass fields destined for hay, seed or silage than in grazed fields (Fig. 2). Numbers in hay fields were usually higher than in silage fields (Fig. 2) as the former were not cut until early to mid-June, whereas the latter were cut twice, usually in mid-May and in late June.

RELATIONSHIP BETWEEN THE NUMBERS OF ADULT *APHIDIUS* AND CEREAL APHIDS ON GRASSLAND

In those years (1972–1976) when numbers of adult *Aphidius* were relatively high on grassland in the spring, numbers of cereal aphids, in particular of *Metopolophium festucae* (Theob.) and *Rhopalosiphum padi* (L.), were also high. In such years, *Metopolophium festucae* was the dominant cereal aphid species in most grass fields and while populations of it reached a peak in mid-May, numbers of *Rhopalosiphum padi* did not normally reach a peak until the end of that month or in early June. Over the period 1972–1979, there was a positive relationship between the mean numbers (/0·5 m²) of adult *Aphidius* and the mean numbers (/0·5 m²) of cereal aphids found on grassland in May in the different years (Fig. 3).

RELATIONSHIP BETWEEN THE NUMBERS OF ADULT *APHIDIUS* IN WINTER WHEAT AND THE NUMBERS ON GRASSLAND

In contrast to the situation on grassland, the first adult *Aphidius* were not usually found in crops of winter wheat until the end of May or in June. In some years (e.g. 1974), adults were found at an earlier date, in particular in those crops that had been sown relatively early (late September/early October) in the previous autumn. Most wheat crops on the three study farms were not, however, normally sown until late October. In the early drilled crops, hatched mummies were frequently found at the same time as the first adult *Aphidius* indicating, perhaps, that the parasitoids had overwintered in these crops. In most crops, however, the first adults were found in the samples long before the first hatched mummies and, in these situations, it was considered possible that the parasitoids were derived from elsewhere, in particular from grassland.

To explore this possibility, the relationship between the numbers of adult *Aphidius* found in wheat crops and the numbers found on grassland in the different years was examined. Between 1972 and 1979 there was a good positive relationship between the mean numbers (/0·5 m²) of adult *Aphidius* found in winter wheat crops (prior to the date when the first hatched mummies were found in the crops) and the mean numbers (/0·5 m²) of *Aphidius* found previously on grassland in May (Fig. 4).

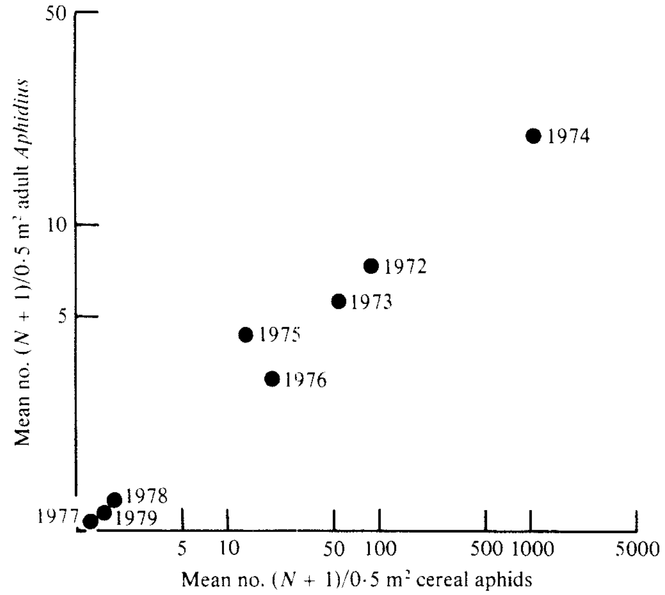

Fig. 3. Relationship between mean numbers (/0·5 m²) of adult *Aphidius* and cereal aphids found in vacuum net samples taken from grass fields in May, 1972–1979.

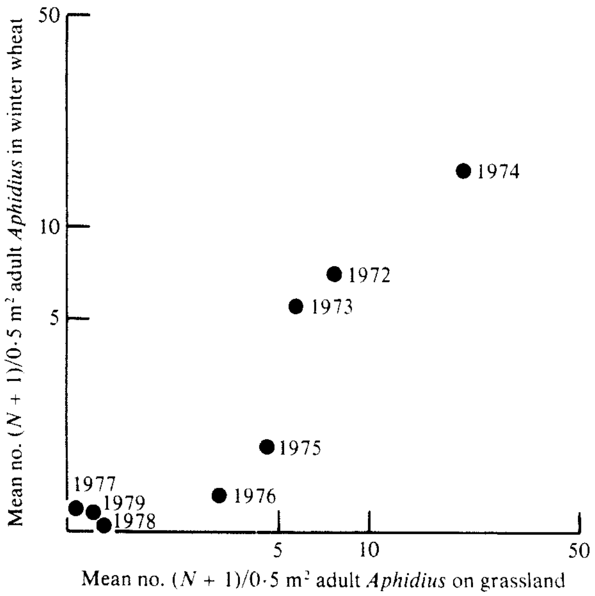

Fig. 4. Relationship between mean numbers (/0·5 m²) of adult *Aphidius* found in winter wheat crops (prior to the date when the first hatched mummies were found in the samples) and the mean numbers (/0·5 m²) found previously in grass fields in May, 1972–1979.

DISCUSSION

Dransfield (1975) obtained information on the numbers of aphids and the species composition of their primary parasitoids on small plots of grassland (mainly *Dactylis glomerata* L.) and spring barley to investigate the role of grassland aphids as a reservoir for cereal aphid parasitoids. However, the cocksfoot aphid, *Hyalopteroides humilis* (Walker), was by far the commonest aphid found on grassland and was parasitised by a member of the *Aphidius urticae* species complex (Dransfield, 1979). While this species of *Aphidius* did not develop successfully in other aphid hosts, *Aphidius uzbekistanicus*, the commonest species found attacking aphids on barley, did not attack *Hyalopteroides humilis* in the field (Dransfield, 1975, 1979). The results of the present investigation were clearly different from those of Dransfield as the species composition of both aphids and primary parasitoids was basically similar on grassland (mainly *Lolium* spp.) and wheat.

It is likely that the adult parasitoids found on grassland in early March were derived from aphids that had overwintered in those fields, as the first hatched mummies were found in the samples at the same time. Indeed, adult *Aphidius* may be found in crops during the winter months in southern England (Dransfield, 1975; Vickerman, unpublished) and the development of parasitoid larvae may continue, provided temperatures are above a threshold of *c* 7 °C (e.g. Dransfield, 1979). In those years when *Aphidius* were not found in the samples until June, it is possible either that adults were present earlier in the year, but at a density too low to be detected by the sampling methods used, or that the adults were derived mainly from mummies that had spent the winter in diapause. Jones (1979) found that two adult *Aphidius* emerged in April or June from mummies that had been collected in the previous summer. The ability to spend the winter months in diapause could, presumably, help to ensure the survival of parasitoids in severe winters, when the numbers of aphids overwintering anholocyclically in the crops would be expected to be low.

