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Entomology Department

C. B. Williams

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ENTOMOLOGY DEPARTMENT

C. B. WILLIAMS

STAFF

G. W. Heath, B. Johnson and Miss S. El-Ziady left during the year, and J. E. V. Davis (A.R.C. scholar) and P. F. Entwistle (Colonial Office scholar) joined the department.

Miss El-Ziady obtained her degree of Ph.D. of London University for a thesis entitled "Field studies in the flight activity of insects in relation to the physical environment".

C. B. Williams visited the West African Cocoa Research Institute by the invitation of the Colonial Office in April 1953 (omitted from last Report), and again in May and June 1954, to advise on insect pests of cocoa, and particularly the mealy bug transmission of virus disease, and damage by Capsidae. He also visited the Netherlands in March 1954 by invitation of the Students Organization of the Dutch Universities, to give four lectures in different universities.

P. W. Murphy went to Austria in June 1954 to work in the laboratory of Dr. Kühnelt in Vienna for about a year.

At the end of the year under review F. Raw was seconded to the West African Cocoa Research Institute in the Gold Coast for a period of 2 years to study insect pests of cocoa.

EFFECT OF WEATHER CONDITIONS ON INSECTS

(C. B. Williams, R. A. French and S. El-Ziady)

No continuous light-trapping was carried out during the year, but suction traps at 5 feet and at 30 feet were working for 2 hours each day, and each night from dusk till midnight. This work was incorporated in a Ph.D. thesis by Miss El-Ziady, and parts of it are now being prepared for publication.

INSECT MIGRATION

(C. B. Williams and R. A. French)

The observations in the Pyrenees, mentioned in the last Report, overlapped into the period of this Report, and during the year a paper has been prepared giving the main results of our expedition. Information on migrant insects continues to be sent in, both from the British Isles and from abroad. R. A. French is preparing a thesis on the migration of the Sphingidae in Western Europe.

GALL MIDGES OF ECONOMIC IMPORTANCE

(H. F. Barnes, Barbara M. Stokes and G. W. Heath)

The twenty-eighth successive annual sampling of the wheat on Broadbalk showed that the percentage grain infestation by the wheat blossom midges was 4.7 in 1954, compared with 11.1 in 1953. Some preliminary experiments were made to test the effect of the freezing and the flooding in the normal soil sampling technique on the

subsequent emergence of the gall midges. Emergence of *C. tritici* and *S. mosellana* took place both after freezing and flooding during the winter and as late as May, but the Saddle gall midge (*H. equestris*), while able to withstand both freezing and flooding in the winter, did not emerge after freezing in May, although it survived flooding in this month.

The study of the biology of *Mayetiola* species attacking the lower part of the stems of cereals and grasses has continued. A stock of the Hessian fly (*M. destructor*) has been maintained on wheat and on couch grass. In experiments this midge intermated with individuals bred on barley, rye and couch grass. Inter-breeding was also obtained. These midges were originally collected on the various host plants on Rothamsted Farm at Harpenden. The host plants of these midges were shown to be interchangeable, and probably only one species is involved. An attempt to estimate the amount of infestation by the Hessian fly in the field was made. The study of a related species, *Mayetiola dactylidis*, from cocksfoot, which differs in life-history and habits, is being continued.

In experiments attempting to measure depression in seed yield of foxtail grass (*Alopecurus pratensis*) as a result of gall midge attack, no differences could be attributed to this group of insects. The experiments involved growing individual plants of a single clone, some of which were infested by gall midges, whilst others were kept free. Unfortunately differences in seed yield due to physiological blindness, thrips and other causes masked any loss due to midge attack.

The investigation into the biology of the lucerne leaf midge (*Jaapiella medicaginis*) was continued. Preliminary attempts to establish the host plant range, using black medick (*Medicago lupulina*), white clover (*Trifolium repens*) and red clover (*T. pratense*), were unsuccessful. Experiments were carried out to assess cocoon populations in the soil. It was found that whereas emergence of the midge was obtained from March and April soil samples that had been kept frozen, but not flooded, the numbers so obtained were considerably lower than from similar samples from which the cocoons were washed without undergoing cold storage.

A paper (134) on the importance of gall midges in the production of the small grains, especially sorghum, as well as a memorandum giving the available published and unpublished information on the gall midges of the sorghums, the panicum millets and rice (135), was prepared for the 6th Conference of Commonwealth Entomologists.

