QUANTIFICATION OF THE IMPACT OF HOVERFLIES (DIPTERA: SYRPHIDAE) ON CEREAL APHIDS IN WINTER WHEAT: AN ANALYSIS OF FIELD POPULATIONS

BY R. J. CHAMBERS AND T. H. L. ADAMS

Department of Entomology and Insect Pathology, Glasshouse Crops Research Institute, Worthing Road, Littlehampton, West Sussex BN17 6LP

SUMMARY

(1) An analysis of predation of cereal aphids by syrphid larvae is described. The analysis uses field data on the absolute densities of predator and prey in winter wheat crops in Sussex in 1981 and 1982. The method calculates and compares two quantities: the estimated kill rate by syrphid larvae, and the kill required to provide the degree of control observed in the aphid population.

(2) This approach provides a separate analysis for each weekly sampling interval to identify when predation was most effective, and permits an initial appraisal of the impact of other antagonists acting concurrently. The method indicates clearly if syrphids were sufficiently numerous to achieve control alone or, alternatively, if they were too few to have had any significant effect on the aphid population.

(3) Syrphid larvae had the potential to halt the aphid increase in four of the six field populations analysed.

INTRODUCTION

There are many species of natural enemies of cereal aphids in winter wheat, but the importance of the stenophagous or 'aphid-specific' predators (certain Coccinellidae and Syrphidae) has been relatively little investigated, e.g., Dean (1974), Basedow (1982), and Holmes (1983, 1984). However, recent evidence now points to their effectiveness in slowing aphid multiplication and limiting maximum population size (Chambers *et al.* 1983), and in halting aphid population growth below the U.K. economic threshold (Chambers *et al.* 1985). The latter study showed a clear synchronization of predator populations with the onset of aphid population declines from low peak densities. Alternative explanations of the decrease in pest numbers, such as the production of alate emigrants, weather conditions and the growth state of the host plants, were discounted. A quantified analysis of predation is necessary since such data are based on an association between the presence of predators and the slowing or cessation of aphid population growth, and it has not been shown whether enough predators were present to cause the control observed.

Quantification serves two other purposes only touched upon here; to determine the number of predators required in a crop, in order to ensure control regardless of the activity of other natural enemies; and to help assess the relative contribution to aphid mortality made by predators in situations where other natural enemies act simultaneously. These are preliminary steps to developing methods of enhancing the effectiveness of the predatory fauna, and to devising monitoring and forecasting schemes (Dewar & Carter 1984) in which the potential of the predator fauna needs to be taken into account.

The present paper describes an analysis of predation by hoverfly larvae (Diptera: Syrphidae) on the cereal aphids *Sitobion avenae* (F.) and *Metopolophium dirhodum* (Wlk.). Field data collected in 1982, where the action of hoverfly larvae was not complicated by an abundance of parasitoids or pathogens, are used to test and validate the method of analysis which is then applied to other instances of natural control.

METHODS

Field sampling

In order to ensure populations of aphids for study, two winter wheat crops (A, B) situated about 1 km apart on North Farm, Worthing, were infested with *S. avenae* from laboratory stocks on 14 and 19 April 1982. Infestation was confined to a plot 20 × 20 m near the centre of each field. A second plot of the same area was marked out approximately 20 m from the infested zone in each field and was left to become infested naturally by immigrant aphids. These are referred to as the 'infested' and 'natural' plots, respectively, in each field.

Samples were taken at approximately weekly intervals. Between 100 and 400 shoots were examined for aphids and aphid-specific predators in groups of twenty-five adjacent shoots, each group randomly chosen within the sampling area. Total aphids of each species were counted on each shoot examined, as well as eggs and larvae of Syrphidae and Coccinellidae. Larvae were identified to instar. Additionally, as soon as predator eggs were found in shoot examinations, ten random samples using a quadrat of $0 \cdot 1$ m^2 were taken in each plot. In each quadrat, the shoots were carefully cut down, counted, and discarded without examination to leave a stubble. The stubble and soil surface were then searched for eggs and larvae of Syrphidae and Coccinellidae.