In the early spring, numbers of adult *Aphidius* were highest in grass fields that had not been grazed throughout the winter and in those fields that had been established by direct seeding in the previous autumn. As the subsequent build-up in parasitoid populations was also greatest in grass fields that were not, or little, grazed, the main grassland reservoirs for *Aphidius* in the spring and early summer are considered to be first-year swards destined for hay or seed.

In the present study, the adult *Aphidius* found in most winter wheat crops in May and June were not considered to have been derived from overwintering populations in those crops. However, adult parasitoids and mummies were found early in the year in some crops, in particular those that were drilled in early October. Such early drilled wheat crops may, therefore, also act as reservoirs for the parasitoids in the spring. On the study area, crops of winter barley and oats were usually drilled before those of wheat and the numbers of *Aphidius* present in these crops in the early spring were much higher than in either wheat or grass in some years, in particular in 1972–1974.

The fact that there was a positive relationship between the numbers of adult *Aphidius* found in wheat crops and the numbers found previously on grassland in May in the different years provided circumstantial evidence that the parasitoids dispersed from one type of crop to the other. It is likely that the adults disperse over a relatively wide area, given that they are caught in relatively large numbers in 12·2 m aerial suction traps (Dean, Dewar, Powell & Wilding, 1980), but the parasitoids may also enter the crop as eggs/larvae in immigrant alate aphids. It would, presumably, be advantageous for the parasitoids to leave the grassland habitat at this time of year, firstly because populations of grassland aphids, in particular of *Metopolophium festucae*, usually crash at the end of May or in early June (Vickerman, 1977 & unpublished) and secondly because aphid populations are also severely reduced when cuts are taken for silage or hay. Vorley (*in litt*) has now obtained evidence, using directional water traps, that adult *Aphidius* do disperse from grassland into adjacent winter wheat crops. Some of the primary parasitoids found in cereal crops may be derived also from crops other than cereals and grassland. For example, *A. picipes* and *A. ervi* are also parasitoids of *Acyrthosiphon pisum* (Harris) and Starý (1976) considered alfalfa to be an overwintering reservoir for these species.

Vickerman (1977) suggested that populations of cereal aphids, in particular of *Sitobion avenae*, in winter wheat in summer were relatively low in those years in which populations of grassland aphids and, consequently, of natural enemies, including parasitoids, were relatively high in the spring. However, modelling techniques will be required to assess the role of parasitoids in this and it is hoped that data such as these will provide an extensive framework for the more detailed information on parasitoid biology now required.

I would like to thank the farmers on the West Sussex study area for all their help and the Agricultural Research Council and Natural Environment Research Council for financing the work.

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The role of natural enemies in cereal aphid population dynamics

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INTRODUCTION

Cereal aphids have achieved high densities (over 40 aphids/tiller) in 4 of the the last 6 yr in the Norwich area. In 1976, 1977 and 1980 the English grain aphid, *Sitobion avenae* (F.), was the commonest species but in 1979 the rose grain aphid, *Metopolophium dirhodum* (Wlk.), reached outbreak levels. *S. avenae*, in particular, regularly causes yield losses exceeding 10% (George & Gair, 1979) and can also reduce grain quality (Lee, Stevens, Stokes & Wratten, 1981).

As many species of natural enemy attack cereal aphids it is difficult to evaluate their individual effects. In an attempt to resolve this problem a simulation approach was used in conjunction with laboratory and field studies of three groups of natural enemies: parasites (in particular *Aphidius* spp.), polyphagous (linyphiid spiders) and aphid-specific (coccinellids) predators. Field data for the spiders and coccinellids were collected at North Farm, West Sussex, and for the parasites at Norwich.

DATA COLLECTION

Parasites

Five species of parasite – *Aphidius rhopalosiphi* (Starý), *Aphidius ervi* Haliday, *Aphidius picipes* Nees, *Aphidius uzbekistanicus* Luzhetzki and *Praon volucre* (Haliday) – commonly attack cereal aphids, while *Ephedrus plagiator* (Nees) and *Aphelinus* spp. have also been recorded. Parasites are themselves attacked by hyperparasites, *Dendrocerus carpenteri* (Curtis) being the most common (McLean, 1980).

Adult parasites are small active insects which are difficult to count in the field. An indication of their abundance can be obtained by counting the number of parasitised aphids. This was carried out in two ways: (i) by counting mummies in the field, and (ii) by collecting aphids in the field to rear them in the laboratory for 2 wk or to dissect. The former method is more convenient and also estimates the degree of hyperparasitism if the mummies are kept until the parasites emerge. It does, however, underestimate the percentage parasitism, compared with the estimate obtained from the live aphid rearing method (Dean, 1974*a*; Carter, McLean, Watt & Dixon, 1980). This is due to (i) the higher survival rate of aphids reared in the laboratory, i.e. in the field more parasitised aphids will die before mummification, and (ii) mummification of the aphid off the plant; Powell (1980) has shown this is the case with *Toxares deltiger* (Haliday). Results from both methods were expressed as a proportion of the toal aphid numbers which were parasitised and entered in the model.

Mummified aphids were found at the beginning of May in 1981 which is earlier than any other year since the study started in 1976 (Carter *et al.*, 1980; S. Gardner, unpublished). In 1981 cereal aphids overwintering in the crops and the mild spring probably assisted the early establishment of the parasites. Mummy densities never rose above 0·1/tiller during the season, while aphid densities never exceeded three/tiller.

Spiders

Linyphiid (money) spiders are the most abundant spiders in cereal fields. They are polyphagous and have been shown to feed on cereal aphids in the field and the laboratory (A. M. Fraser, unpublished). They build horizontal non-sticky webs between cereal tillers, into which aphids either fall or walk, and from which they may escape. The rate at which aphids encountered webs was estimated from two parameters: (i) area of web cover, and (ii) aphid density. Web cover was estimated by measuring the percentage cover in 15 quadrats, each 0·1 m^2, placed at random. An atomiser was used to show up the webs and a pair of dividers to measure the two longest dimensions of each web which was assumed to be rectangular. Aphid densities were estimated in two ways: on a per stem basis to provide an absolute measure of the population, and using sticky traps, each 200 cm^2, placed at ground level and at 6 cm to give the number falling off plants/m^2. Web cover and the number of aphids falling off were used to calculate the encounter rate, which was corrected for the proportion of each aphid instar which can escape from adult spiders in the laboratory.