Since writing up the account of an investigation into the gall midges living in chrysanthemum flowers (129), it has been shown that *Contarinia chrysanthemi* can breed on the Daisy (*Bellis perennis*).

A study has been started on the gall midges living in white clover flowers (132). A *Dasyneura* species, injurious to seed production, was found to be widespread in England and Wales. Three other species were also discovered breeding in the flowers. Preliminary experiments indicate that this *Dasyneura* from white clover will intermate with a *Dasyneura* whose larvae feed on the developing seeds of red clover and will breed on red clover.

New gall midges whose larvae live respectively as predators of the eggs of *Pulvinaria* in Indonesia, as internal parasites of aphids

in Trinidad and in the blossom of privet (*Ligustrum*) in Britain have been described (137, 131, 133).

The object of this section has been to build up an international collection of gall midges and a library, while carrying out long- and short-term biological studies particularly on fluctuations and host-plant range, as well as providing facilities for training other workers and serving as a centre of information (130).

APHID PROBLEMS

(C. G. Johnson, L. R. Taylor, Elsa Haine and B. Johnson)

Suction traps

In order to estimate insect densities two parameters must be known: the volume of air sampled and the proportion of insects in that air which are caught. With suction traps, the volume of air sampled varies with voltage, frequency and wind-speed; therefore the climate of the trapping site and the length of the cable cause fluctuation in air delivery. This difficulty is acute when sampling high in the air on a barrage balloon; and when different sized traps are used each must be accurately standardized for air flow. This has now been done by L. R. Taylor for six types of trap and the limits of error under all likely conditions assessed; for this work Taylor devised a new type of manometer.

The second problem—the proportion of insects in an air mass which elude the trap should, *a priori*, vary with the mass and flight speed of the insect and with the wind-speed; this is being investigated.

High-altitude dispersal

The work at Cardington continues, but much time has been spent dealing with 6 years' work and in analysing the results of other authors. Past workers failed to distinguish two processes in aerial dispersal: the distributive effect of meteorological forces on airborne insects and the effects of meteorological factors on the biological processes causing changes in numbers flying. When insects were trapped at various high altitudes, the catches at each height were often correlated with the meteorological factors at each height. It is, however, more convenient to combine the catches at all heights into a single parameter—the density-height gradient: this is independent of gross numbers flying and is an expression of the degree of mixing. The gradient varies with time of day and with season; it is steeper (i.e. a greater proportion of aphids are in lower levels of the atmosphere) with low lapse rates; and this type of distribution is often characteristic of the autumn. High lapse rates and shallow gradients (i.e., more mixing) are often characteristic of spring and summer. The gradient can be integrated to give an estimate of total insects in the air: and the total number of aphids flying up to at least 1,000 feet often shows the double peak characteristic of density change near the crop.

Moulting, parturition and flight rhythms

We have shown that the number of *Aphis fabae* flying are strongly affected by the rhythm of moulting into the alatae. In

the field this rhythm is characterized by a peak of moulting in the morning, followed by a decline, with a later resurgence in the afternoon and evening, and it is to some extent correlated with temperature. Dr. E. Haine has now shown that this rhythm persists for many weeks, even when the insects are kept under constant illumination at constant temperature. A similar rhythm exists for parturition. Thus the rhythm at birth continues in moulting, flight, and eventually often in the rise and fall of total numbers in the air up to 1,000 feet and probably more. In connection with this work L. R. Taylor has investigated the flight rhythms of *Drosophila*.

Aphid flight

Dr. E. Haine has also shown that some tree aphids (e.g., *Drepanosiphon platanoides*, *Phyllaphis fagi* and *Euceraaphis punctipennis*) are able to fly when they are a considerable age (30 days at least with *Drepanosiphon*): they differ, therefore, from *A. fabae*, *M. persicae* and others whose wing muscles autolyse after a few days of activity.

B. Johnson has been working on the behaviour of alate aphids. After the final moult young alatae enter into an excited state in which they are indifferent to their host plant, and require a short flight or other exercise before they will become responsive to it. The main factors influencing the acceptance or rejection of a host are the age and quality of the plant, and the experience of the aphid immediately before alighting, e.g., the length of flight it has undertaken. The physical environment is of less importance, although adverse conditions for flight may have an effect on the larviposition response in some species of aphids, as distinct from the physiological processes of embryo development and flight muscle histolysis, which are dependent on the aphid fully accepting a host plant.