Estimates of aphid density (m^{-2}) were calculated from the number per shoot and the shoot density in the quadrats. Total numbers of larvae per square metre were calculated from numbers on the shoots, shoot density, and numbers found on the weeds, stubble and soil surface in the quadrats.

Similar sampling methods were used in winter wheat crops in 1981 (Adams 1984; Chambers *et al.* 1985) and the data from two such fields (crops C, D) are analysed here for comparison with the 1982 results.

Analysis

A decision on whether there were sufficient predators present in a particular case depends upon the kill rate of each predator, the capacity for increase of the aphid prey, and the ratio of predator and prey densities. Whereas it is comparatively straightforward to estimate the latter, field measures of rates of kill and aphid increase in the absence of predators are more difficult to obtain. However, the problem can be restated by calculating the kill of aphids required of each predator to cause the observed change in aphid population for a given aphid potential increase rate, and by comparing this with the predator's estimated kill. If the required kill exceeds the estimated kill, then there were insufficient predators to account wholly for the aphid population changes seen.

Computer programs were written to calculate required kill and estimated kill for each weekly sampling interval. Programs are available from the authors and are listed by Adams (1984).

Required kill

Required kill is the aphid mortality due to the predator population at a given aphid increase rate, which results in the observed change in aphid population density between two subsequent sampling observations.

The rates of aphid increase chosen for the analysis are representative of field populations in the absence of aphid-specific predators. Field sampling has been undertaken by Glasshouse Crops Research Institute workers on the Sussex study area since 1975. Rates of increase prior to the arrival of aphid-specific predators were about fivefold per week in June of the outbreak years 1975 and 1977, while in 1980 and 1981 (where natural enemies were subsequently effective in limiting aphid numbers (Chambers *et al.* 1985)), rates ranged from approximately 2-fold to 5·5-fold per week during May and June. Therefore, aphid increase rates of two-, three-, four-, five- and sixfold per week were selected for this analysis. This range covers the rates of increase normally observed in May when aphid-specific predators arrive in June, and in June itself when predators do not appear until late June or July. Before the arrival of predators, aphids may increase due to both immigration and reproduction while polyphagous predators and other antagonists may be present. The range chosen for the analysis therefore represents the extent of variation in increase rates found in the field due to the combined effects of these factors. The use of a range of increase rates is necessary because, other than reproduction, these factors cannot or have not yet been fully quantified. The analysis is therefore designed to assess the impact of aphid-specific predators against a possible background of mortality due to other beneficial organisms. This permits the identification of instances where aphid-specific predation was the major mortality acting on the prey (when required kill is markedly less than estimated kill even at a sixfold increase per week), and conversely where predation was of minimal importance.

The observed increase rate of an aphid population can occasionally be higher than sixfold per week; at or immediately after the initiation of an infestation by alate immigrants, the rate may, for mathematical reasons, take any value up to infinity between two sampling occasions. Additionally, increase rates may be unusually high in exceptionally hot weather, such as occurred in 1976 when a figure of ninefold per week was recorded during June.

The required kill was found by means of a simple short-run simulation with step-lengths of one day, which started from the observed aphid population density at the beginning of the sampling interval and then calculated a projected population trend to the next observation. An initial value chosen for the number of aphids killed per predator per day was corrected by an iterative procedure until the population passed through the second observation. The predator population between observations was estimated by interpolation. The model chosen for the simulation was first used by Bombosch (1963), later evaluated by van Emden (1966) and further developed by Tamaki, McGuire & Turner (1974) and Wyatt (1983a, b). To simulate reproduction and predation occurring simultaneously, two calculations were used to obtain each subsequent day's aphid population and the mean calculated. These assume that reproduction acts before predation, and vice versa, i.e.,

$$N_{d+1} = \{[(N_d L) - (P_d k)] + [(N_d - (P_d k))L]\}/2 \tag{1}$$

where N_d = number of aphids m^{-2} on day d, L = daily proportional rate of increase assumed, P_d = number of predators m^{-2} on day d, and k = required kill predator^{-1} day^{-1}.