Web cover, in April, was 0·3% of the ground and increased rapidly to 30% in July. Aphid densities rose to just over one/tiller in the same period. The capture efficiencies of the adult spiders with different aphid instars were: 100% for first and second; 74% for third; 53% for fourth and 12% for adult aphids. The numbers of aphids captured in webs were expressed as percentage mortalities from birth to maturity. These values increased from 3% to over 80%. No allowance was made, however, for the proportion of immature spiders whose capture efficiencies are lower than those of the adults or the presence of alternative prey. Both of these factors will tend to reduce the mortality inflicted by spiders.

Coccinellids

Several species are found in cereal fields but in the present study addtention was centred on *Coccinella 7-punctata* L. This is one of the commonest species (McLean, 1980), although its abundance varies from year to year (Dean, 1982; Heathcote, 1978). The adults hibernate in a variety of habitats such as leaf litter and grass tussocks. From early spring onwards they disperse to crops, including cereals where they lay eggs.

In 1980 and 1981 at North Farm, West Sussex, weekly estimates were made of coccinellid numbers/0·25 m^2, initially based on 20 samples decreasing as coccinellid densities increased. The instars were identified from appearance and size.

In 1980 adult coccinellids arrived in the crop in April, and eggs were found on 21 May. Aphids which had overwintered on the crops supplied the adult coccinellids and the emerging larvae with food early in the year. By 10 June fourth instar coccinellids were present whilst the density of *S. avenae* was only 2·9/tiller. After this, aphid numbers declined. In 1981, coccinellids were generally uncommon in cereal crops.

Laboratory consumption rates for each larval instar and adults of *C. 7-punctata*, given excess food, are available for two temperatures, 15 and 20 °C (McLean, 1980). These values together with the field densities were used in the model to estimate the effect of coccinellids on aphid population dynamics.

SIMULATION

Description of the model

A listing and detailed account of the model have been presented elsewhere (Carter, 1978; Carter, Rabbinge & Dixon, 1982), and only a brief description is presented here.

The model used the number of alate *S. avenae* caught in the nearest suction trap as an index of the number of aphids colonising crops. Carter *et al.* (1980) have shown that the catches of the Brooms Barn suction trap are significantly correlated with catches in water traps located in study fields near Norwich. There is also now the additional facility of inserting into the model the numbers in each aphid instar. This is especially important in those crops where overwintering has occurred.

Subsequent development and reproduction were dependent on daily minimum and maximum temperatures and the crop development stage. The majority of the first generation nymphs developed into apterous adults. These in turn produced more nymphs, an increasing proportion of which developed into alate adults, which emigrated. Much of the information concerning development, survival and reproductive rates used in the model, comes from Dean (1974*b*), Wratten (1977) and Watt (1979).

Mortality caused by parasites was introduced into the model empirically. A proportion of the newly-moulted adults was removed to give approximately twice the number of mummified aphids observed in the field. This doubling was done to compensate for the underestimate of mortality that results from mummy counts. The mortality caused by the fungus *Entomophthora* spp. was handled in the same way as parasitism.

The mortality caused by spiders is to be incorporated into the model as a reduction in the aphid nymphal survival rate.

Field counts of the four larval instars and adult coccinellids were entered into the model. The number of aphids in each instar was expressed in aphid units: one aphid unit being equivalent to one adult; one and a half fourth; two third; three second or five first instar aphids. The numbers of larval and adult coccinellids were multiplied by their respective consumption rates (McLean, 1980) to give the number of aphid units which were eaten by each instar. These were then subtracted from the instar totals. As it is unlikely that coccinellids will eat prey at the maximum rate at low aphid densities, an option for a Type 1 functional response (Holling, 1959) was incorporated into the model.

RESULTS

Parasites

In 1981 *S. avenae* reached 2·6/tiller at the end of June at the start of the milky-ripe stage (Fig. 1). In the simulation, with no parasites included, aphid densities rose very rapidly to over 100/tiller. Inclusion of the parasites, either using the mummy counts or the live aphid samples, still resulted in high aphid densities although the aphid population growth was slower. Aphids killed by *Entomophthora* were not observed in the field until the end of May, and the incorporation of this mortality factor into the simulation had little effect on early aphid population development although it did reduce the final peak density. This, however, was still high when compared with the peak observed in the field.

Coccinellids

In contrast to the population trends for *S. avenae* in fields near Norwich, those at North Farm in 1980 *peaked at* flowering at 2·9/tiller (Fig. 2). The simulation with no coccinellids included gave a peak density greater than 40/tiller at the end of June during the milky-ripe stage. Up to the time of the observed peak aphid population development was accurately predicted. Inclusion of coccinellids led to rapid extinction of the aphid population at the time when fourth instar coccinellids appeared, although again the early phase of population development was accurately predicted. When the number of aphids eaten by the