A NEW METHOD OF SAMPLING INSECTS IN HERBAGE BY SUCTION PUMP

(C. G. Johnson, C. J. Banks and T. R. E. Southwood)

A new sampling method for insects on grassland, herbage, hedges, etc., has been developed in which a powerful suction pump removes the insects and deposits them in a detachable bag. It is particularly suitable for removing the free-living population in the deep interstices of matted vegetation; preliminary tests show that a high proportion of the total insects, and in some cases (e.g., capsids) a complete extraction, of a given area is possible in a very few minutes without removing plants, etc., to the laboratory.

THE NATURAL ENEMIES OF APHIDS

(C. J. Banks)

Some of the conclusions from earlier studies on the movements and behaviour of ladybird larvae (Coccinellidae) have been given in the Report for 1953. The high mortality in the field of young larvae occurs, it seems, soon after they have dispersed from the egg shells. The studies were resumed during 1954, with special reference to the movements of unfed, newly-hatched larvae, whose small size called for the development of a technique for locating them on plants in the field.

Satisfactory results were obtained for well-grown larvae of the large species *Coccinella 7-punctata* by attaching labels containing radium sulphate to the insects. For the small, very active, first-stage larvae these labels were too large and other materials had to be found; experiments with ^{32}P , mixed with an adhesive applied to the thorax, were unsuccessful, but radioactive tantalum (^{182}Ta) was found to be a suitable material for attachment with glue or cellulose paint to the larvae. Labels, cut from a strip of the irradiated metal, measured approximately 0.05 mm. \times 0.10 mm. \times 0.23 mm. and on the average weighed 0.03 mg. Simple techniques were developed for cutting the labels and for holding the larvae still while labels were being attached. These labels could be detected at a distance of 1-1.5 feet, and were suitable for larvae of all sizes and, no doubt, could be used for other small crawling insects.

Injurious effects of this treatment of larvae were sought. No changes in the behaviour or in the growth of first-stage larvae carrying labels of unirradiated tantalum could be observed, but labels of an initial specific activity of 250 $\mu\text{c.}/\text{mg.}$ specific activity, while not so readily detected, proved satisfactory, for no adverse effects could be observed on the behaviour of the larvae or on the rate of growth of any immature stage of the insects.

The results of laboratory and field studies in which these techniques were used are being prepared for publication.

HETEROPTERA

(T. R. E. Southwood and P. F. Entwistle)

T. R. E. Southwood has continued his study of the ecology of various Heteroptera associated with field margins and hedgerows. During the winter, grass stems were examined and the number, conditions and species of Mirid eggs recorded; mortality factors recognized were parasitism by Mymarids and crushing when the grass stem twisted and contracted on drying. The numbers of parasites emerging per unit area of ground was estimated by means of emergence traps. During the summer, samples of the larvae and adults of Heteroptera were taken by sweeping and with the vacuum method of sampling (see above). Each species was found to have its own special habitat within the grassland, for example the larvae of *Capsus ater* L. occur only around the bases of the grass; whilst those of *Stenotus binotatus* Jak. are confined in the early instars to the flower heads of Cocksfoot grass (*Dactylis glomerata* L.), and later instars live on the heads of other grasses and wheat.

An estimation of the population of adult *Leptopterna dolabrata* L. by marking and recapture was carried out in July; from a preliminary analysis of the results it would appear that the expectation of life, after capture, was low, in the order of 5 days. By sweeping the wheat adjacent to the experimental area and from the catches of a suction trap running in the area, it was found that very little migration of *L. dolabrata* occurred during the experiment. A study of the bionomics of the two thistle lace bugs, *Tingis ampliata* H.-S. and *T. cardui* L., has been completed; in this Mr. G. G. E. Scudder has collaborated.

A survey has been made of the morphology of the salivary glands of terrestrial Heteroptera; this work and that on egg structure,

which is continuing, have contributed to a revision of the super-family classification.

A taxonomic revision of the world species of the Mirid genera *Cyrtorhinus* Fieber and *Mecomma* Fieber, the first of which is important in biological control, is being carried out in collaboration with Dr. J. C. M. Carvalho of Brazil.

During July a short visit was made by T. R. E. Southwood to the Nature Conservancy's Merlewood Research Station to survey, with Dr. J. E. Satchell, the Heteroptera of natural woodlands in the Lake District.

In collaboration with Mr. D. Leston a study is being made of the range of variation of taxonomic characters of various Heteroptera, including *Blepharidopterus angulatus* Fallen, an important predator of the red spider mite.