Estimated kill

Estimated kill is the predation capacity of the predator population, expressed for comparison in the same units as required kill (number of aphids per predator per day). Estimated kill was calculated using field temperatures and counts of the instar distribution of the predator population, together with laboratory measurements at constant temperatures of rates of kill on excess prey in relation to the biomass of the larvae.

Laboratory figures for the rate of kill by larvae of *Metasyrphus corollae* (F.) were obtained at 10 and 15 °C by Adams (1984). It was found that means of 0·29, 0·16 and 0·09 mg fresh weight of aphids were consumed per mg of larval fresh weight per development unit in the first, second and third larval instars, respectively. (One development unit is here defined as 1% of the total development period of the larval stage.)

Field populations in 1982 were almost entirely *Episyrphus balteatus* (Degeer) (see results section), and we have assumed that the same relationship between larval weight and kill rate applies to this species. Predator numbers between sampling dates were estimated by linear interpolation and the number in each predator instar from field counts was converted to biomass by a mean larval weight. The mean weights were obtained from a larger sample of larvae taken from six fields of winter wheat in 1981. A sine curve was fitted to field daily maximum and minimum temperatures to estimate the number of development units accumulated on each day. Daily development units were obtained by interpolation of temperature on a sigmoid curve fitted to the relationship between rate of development and temperature (Adams 1984).

The estimated biomass consumed each day was then found from:

$$k_d = \sum_{i=1}^{3} P_{id} R_i D_d \tag{2}$$

where K_d = biomass of aphids killed m^{-2} on day d, P_{id} = biomass of syrphid larvae m^{-2} of instar i on day d, R_i = rate of kill by instar i, as mg aphids killed per mg syrphid biomass per development unit, and D_d = development units accumulated on day d.

Biomass killed was converted to numbers of aphids killed for a mean aphid weight of 0·5 mg. This figure was obtained from aphid samples taken during April and May from the infested plots, supported by results from Vereijken (1979).

RESULTS

Field populations

In the infested plots, *Sitobion avenae* numbers grew steadily for most of May and into early June. In the natural plots, both *S. avenae* and *Metopolophium dirhodum* colonized the wheat from mid-May. Peak aphid population densities occurred in June at 1·85 and 2·98 per shoot in the infested and natural plots of crop A respectively (Fig. 1a, b), and at 2·09 and 1·95 per shoot in the corresponding plots in crop B (Fig. 1c, d). The population peak occurred at the watery-ripe growth stage in the natural plot of crop B (Fig. 1d), but was at flowering in the other three plots. *M. dirhodum* was less numerous than *S. avenae* in the infested plots but about equally common in early June in the natural plots. Aphid numbers did not exceed the recommended spray threshold which in the U.K. is five *S. avenae* per ear at the start of flowering or thirty *M. dirhodum* per flag leaf until the start of milky-ripe (George & Gair 1979; Anon. 1984).
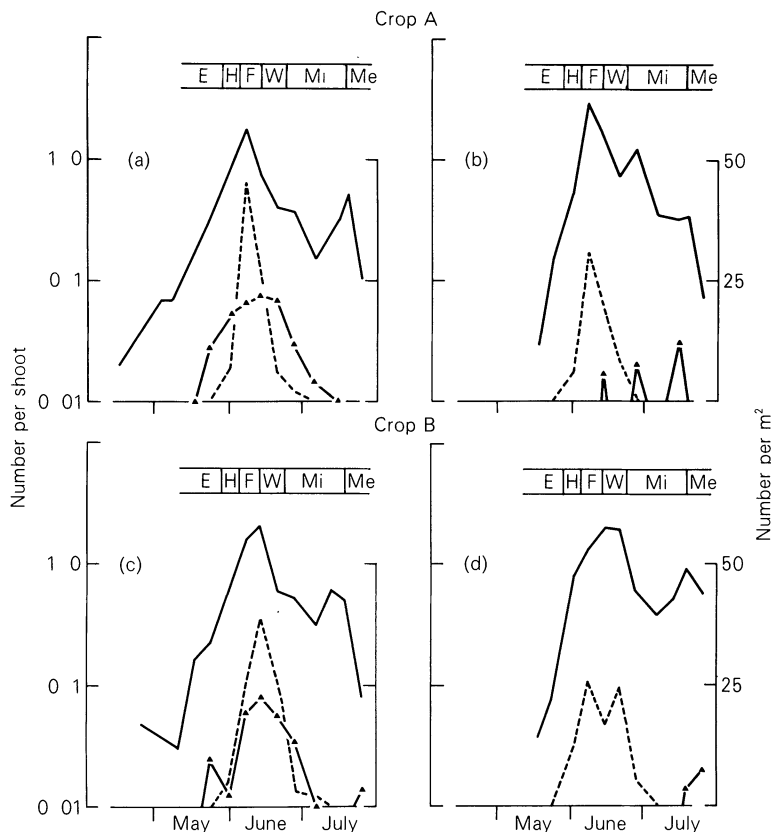
FIG. 1. Mean total number of aphids (———) and parasitoid mummies (▲———▲) per shoot, and number of syrphid larvae per m^2 (————) in infested (a, c) and natural (b, d) plots. Plant growth stages: E, stem extension and booting; H, heading; F, flowering; W, watery-ripe; Mi, milky-ripe; Me, mealy-ripe.