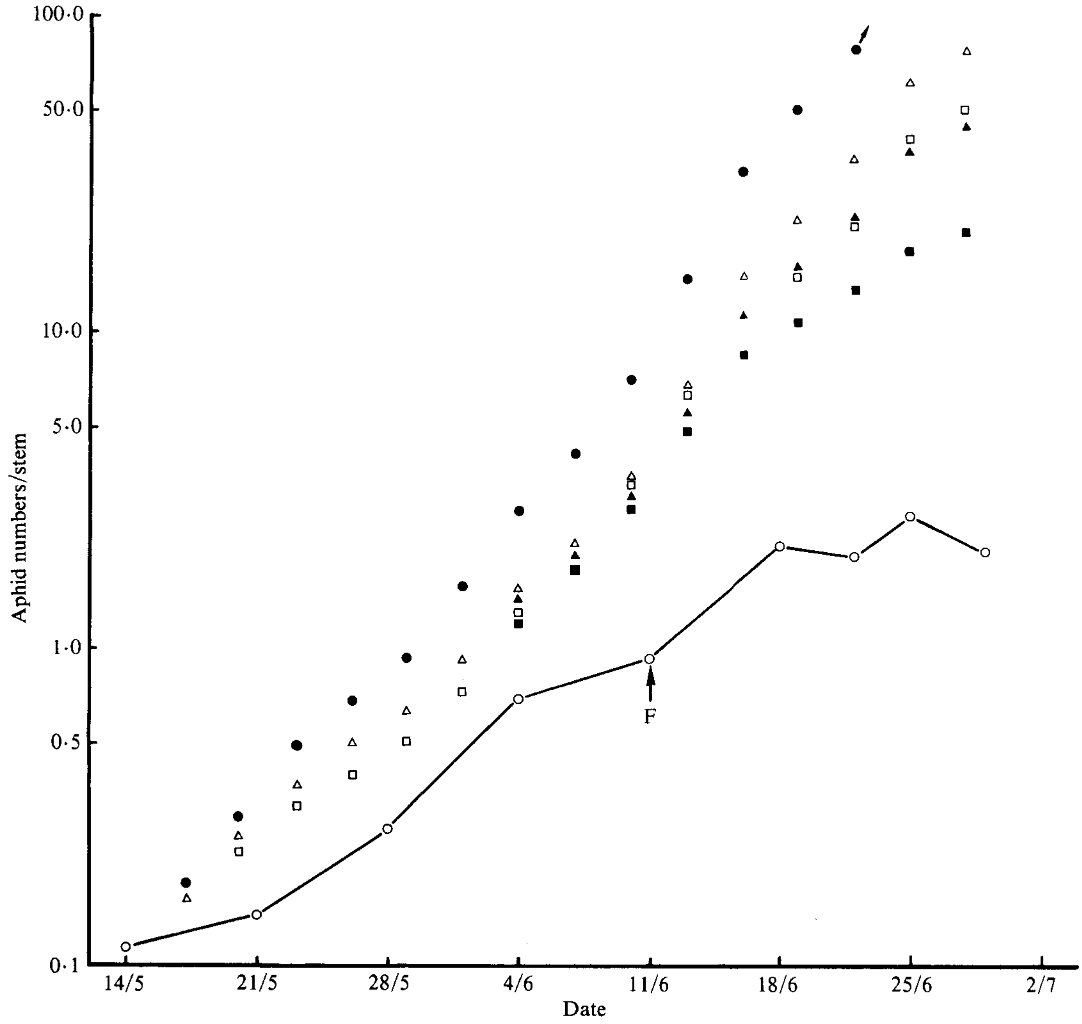

Fig. 1. Simulation of the effects of parasites and *Entomophthora* spp. on *S. avenae* population, Norwich 1981. (○) field results: simulation predictions; (●) no parasitism or disease, (△) parasitism estimated from mummy counts, (▲) parasitism (mummies) and disease, (□) parasitism estimated from live aphid samples and (■) parasitism (live aphid samples) and disease. (F) flowering.

coccinellids was determined by a functional response, with a threshold of three aphid units, the aphid population increased to over 30/tiller, but accurately followed the observed population development up to the start of flowering. It was only at the end of the season that the predictions of this simulation deviated from that obtained when mortality due to coccinellids was omitted.

DISCUSSION

The incorporation of natural enemy data into the simulation model caused a reduction in the predicted aphid numbers. Discrepancies, however, still remained between the observed and predicted aphid populations.

Inclusion of the numbers of parasitised aphids – in isolation and in combination with the incidence of *Entomophthora* – lowered the predicted aphid peak, but was still too high when compared with the field results. This suggests that either the aphid population was being affected by another mortality factor, or the current method of assessing the impact of parasitism and disease is inaccurate. Mummy counts and live aphid samples provide different estimates of aphid mortality due to parasites, thus complicating the evaluation of the actual mortality.

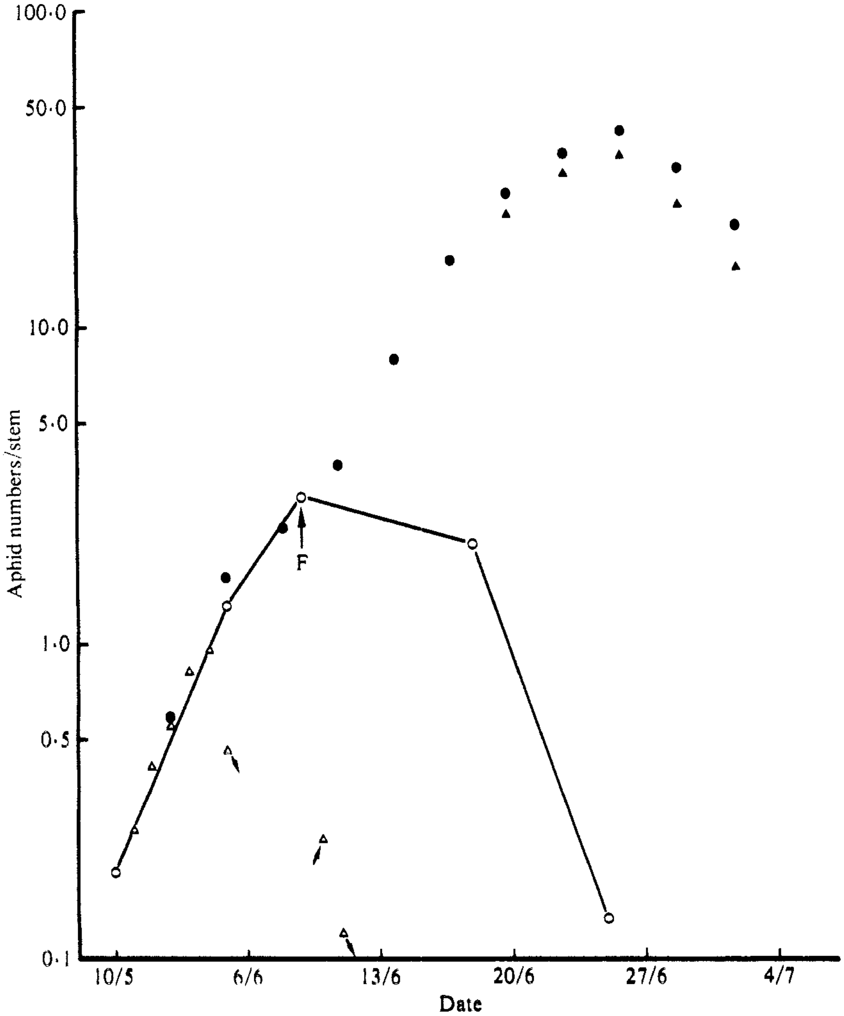

Fig. 2. Simulation of the effects of coccinellids on *S. avenae* population, North Farm 1980. (○) field results: simulation predictions; (●) no coccinellids, (△) with coccinellids, (▲) with coccinellids and a functional response. (F) flowering.

Few aphid specific predators were found in Norwich in 1981, early in the season, although polyphagous predators and wet weather during the colonisation period may have adversely affected the aphid population. Determination of the role of polyphagous predators, particularly spiders, is still at an early stage. Their effect will be entered empirically into the model, as aphid nymphal mortality, which may be important during the early stages of aphid population development.