P. F. Entwistle has commenced a comparative study on the oviposition sites, eggs and larvae of the various mirids occurring on oak; in connection with this work he is investigating the structure of the female genitalia of mirids.

EFFECTS OF POPULATION DENSITY ON INSECTS

(D. B. Long)

The work on the effects of population density on larva of Lepidoptera has been continued, and a more detailed study of the processes involved in larval darkening and the faster rate of development is being made. The work has been extended to include Heteroptera, and aggregation has been observed to induce a faster rate of development in *Stollia fabricii* Kirk. The fact that the population density may produce similar effects in orders other than Lepidoptera or Orthoptera is supported by a recent observation in the literature on Coleoptera, which with a consideration of the small numbers that may be involved, will indicate the potentialities of these biological principles in the field.

Photo-colour response in lepidopterous larvae

The colour of the spots of the older larvae of the Emperor moth (*Saturnia pavonia* L.) are known to be variable, the spot colour of the individual larva generally being uniform. Apart from certain larvae in which they are black or white, the colour of the spots may range from pale yellow through orange to pink. Experiments showed that the colour which appeared during each of the last two instars could change from yellow to pink and that the extent of the change depended on the intensity and duration of the light to which the larvae were exposed. This photo-response was locally determined for each spot, and did not involve a central nervous reflex depending on light entering the ocelli.

SOIL SECTION

Wireworm studies (F. Raw, R. M. Dobson, J. W. Stephenson and J. R. Lofty)

The studies of wireworm populations on the ley and arable rotations are now almost complete and will be concluded when the present first- and second-year plots have reached their third year.

The results of the Geescroft experiment on the chemical control of wireworms are now being prepared for publication in collaboration with the Insecticides Department.

Experiments to investigate the populations and movements of *Agriotes* adults were carried out in Geescroft and on Highfield pasture. The method used was that of marking and recapture, and the results are being considered together with those of the essentially similar experiment carried out last year.

Earthworm studies (F. Raw and R. M. Dobson, in collaboration with Soil Survey)

It has been suggested that soil organisms, especially earthworms, may play a considerable rôle during the rehabilitation of grassland which, due to the combined effects of acid soil, sheep grazing and neglect, has reverted to Nardetum. The organisms may help to break up the characteristic surface mat of rhizomes and to improve the physical structure of the soil. Experiments have been laid out on two hill farms in Lancashire in which, after a basic treatment of liming and surface cultivation has been applied to all plots, the effects of dung and balanced artificials at two levels of earthworm populations will be studied. Changes in the vegetation, the soil profile and the populations of earthworms and soil arthropods will be noted, and the productivity of the plots will be assessed by taking periodic grass cuts. Preliminary observations have indicated very low populations of earthworms on both sites.

Studies on Protura (F. Raw)

The results of the observations on the Protura of Park Grass have been prepared for publication. 1,425 Protura were extracted from ninety soil samples by flotation (each sample was 2 inches diameter and 9 inches deep). Eighty-five per cent of these were *Proturentomon minimum* Gisin and the remainder a species of *Eosentomon*, probably *E. armatum*. They were aggregated in such a way that the majority of individual sample counts fell within the range one-half to twice the geometric mean of the population. The degree of aggregation appeared to be independent of the population density. Their distribution was associated with conditions induced by liming, and both species were correlated with exchangeable calcium. *P. minimum* was also correlated with soil pH, and the abundance of *Avena* spp. and *Dactylis* spp.

Studies on millipedes (J. W. Stephenson)

Work on the biology of millipedes has continued. Cultures have been successfully maintained in the laboratory in order to investigate life-cycles, and last year's feeding experiments are being repeated so that differences between species can be more accurately assessed. Regular field collections and associated ecological studies have been made since spring.

Studies on Coleoptera (R. M. Dobson)

Limited field and laboratory observations on the bionomics of the cabbage stem flea beetle (*Psylliodes chrysocephala* L.) have been carried out. The results are now being prepared for publication. Some systematic work has been carried out on the species of *Carp-*

philus (Nitidulidae) associated with stored produce. Three new species have been found amongst material submitted for identification.

WHEAT BULB FLY (*LEPTOHYLEMYIA COARCTATA* FALL.)