In common with many of the observations in 1980 and 1981 (Chambers *et al.* 1985), the aphid population declines were synchronized with the presence of larvae of aphid-specific predators (Fig. 1). The only abundant aphid-specific predator species found at this time was *Episyrphus balteatus*, the larvae of which were present from the end of May until all had pupated in early July. Since there is, at present, no reason to assume that *E. balteatus* would selectively attack one aphid species in preference to another, population counts have been added for the analysis. In three of the plots, the aphid populations showed a slight resurgence after syrphids had pupated (Fig. 1a, c, d). The absence of this recovery in the natural plot in crop A was probably due to coccinellids, mainly *Coccinella septempunctata* L., which first appeared as adults at the end of June when the last syrphid larvae pupated. (Weekly sweep-net catches of 200 sweeps were taken around the natural plots. Total coccinellid catch for 7, 13 and 19 July was 56 in crop A where there was no resurgence and 21 in crop B).

Dead, diseased aphids were uncommon, being recorded at a level of about 0·01 per shoot in all plots. A few were present in the natural plots from early June, but none before the end of June in the infested plots. Their near-absence signifies that little mortality can be

attributed to pathogenic fungi. The mummies of hymenopterous parasitoids were infrequent in the natural plots in both fields (Fig. 1b, d) but were noticeably more common in the infested plots (Fig. 1a, c), probably because of early aphid establishment and a steadily growing host population during May. There was, however, no substantial increase in numbers of mummies in the shoot samples when the aphid populations were decreasing from their peaks, which suggests that parasitoids were not a major agent of aphid mortality at this time.