The predictions of the model were very sensitive to changes in the aphid–coccinellid interaction; Carter & Dewar (1981) have shown that they are affected by fluctuations in coccinellid density, the threshold level of the functional response and possibly consumption rates assigned to the coccinellid instars. During 1980 at North Farm, a number of cereal aphids were found in the grass weeds in the crop. These will have formed an alternative source of prey, early in the season, which may help to explain why the crop aphids did not reach extinction as quickly as the model predicted. Before a complete assessment of the coccinellid effect can be made, reliable methods for measuring coccinellid density, together with accurate estimates of field consumption rates and functional and numerical responses are required.

Demonstration by the model of the effect of natural enemies in controlling aphid populations is still highly variable. Field observations at North Farm 1980 showed that coccinellids and, possibly later, syrphids reduced aphid population growth so that the decline occurred at flowering rather than at the more usual time of the milky-ripe stage (Carter *et al.*, 1980). Similarly, in 1981 in Norwich, the early appearance of parasites followed by outbreaks of *Entomophthora*, may well have checked aphid growth rates, holding the population below the economic threshold. In both cases, the influence of natural enemies seemed to depend on their early appearance in the crops, in association with the occurrence of overwintering aphids or the early immigration of another another aphid species such as *Metopolophium festucae sensu lato.* This synchronisation of the natural enemy and aphid populations is essential if the natural enemies are to exert any form of control (Dean, 1974*a*). Dean (1974*a*) suggests that parasites may achieve better synchronisation than predators. Some parasites enter crops inside immigrant alate aphids (S. Gardner, unpublished) and although the proportion of parasitised alates at Norwich in 1980 and 1981 were similar (6–7%) subsequent parasite abundance was higher in 1981.

Present studies are being directed towards a more comprehensive interpretation of the population dynamics of the three natural enemy groups. These will provide a more accurate assessment of the actual aphid mortality inflicted by each group, which can be used in the model to study their effects on the development of cereal aphid populations.

While the work was being carried out, N. Carter was in receipt of an A.R.C. Senior Research Assistantship, Sarah Gardner an S.R.C. Studentship and A. M. Fraser and T. H. L. Adams S. R. C. C.A.S.E. awards between U.E.A. and the Glasshouse Crops Research Institute. We would like to thank G.C.R.I. for the use of their aphid data.

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Predation of a chrysomelid beetle (*Gastrophysa polygoni*) in cereals by polyphagous predators

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INTRODUCTION

Gastrophysa polygoni (L.) (Coleoptera: Chrysomelidae) feeds on species of the genus *Polygonum* e.g. knotgrass (*Polygonum aviculare* L.) and black bindweed (*Polygonum convolvulus* L.) found in cereals. *G. polygoni* overwinters in the soil in the adult stage and emerges in the spring. The first eggs are usually found in early May, reaching a peak 3 or 4 wk later. The yellow eggs are laid in batches of about 20 on the undersides of the leaves. On hatching, the first-instar larvae feed upon any infertile or unhatched eggs in the batch and then tend to remain feeding on the plant on which the egg batch had been laid. The more mobile second- and third-instar larvae may feed on different plants. Once fully fed, third-instar larvae leave the plant and enter the soil where they pupate. There are usually two generations each year. Further information on the biology of *G. polygoni* may be found in Sotherton (1980).

METHODS AND RESULTS

During the first generation, mortality of the egg stage was very high, varying from 51% in 1977 to 65% in 1979. Mortality during the egg stage was the key factor determining population change, with mortality during the second-larval instar the next most important factor (Sotherton, 1980). During the egg stage the most likely causes of mortality were parasitism, disease, weather, cannibalism, infertility and predation. However, no parasites were ever bred from them and no diseased eggs were found during the 3-yr study. Waterlogging had no effect on the survival of eggs and given that the eggs are cemented onto the undersides of the leaves, it is also unlikely that rainfall, for example, was an important mortality factor. In the laboratory, cannibalism and infertility were estimated as causing 2% and 5% mortality respectively. Predation was the only remaining mortality factor, and the remains of predated eggs were frequently found on the leaves.

The effects of both weather and plant condition may have contributed to the mortality of the larvae but only one parasite adult was bred from the larvae and although some diseased larvae were found in the first generation in 1977, none was found at other times. As with the eggs, predators appeared to be the most likely mortality agents. Predator exclusion experiments were therefore carried out in 1978 and 1979 to assess the importance of arthropods as potential predators of the development stages of *G. polygoni.*

Predators were excluded by enclosing 1 m^2 areas of spring barley or winter wheat with barriers of weather-proofed plywood (0·5 m high). A band of tree-banding grease was smeared around the outsides of each barrier, to prevent predatory arthropods climbing into them. Predators emerging from the soil within the enclosed areas were removed using pitfall traps.

Individual gravid female *G. polygoni* were then confined with individual *Polygonum* plants, within these barriers or in the open field, using rigid, transparent, plastic cylinders, capped with cotton fabric. After 24 h the females were removed and the numbers of eggs laid were recorded. Numbers of eggs and larvae were then counted daily.

Four types of predator exclusion were carried out, each allowing access to a different number and range of predators:

1. Total exclusion of predators (control).
2. Ground-living predators excluded.
3. Aerial predators excluded.
4. No exclusion; free access to all predators.

Each treatment was replicated three times.

Total exclusion of all predators was achieved by burying the sides of the exclusion boxes into the soil to a depth of 15 cm. The boxes were also covered with a fine-meshed cotton fabric. Ground living predators were excluded by digging the boxes into the soil but omitting the cotton fabric. Aerial predators were excluded by siting covered boxes on legs 10 cm off the ground. The open field constituted the area in which all predators had free access.

In the second generation in 1978, the second treatment (exclusion of ground predators only) was excluded from the trial. This was so that more time and resources could be used to produce worthwhile results for the other three treatments.

It was possible to separate the total egg mortality into a 'pre-hatching mortality' and a 'hatching mortality'. The pre-hatching mortality was calculated as the difference between the mean initial number of eggs and the mean number of eggs present on the sampling date immediately prior to hatching. The hatching mortality was calculated as the difference between the mean number of eggs present immediately prior to hatching and the mean initial number of first-instar larvae.

Comparisons were made between the mean percentage losses of the eggs and the first-instar larvae in the different treatments. With the second- and third-instar larvae, the mean numbers (/m^2) surviving in the different treatments were compared. This was because the more mobile, older larvae could not always be attributed to a particular marked egg batch. Mean percentage losses and mean numbers (/m^2) surviving in the four treatments were compared using analysis of variance techniques. Data for the treatment in which predators were totally excluded (control) were compared with the data of the other three treatments. Mean differences with their standard errors were used and referred to the *t*-distribution.