Analysis

Estimated kill and required kill were compared for each sampling interval in all four plots (Fig. 2). The required kill was calculated for increase rates of two-, three-, four-, five- and sixfold per week, but only two of these, an upper and lower rate, are illustrated. In each plot, the lower required kill is for the maximum aphid increase rate at which estimated kill exceeds required kill in every week of the analysis. The higher required kill is for the maximum increase rate at which estimated kill exceeds required kill in the weeks around the aphid population peak. Thus, the upper and lower required kills illustrated are not the same in all plots.
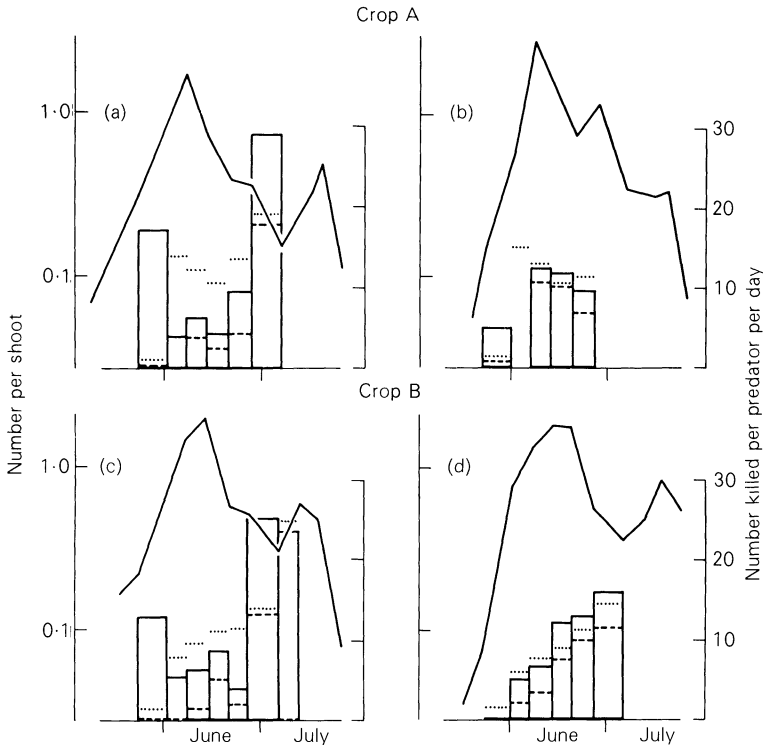

FIG. 2. Mean total number of aphids per shoot (———) with required kill (histograms) and estimated kill (· · · · · ·) in infested (a, c) and natural (b, d) plots. For (a, c): upper histogram bars (———), sixfold increase rate per week; lower bars (– – – –), twofold increase per week. For (b): upper histogram bars (———), fourfold increase per week; lower bars (– – – –), threefold increase per week. For (d): upper histogram bars (———), sixfold increase per week; lower bars (– – – –), threefold increase per week. The required kill is zero when the increase rate assumed is less than the observed rate.

In both infested plots (Fig. 2a, c), the required kill per predator was below ten aphids per day throughout June, even at aphid increase rates of sixfold per week. Over this period, which included the one or two weeks before the peak population and the two or three weeks of the initial decline, the estimated kill was well in excess of the required kill. Extra program runs revealed that increase rates could be as high as ninefold per week in crop B, or fifteenfold per week in crop A, before estimated kill was exceeded by required kill at any time in June. The estimated kill exceeded the required kill for the entire period of the analysis at the lower increase rate of twofold per week. Thus, there were sufficient syrphids for control, and the analysis identified clearly when syrphid larvae achieved control with low levels of mortality due to other antagonists.

Owing to aphid immigration, the increase rates in the natural plots (Fig. 2b, d) at the start of the infestation approximated the maximum used in the analysis. In crop A in the first week of June, 6·2-fold per week; in crop B at the end of May, 5·9-fold per week. This resulted in a zero value for kill required in crop A (Fig. 2b) and a very low value in crop B (Fig. 2d). In both natural plots (Fig. 2b, d), because there were fewer syrphids, required kill rates were generally higher than in the infested plots during June. Required kill was under thirteen aphids per predator per day throughout June at increase rates of sixfold per week, reaching sixteen per day by the end of June and early July in crop B. In both plots, the estimated kill exceeded the required kill for the full period of the analysis at aphid increase rates up to threefold per week. In crop B, required kill was exceeded in the 3-week period prior to the aphid peak at an increase of up to sixfold per week; it is also exceeded in the week following the peak in crop A at an increase of up to fourfold per week. Thus, syrphids were sufficiently numerous to have initiated the fall in numbers in the crop A natural plot providing that the increase rate did not exceed fourfold per week, and to have perpetuated the decline if the increase rate was below threefold per week. There were enough of them to have caused the observed slowing of population growth in the crop B natural plot prior to the population peak, even at an increase rate of sixfold per week, and enough to cause the ensuing decline if aphid increase at this time was threefold per week or less.