Losses of eggs

In both 1978 and 1979, total egg losses were significantly higher in areas of spring barley or winter wheat where predators had access than in areas of the crop where predators had been excluded. These differences in total egg mortality were attributed to the significant differences between treatments in pre-hatching egg losses (Table 1). Hatching losses did not significantly differ between treatments in any generation (Table 1). No significant differences in egg loss occurred between replicates within treatments in any generation.

Table 1. *Mean percentage egg losses* (± *one standard error*) *of* G. polygoni (*based on numbers/plant*) *in predator exclusion experiments in 1978 and 1979.* (*Transformed data: arcsin*)

	Control or total exclusion	Ground exclusion	Aerial exclusion	No exclusion or total access	Sig. level of F. ratio
1978 Generation 1					
Total egg loss	11 ± 3·8	33 ± 9·5	42 ± 10·5	60 ± 12·7	<0·001
Pre-hatching loss	0·3 ± 0·3	19 ± 5·2	29 ± 7·9	50 ± 4·4	<0·001
Hatching loss	10 ± 3·7	16 ± 5·2	18 ± 5·2	17 ± 4·3	>0·05
1978 Generation 2					
Total egg loss	12 ± 2·6	—	41 ± 8·1	56 ± 8·0	<0·001
Pre-hatching loss	0·6 ± 0·4	—	37 ± 10·5	46 ± 9·8	<0·001
Hatching loss	20 ± 2·4	—	13 ± 2·9	13 ± 2·9	>0·75
1979 Generation 1					
Total egg loss	15 ± 5·3	27 ± 7·7	70 ± 13·9	36 ± 8·5	<0·001
Pre-hatching loss	5 ± 1·6	10 ± 3·5	59 ± 12·0	26 ± 65·5	<0·001
Hatching loss	13 ± 4·8	19 ± 5·9	26 ± 6·0	13 ± 4·0	>0·05

—, No data available.

When predators were totally excluded, total egg losses were significantly ($P < 0{\cdot}05$) lower than when either ground predators alone (aerial exclusion) or all predators had access. Total egg losses were similar when predators were totally excluded or when ground predators alone were excluded ($P < 0{\cdot}1$).

Losses of first-instar larvae

There were also significant differences ($P < 0{\cdot}001$) between the losses of first-instar larvae in the different predator exclusion treatments (Table 2). Compared with total exclusion, losses of first-instar larvae were significantly greater when either aerial predators were excluded or when all predators had access.

Table 2. *Mean percentage losses of first-instar larvae of* G. polygoni (± *one standard error*) (*based on numbers/plant*). *Predator exclusion experiments in 1978 and 1979.* (*Transformed data: arcsin*)

Year	Generation	Control or total exclusion	Ground exclusion	Aerial exclusion	No exclusion or total access	Sig. level of F. ratio
1978	1	37 ± 8·5	12 ± 5·3	65 ± 17·5	60 ± 16·5	<0·001
1978	2	29 ± 4·4	—	56 ± 6·4	48 ± 4·2	<0·001
1979	1	33 ± 8·5	25 ± 7·3	64 ± 14·9	58 ± 14·4	<0·001

—, No data available.

Survival of second- and third-instar larvae

There were significant differences between the maximum numbers of both second- and third-instar larvae surviving in the different predator exclusion treatments (Table 3). There were no significant differences between the numbers of larvae surviving when either predators were totally excluded or when ground zone predators alone were excluded. However, by comparison with total exclusion, significantly fewer larvae were usually found when aerial predators alone were excluded or when all predators had access ($P < 0·02$).

Table 3. *Mean numbers* $(/m^2)$ *of second- and third-instar larvae of* G. polygoni (± *one standard error*) *surviving in the predator exclusion experiments in 1978 and 1979*

Year	Generation	Control or total exclusion	Ground exclusion	Aerial exclusion	No exclusion or total access	Sig. level of F. ratio
Second-instar larvae						
1978	1	33 ± 8·3	30 ± 9·3	9 ± 3·2	13 ± 1·2	<0·05
1978	2	30 ± 6·1	—	9 ± 2·1	12 ± 1·8	<0·025
1979	1	17 ± 1·5	20 ± 1·4	7 ± 2·7	12 ± 1·8	<0·01
Third-instar larvae						
1978	1	6 ± 4·3	7 ± 0·6	1 ± 0·0	0	>0·05
1978	2	6 ± 0·6	—	1 ± 0·3	1 ± 0·3	<0·001
1979	1	4 ± 0·6	5 ± 0·3	1 ± 0·3	1 ± 0·0	<0·001

—, No data available.

Throughout the 1978 and 1979 predator exclusion experiments, there were no significant differences in the mean losses of eggs and first-instar larvae and the mean numbers of second- and third-instar larvae surviving when either predators were totally excluded (control) or when ground predators alone were excluded (treatment 2). In the treatments where ground zone predators had access (treatments 3 and 4) losses of the developmental stages of *G. polygoni* were always higher than in treatments where this range of predators was excluded. Ground zone predators were therefore considered to be most responsible for the losses of the stages of *G. polygoni* in the predator exclusion experiments.

The suggestion that the losses of both eggs and larvae were primarily due to predators was supported by laboratory experiments in which arthropods were screened as potential predators of *G. polygoni.* Collections of predators were made in the field and they were confined individually in Petri dishes (8·5 cm diameter), lined with damp filter paper, and presented with the development stages of *G. polygoni.* In these trials, ground-zone 'polyphagous' predators, such as many of the Carabidae and the Staphylinidae, fed on eggs and larvae of *G. polygoni.* In marked contrast, predators such as Coccinellidae, Syrphidae, Nabidae and Anthocoridae did not readily take these prey items. *Agonum dorsale* (Pont.), *Demetrias atricapillus* (L.), *Philonthus cognatus* (*Stephens*), *Philonthus laminatus* (Creutzer), *Tachyporus hypnorum* (F.), *Nebria brevicollis* (F.) and the common earwig, *Forficula auricularia* (L.) were the major predators of eggs and first-instar larvae, whereas *Pterostichus madidus* (F.), *Pterostichus melanarius* (Illiger), *Philonthus* spp. and *F. auricularia* were the major predators of older larvae and adults.

During 1977 and 1978 many of the predatory arthropods screened in the laboratory trials were captured in the field using pitfall traps. The traps consisted of 7-cm diameter plastic beakers, set into the soil so that the rims were at ground level and were filled with a mixture of water and detergent. In each year, 15 traps were laid out 5 m apart in a transect parallel to and 50 m from the field edge. The traps were operated between April and September and were emptied at intervals of 7–10 days. Catches were preserved in 95% alcohol.