Similar analyses have been performed on syrphid data collected from two fields in 1981 (Adams 1984). Shoot counts of other natural enemies in these two fields are illustrated by Chambers et al. (1985). In crop C in 1981 (Fig. 3a), *Metopolophium festucae sensu lato* was present at a maximum abundance of 0·49 per shoot on 28 May. It is believed not to be an economically damaging aphid because of the habit of leaving the crop relatively early, in June. It was considered important not to attribute this loss to predators, so the analysis was conducted on the *S. avenae* population alone. For each weekly sampling interval, the required kill was increased on the assumption that kill was partially expended on the available *M. festucae* in proportion to their abundance relative to the total aphid population. For the fortnight prior to the *S. avenae* peak (at 0·93 per shoot) and for the following week, the required kill vastly exceeded the estimated kill of the predator population, even when the aphid increase rate was assumed low, at twofold per week. From mid-June onwards however, estimated kill was greater than the kill required for every sampling interval at increase rates up to 4 times per week. So, although syrphids were ineffective against *S. avenae* in this field during late May, they were sufficiently abundant to prevent a resurgence in aphid numbers, providing that the increase rate was fourfold per week or less. The major mortality agents were either parasitoids or pathogenic fungi, since mummies and diseased aphids were at their most numerous at the beginning of June.

In crop D (Fig. 3b), which was in the same field as crop A in 1982, *S. avenae* numbers stopped increasing in late May at 1·4 per shoot, fell to a minimum at flowering and then
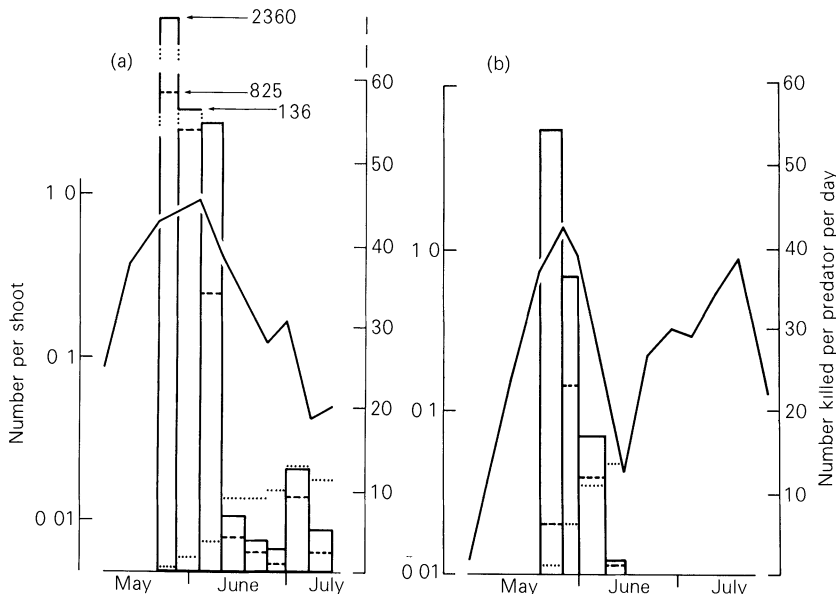
FIG. 3. (a) Crop C. Legend as for Fig. 2 except: mean number of *S. avenae* per shoot (——);
upper histogram bars (——), fourfold increase rate per week; lower bars (– – – –), twofold
increase per week. Numbers on histogram are required kill. (b) Crop D. Legend as for (a).

recovered to a second peak in July. *M. festucae* was numerous at the time of the *S. avenae*
peak, at 6·2 per shoot, but declined rapidly in the first week of June. The division of
predation pressure between the two aphid species resulted in very high required kills for the
control of *S. avenae* in the second half of May. By the first week of June, however,
estimated kill amounted to 92% of the required kill at an increase rate of twofold per week,
or 64% of required kill at a fourfold increase rate. Therefore, there were too few syrphids to
account for the entire decline observed in this week, even though there were an estimated
thirty-four larvae per square metre. Diseased and parasitized aphids were numerous the
week after the aphid population peak and were most probably the main controlling agents,
with syrphids contributing to aphid mortality in the first week of June. Estimated kill was
well in excess of required kill only in the final week of the population decline. The presence
of *M. festucae* in May probably stimulated extra oviposition by female syrphids, but the
higher total aphid density was likely to have diverted a large proportion of predation
pressure away from *S. avenae*.