In 1977, a total of 187 *N. brevicollis*, 87 *P. melanarius*, 132 *A. dorsale* and 61 *Bembidion lampros* (Herbst.) were examined. In 1978 too few *B. lampros* were captured to merit dissection, and both *P. melanarius* and *P. madidus* were dissected. The results from the latter two species were pooled and 301 *Pterostichus* spp. were dissected, along with 104 *N. brevicollis* and 138 *A. dorsale*. Although *Harpalus rufipes* (Degeer) and *Philonthus* spp. (*P. cognatus* and *P. laminatus*) were also caught in large numbers, they were unsuitable for gut dissection. These predators ingest only the fluid contents of their prey (Sunderland, 1975).

Many other species of predator were considered suitable for examination by gut dissection, but too few were captured.

The remains of *Gastrophysa* larvae were found in the guts of the following predatory arthropods captured in the field in 1977: *P. melanarius*, *N. brevicollis* and *A. dorsale*. The peak percentage of predators that had fed on *Gastrophysa* larvae in 1977 were: *N. brevicollis* 14·3%; *A. dorsale* 5·7% and *P. melanarius* 3·3%. Remains of *Gastrophysa* were never found in the guts of *B. lampros*.

In 1978, the remains of *Gastrophysa* larvae were found in the guts of *N. brevicollis*, *P. melanarius* and *P. madidus*. Both species of *Pterostichus* contained fragments of older larvae whereas *N. brevicollis* contained only the remains of first-instar *Gastrophysa* larvae. The peak percentage of *N. brevicollis* containing fragments of first-instar larvae was 13%. Three wk later, the peak percentage of *Pterostichus* spp. found to contain fragments of older larvae was 16·7%. In 1978 remains of *Gastrophysa* were not found in the guts of *A. dorsale*.

Although first-instar larvae tended to remain on the host plant, they were nevertheless found in the guts of *N. brevicollis* and *A. dorsale*, species capable of climbing (Vickerman & Sunderland, 1975). The second- and third-instar larvae, in particular the latter, would be vulnerable to a greater range of predators than would the eggs or first-instar larvae, because larvae of both these instars moved from plant to plant and the third-instar larvae had to move onto the soil surface to find pupation sites. In the feeding trials these later instar larvae were predated mainly by the larger non-climbing predators and the remains of third-instar larvae were also found in the guts of two species of *Pterostichus*. Gut dissection is clearly only of use for those predators that ingest the solid remains of their prey and even with these species, when few remains are present in the gut it is impossible to identify the prey with certainty. The proportion of the different predator species feeding on *G. polygoni* larvae must therefore be regarded as underestimates. It was also impossible to detect remains of *G. polygoni* eggs in the guts of the predators and serological techniques would be required in future work.

I thank the Natural Environment Research Council for support and Drs G. P. Vickerman and S. D. Wratten for supervision.

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Effects of natural enemies on a population of codling moth *Cydia pomonella*

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In order to investigate whether the natural enemies of codling moth *Cydia pomonella* (L.) could usefully contribute to a programme of integrated control, codling moth numbers were studied in relation to the activity of natural enemies from 1972 to 1977 in an apple orchard at Long Ashton Research Station which received no insecticides after blossom.

Many codling moth eggs (placed singly on fruit and nearby leaves) were killed by insect predators (Glen, 1975, 1977), mainly mirids and anthocorids (Heteroptera) which are also predators of the fruit tree red spider mite *Panonychus ulmi* (Koch). The number of codling eggs killed depended on the number and size of the Heteroptera and their tendency to search, which in turn depended on the numbers of spider mites and sunshine (Glen & Brain, 1978). Earwigs *Forficula auricularia* L. also took some eggs. An estimated 28–62% of the eggs laid by the moths were taken by predators. Heteroptera took 19–50% and earwigs 7–13% of first generation eggs. In contrast, second generation eggs (laid only in 1975 and 1976) were taken more frequently by earwigs (33–34%) than by Heteroptera (18–28%).

Predators probably killed few newly hatched larvae before the latter entered the fruit. Few codling larvae died or were attacked by insect parasitoids whilst feeding inside fruit. When mature, larvae left the fruit at night and formed cocoons, mainly under bark, where they usually spent the winter. Some of these wandering larvae were eaten by carabid and staphylinid beetles. However, this had little effect on the numbers that survived to adulthood, because of the overwhelming importance of subsequent predation by birds, mainly blue tits *Parus caeruleus* L., on larvae in cocoons (Glen & Milsom, 1978). Birds removed about 95% of cocooned larvae (Solomon, Glen, Kendall & Milsom, 1976), taking more females than males because the latter were better hidden (Glen, Milsom & Wiltshire, 1981); and they reduced the number on different trees to similar levels irrespective of initial numbers (Solomon & Glen, 1979). However, tits did not reduce the number of larvae to similar numbers each year. In particular, in 1976 more than twice as many adults emerged as in other years. In 1976, there was a substantial decline in the number of tits nesting in Marley Wood, Oxford (Perrins, 1979). Since tit numbers fluctuate synchronously over large areas, it is likely that predation at Long Ashton in 1975–76 was less intense because fewer tits visited the orchard. If 1975–76 is excluded from the analysis of codling moth mortality, the loss of mature larvae and pupae in other years was density-dependent. However, this loss was slightly undercompensating so that when more larvae were present initially, more survived to emerge as adults in the following year.

On tree trunks protected by netting from bird attack, 5–30% of overwintering larvae were killed by fungi, of which *Verticillium lecanii* was the most important. In addition, up to 50% of the pupae that developed in spring were attacked by insect parasitoids, the most important being *Pimpla turionellae* (Glen & Curtis, 1978). Both fungal disease and pupal parasitism were density dependent, but markedly under-compensating. Thus if for some reasons birds did not prey on codling moth larvae, fungi and pupal parasites would probably increase in importance, but they could not prevent codling moth numbers from increasing.

All the natural enemies of codling moth attack a wide range of species and, for most, the codling moth is probably of relatively little importance to their survival. Thus the impact of natural enemies cannot be predicted from year to year from a study of codling moth numbers alone. Furthermore, warm summer weather favours egg laying by the moth and rapid development of larvae to give a partial second generation, so that, despite the effects of natural enemies, the numbers of larvae attacking fruit may rise to unacceptable levels. Thus insecticides are needed in some years to ensure low levels of codling moth damage to fruit. The use of any effective insecticide would result in a disproportionate decline in bird predation, because of its relationship to larval density. However, an insecticide that affected only the codling moth would not affect the percentage of eggs eaten by insects, since predation of eggs is not density dependent.