DISCUSSION

The six cases of aphid-specific predation analysed here differed in the relative importance
of hoverfly larvae in the control of *Sitobion avenae* and *Metopolophium dirhodum*. The
analysis clearly identified cases in which predators were too few to make a significant
contribution to control and, conversely, in which predation was a major component of the
total mortality acting on an aphid population. The method gives unambiguous conclusions
when there are too few predators at the lowest aphid increase rate, or enough predators at
the highest increase rate.

Because the estimated kill values calculated here are derived from laboratory experiments with surplus prey, no allowance has been made for the effect of low aphid densities where predators may have difficulty in finding aphids; this aspect of the analysis could overstate estimated kill. Conversely, other field factors not taken into account here may have resulted in underestimation of syrphid effectiveness. For example, the laboratory data were collected at a relative humidity of 86–88%, but low humidities can cause higher rates of kill by *Metasyrphus corollae* (Wahbi 1967). The importance of prey density and relative humidity to syrphid effectiveness will be determined by field experimentation. Adams (1984) has conducted experiments to assess the functional response of *C. septempunctata* larvae in small areas of winter wheat, and similar experiments with syrphids are planned. Likewise, smaller syrphid instars are more easily overlooked during sampling and this could result in required kill being overstated.

A simulation modelling and systems approach to the analysis of aphid-specific predation has been used by Rabbinge, Ankersmit & Pak (1979) and by Carter, Dixon & Rabbinge (1982) and for the cabbage aphid, *Brevicoryne brassicae* (L.) by Raworth (1984). These studies attempted an appraisal of the impact of predator populations, but were hampered either by the lack of adequate estimates of predator and prey densities or by unrealistic values for predator rates of kill. The present study sought to partially overcome these handicaps in two ways. Firstly, by using field sampling methods chosen with a quantitative analysis in mind and, secondly, by devising a method of analysis in which the results were expressed in readily-interpreted quantities. Division into weekly intervals also avoided the cumulative errors of a long-run simulation.

There are potentially two ways of making better use of the existing aphid-specific fauna in cereals: predator and pest monitoring coupled with short-term forecasting; and modifications to crop husbandry that enhance predator effectiveness. Field assessment of predator and aphid abundance by a farmer or his advisors, either in local fields or in crops known to be representative of a wider area, would save unnecessary spray applications. If varieties identified as possessing a degree of resistance to *S. avenae* (Lowe & Angus 1985) cause lower aphid increase rates in field crops, this would raise the likelihood of control by aphid-specific predators (van Emden & Wearing 1965). Not only would this reduce the kill required per predator for control, but after oviposition larvae would be present at a lower aphid density. For the same reasons, farming methods that encourage a more effective polyphagous predator fauna (Sunderland, Chambers & Stacey 1984) could result in more frequent control by aphid-specific predators.

ACKNOWLEDGMENTS

REFERENCES

Adams, T. H. L. (1984). *The effectiveness of aphid-specific predators in preventing outbreaks of cereal aphids.* Ph.D thesis, University of East Anglia, Norwich.

Anon., (1984). Use of fungicides and insecticides on cereals in 1984. *Ministry of Agriculture, Fisheries and Food*, Booklet number 2257.

Basedow, Th. (1982). Untersuchungen zur populationsdynamik des Siebenpunktmarienkafers, *Coccinella septempunctata* L. (Col., Coccinellidae) auf Getreidefeldern in Schleswig-Holstein von 1976–1979. *Zeitschrift fur Angewandte Entomologie*, **94,** 66–82.

Bombosch, S. (1963). Untersuchungen zur Vermehrung von *Aphis fabae* Scop. in Samenrubenbestanden unter besonderer Berucksichtigung der Schwebfliegen (Diptera, Syrphidae). *Zeitschrift fur Angewandte Entomologie*, **52,** 105–141.

Carter, N., Dixon, A. F. G. & Rabbinge, R. (1982). Cereal aphid populations: biology simulation and prediction. *Simulation Monographs*. Pudoc, The Netherlands.

Chambers, R. J., Sunderland, K. D., Wyatt, I. J. & Vickerman, G. P. (1983). The effects of predator exclusion and caging on cereal aphids in winter wheat. *Journal of Applied Ecology*, **20,** 209–224.

Chambers, R. J., Sunderland, K. D., Stacey, D. L. & Wyatt, I. J. (1985). Control of cereal aphids in winter wheat by natural enemies: aphid-specific predators, parasitoids and pathogenic fungi. *Annals of Applied Biology*, **108,** 219–231.

Dean, G. J. (1974). Effects of parasites and predators on the cereal aphids *Metopolophium dirhodum* (Wlk.) and *Macrosiphum avenae* (F.) (Hem., Aphididae). *Bulletin of Entomological Research*, **63,** 411–422.

Dewar, A. M. & Carter, N. (1984). Decision trees to assess the risk of cereal aphid (Hemiptera, Aphididae) outbreaks in summer in England. *Bulletin of Entomological Research*, **74,** 387–398.

George, K. S. & Gair, R. (1979). Crop loss assessment on winter wheat attacked by the grain aphid, *Sitobion avenae* (F.), 1974–1977. *Plant Pathology*, **28,** 143–149.

Holmes, P. R. (1983). *A field study of the ecology of the grain aphid* Sitobion avenae *and its predators*. Ph.D thesis, Cranfield Institute of Technology.

Holmes, P. R. (1984). A field study of the predators of the grain aphid, *Sitobion avenae* (F.) (Hemiptera: Aphididae), in winter wheat in Britain. *Bulletin of Entomological Research*, **74,** 623–631.

Lowe, H. J. B. & Angus, W. J. (1985). Grain aphid infestations of winter wheat variety trials, 1984. *Annals of Applied Biology*, **106,** 591–594.

Rabbinge, R., Ankersmit, G. W. & Pak, G. A. (1979). Epidemiology and simulation of population development of *Sitobion avenae* in winter wheat. *Netherlands Journal of Plant Pathology*, **85,** 197–220.

Raworth, D. A. (1984). Population dynamics of the cabbage aphid, *Brevicoryne brassicae* (Homoptera, Aphididae) at Vancouver, British Columbia. V. A simulation model. *Canadian Entomologist*, **116,** 895–911.

Sunderland, K. D., Chambers, R. J. & Stacey, D. L. (1984). Polyphagous predators and cereal aphids. *Report of the Glasshouse Crops Research Institute for 1982*, pp. 94–98.

Tamaki, G., McGuire, J. U. & Turner, J. E. (1974). Predator power and efficacy: a model to evaluate their impact. *Environmental Entomology*, **3,** 625–630.

van Emden, H. F. (1966). The effectiveness of aphidophagous insects in reducing aphid populations. *Ecology of Aphidophagous Insects* (Ed. by I. Hodek), pp. 227–235. Academia, Prague.

van Emden, H. F. & Wearing, C. H. (1965). The role of the aphid host plant in delaying economic damage levels in crops. *Annals of Applied Biology*, **56,** 323–334.

Vereijken, P. H. (1979). Feeding and multiplication of three-cereal aphid species and their effect on yield of winter wheat. *Agricultural Research Report (Verslagen van Landbouwkundige Onderzoekingen)*, No. 888, pp. 1–58.

Wahbi, A. A. (1967). *Untersuchungen Uber den Einfluss der Temperature und der Relativen Luftfeuchtigkeit auf das Frassvermogen von Syrphiden larven (Diptera, Syrphidae)*. Dissertation zur Ehrlangung des Doktorgrades der Landwirtschaftlichen Fakultat der Georg-August-Universitat, Gottingen.

Wyatt, I. J. (1983a). Simple calculator models of predator–prey interactions: exponential population growth. *Protection Ecology*, **5,** 235–244.

Wyatt, I. J. (1983b). Simple calculator models of predator–prey interactions: logistic population growth. *Protection Ecology*, **5,** 327–336.