If insecticides were applied in such a way that they killed the predators of eggs, but not the codling moth, a model of the codling moth population shows that the number of larvae feeding in the fruit would have risen to a peak, in 1976, six times greater than that observed. The egg predators present in any one year did not only reduce larval numbers in that year by killing a percentage of the eggs; since fewer larvae matured, fewer survived to become adult in the following year, because of the under-compensating nature of the density-dependent loss of overwintering larvae.

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Phytophagous mites and their predators in apple orchards.

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INTRODUCTION

The fruit tree red spider mite *Panonychus ulmi* Koch is the principal mite pest in apple orchards. Many predators attack *P. ulmi* (Collyer, 1953) and the relative effectiveness with which they regulate the numbers of the mite is influenced not only by the intrinsic differences among the species of predator, but also by external factors, in particular by the nature of the vegetation surrounding the orchard, and by the availability of alternative prey in the orchard. Some of these factors are outlined here.

In orchards receiving a broad-spectrum pesticide programme, few predators survive. The relationships discussed here apply to orchards under an integrated pest management programme, in which the pesticides used are not toxic to predators (Easterbrook, Souter, Solomon & Cranham, 1979).

RESPONSE OF PREDATORS TO CHANGING PREY NUMBERS

The mirid *Blepharidopterus angulatus* (Fall.) is a voracious predator of *P. ulmi* and is one of the first to colonise apple orchards sprayed with selective pesticides. It is univoltine, and overwinters in the egg stage. Thus apart from immigration from outside the orchard, *B. angulatus* can increase its numbers in response to increasing prey numbers only the following season. In orchard experiments *P. ulmi* population densities of two mites per leaf were high enough to sustain populations of *B. angulatus* on the trees, and for the predators to lay large numbers of eggs (Solomon, 1975). A spider mite population level of about 0·5 per leaf the following year was not a sufficient food supply for the resulting large numbers of the predator, and many of them died before reaching the adult stage, and few eggs were laid by the survivors. The resulting small numbers of *B. angulatus* the next year were unable to prevent a rapid increase of *P. ulmi*. *Malacocoris chlorizans* (Panz.), another univoltine predacious mirid, responds in a similar way but is less able to survive at low prey densities, so that in the season when *P. ulmi* was at about 0·5 per leaf, no individuals of this predator completed larval development.

Anthocorids are the other important group of insect predators of *P. ulmi*, *Anthocoris nemorum* (L.) and *A. nemoralis* (Fab.) being usually the most abundant. These predators pass through two generations per year, and overwinter as adults. In years of low *P. ulmi* numbers, anthocorids declined in numbers just as the mirids did, but when the mite increased the following season the anthocorids were able to increase to a high density within the year, by the second generation.

The third group of important predators are the phytoseiid mites, and of these *Tryphlodromus pyri* Scheuten is the species that regularly colonises and establishes itself in apple orchards sprayed with selective pesticides. It passes through three or four generations per year, and thus can increase within the season in response to increasing spider mite numbers. It survives when spider mite numbers are very low; in the experiment mentioned above, *T. pyri* maintained itself at 0·01 per leaf in the season in which *P. ulmi* remained below 0·5 per leaf, and the predator was able to increase rapidly the following season.

THE INFLUENCE OF ALTERNATIVE PREY

All of these predators feed on other prey species in addition to *P. ulmi*, and are influenced in various ways by the abundance of these alternative prey. The main alternative food source for *T. pyri* on apple is the apple rust mite *Aculus schlechtendali* (Nal.) This very small mite occasionally causes fruit russet (Lyne, 1981), but it is not usually damaging. *T. pyri* feeds on apple rust mite, particularly when spider mite numbers are very low (Solomon, 1975). Tydeids are another group of phytophagous mites on which *T. pyri* feeds, and which are often present in low numbers on trees sprayed with selective pesticides.

Mirids and anthrocorids feed on aphids and leafhoppers in addition to spider mites. *A. nemoralis* in particular feeds on the apple psyllid *Psylla mali* (Schmid.), and tends to colonise orchards where this psyllid is abundant.

The possibility that mirids feed on *T. pyri* when spider mite numbers are low has been investigated in a field trial in which mirid numbers were reduced to a low level on some plots by application of diflubenzuron, which is toxic to the mirid larvae (Solomon, 1980). Numbers of *P. ulmi* were low, yet there was no reduction of *T. pyri* numbers on unsprayed plots compared with those on the sprayed plots. The fact that the mirids did not reduce the numbers of *T. pyri* even when other food sources were scarce, suggests that they are unlikely to do so in other circumstances.

THE SURROUNDINGS OF THE ORCHARD

Hedgerows, windbreaks, and woodland are all potential sources of predators of apple pests, and their proximity to an apple orchard can influence the abundance of predators in the orchard. *T. pyri* occurs on several species of plant found in hedgerows (Chant, 1959) and is particularly abundant on bramble (*Rubus fruticosus* L.). Other nearby orchards under integrated pest management are also likely to be a source of wind-blown *T. pyri*. Two other species of phytoseiid mites not normally found in orchards sprayed with selective pesticides, but abundant on unsprayed apple trees, are also numerous on some woodland trees. They are *Typhlodromus aberrans* (Ouds.) on hornbeam (*Carpinus betulus* L.) and hazel (*Corylus avellana* L.), and *Amblyseius finlandicus* (Ouds.) on horse chestnut (*Aesculus hippocastanum* L.).

Anthocorids are very mobile predators and are present on a wide range of herbaceous and woody plants, but during late March or early April they occur on willow (mostly *Salix caprea* L. and hybrids) in very large numbers (Anderson, 1962). After a week or so, when the flowering of the willow has finished, the anthocorids move onto other plants, and may colonise apple orchards, particularly those in which *Psylla mali* is abundant.

The increasing practice of planting a single row of alder (*Alnus* spp.) as a windbreak has brought an important reservoir of the mirid *B. angulatus* close to many orchards. This predator is abundant on alder, where it feeds on the aphid *Pterocallis alni* (DeG.) and on leafhoppers. *B. angulatus* becomes adult in August, when *P. alni* is declining. Many of the *B. angulatus* then leave the alder, and may colonise nearby apple orchards. In a trial at East Malling in an orchard close to alder windbreaks, the mirid colonised the apple trees in response to spider mite densities as low as two per leaf. In another trial in an orchard with greater numbers of spider mite, but with no alder windbreak, hedgerow or woodland within 800 m, colonisation by *B. angulatus* was much slower (Solomon, 1981).

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