(Barbara M. Stokes, D. B. Long and F. Raw)

Barbara Stokes reports that an investigation into the host plants of wheat bulb fly was begun. Flies were reared in experiments from newly hatched larvae on seven different common British grasses, from four plants related to wheat, and from wheat and rye. Larvae were also found feeding in experiments in three further plant species and typical damage occurred in six others, all in the Gramineae.

Larvae were able to move in the soil at least 7 inches (a usual drill width).

Breeding stocks of flies were maintained successfully in captivity in order to continue the host-plant experiments.

Larval studies (D. B. Long)

A survey was made in early spring of 1954 of larval infestation on the Rothamsted and Woburn soils in which samples were obtained from seventy plots of winter wheat involving different manurial treatments, and ten different previous crops.

From the samples taken, the sandy loam of Woburn did not appear to be so heavily infested as the clay loam at Rothamsted, though in both cases the heaviest infestations followed a summer fallow. At Rothamsted the highest infestation occurred in wheat of the four-course experiment on Hoosfield, where 87 per cent of the plants contained larvae, although 98 per cent of them had been attacked at the time of sampling, involving the destruction of 75 per cent of the existing shoots. Other plots carrying high infestations were Broadbalk, the wheat in the six-course experiment on Long Hoos 4, and the Wheat and Fallow experiment in decreasing order of intensity. Some infestation occurred in wheat following potatoes, whilst relatively low attacks followed previous crops of barley, wheat, lucerne, ley and cut grass.

Adult studies

Observations were made on the relative numbers of flies occurring on wheat plots. Male flies were first caught on 21 June and females a day later. The largest numbers of flies were always obtained in the sweeps made at 6.30 a.m. The minimum flight temperature was found to be 12° C. The results showed that as the daily temperature rose above this value the flies dispersed from the wheat and generally did not settle again in any number on the crop until dusk. From the recaptures from 2,000 flies which had previously been marked and released, and from the uneven distribution of the existing population, the flies appeared to stay in the vicinity of the plots from which they emerged. They also tended to aggregate on the lee side of the crop. Generally at low wind speeds the flies were found to be on the top of the wheat, but with higher speeds, i.e., 15 m.p.h., they were found close to the ground.

Oviposition rhythm

Although looked for, oviposition was not observed in the field. Observations on caged females under laboratory conditions showed a distinct diurnal rhythm. Egg laying began in the afternoon and rapidly rose to a maximum during the 2 hours before dark. Few or no eggs were laid during the night or morning. The rhythm was not dependent on light, but was influenced by it.

Eggs

Eggs are known to develop for a period of up to 2 weeks before entering diapause, and a study was made of the water relations during this period. The eggs were found to lose water rapidly unless kept at 100 per cent relative humidity. Eggs kept at 77 per cent relative humidity lost one-fifth of their total water in 13 days, resulting in 50 per cent mortality. The rate of water loss was found to depend on both physical and physiological factors. Water once lost could not be recovered when returned to saturated conditions.

F. Raw reports as follows :

Preliminary observations on Broadbalk suggested that the intensity of wheat bulb fly attack might be affected by the quantity of organic residues in the soil influencing oviposition and by the density of wheat shoots available to the larvae at hatching time. A factorial experiment laid out on Pennell's Piece to investigate the effect of various soil conditions on oviposition showed that manuring had no effect on the number of eggs laid, but that a rough tilth was preferred for oviposition to a smooth one. Cultivation of the soil during the oviposition period appeared to create conditions favourable to oviposition, but it could not be ascertained whether this was due to an increase in the number of possible oviposition sites or to some property of freshly cultivated soil which was attractive to the insects.

By covering parts of selected plots on Broadbalk fallow with mosquito netting during the oviposition period, small areas free from wheat bulb fly eggs were obtained. These will be harvested separately so that the effect of the infestation on the yield of the crop can be estimated.

FOREST SOIL INVESTIGATIONS

(P. W. Murphy)

Preliminary investigations have commenced to consider in greater detail the litter fauna of different tree species, singly and in mixture, together with their associated "humus" formations. It is intended to consider especially the food habits of individual species of Acarina and Collembola occurring in the litter. A problem encountered in the search for suitable sites for this work is the absence of information concerning the soil properties of what are otherwise suitable locations. However, some plantations in Thetford Chase, Norfolk, appear promising, and the investigations of Dr. J. D. Ovington of the Nature Conservancy provide valuable information on the chemical and physical attributes of the soils in this area. A preliminary survey has been made of the meiofauna of single-species plots at

Olleys Farm, Thetford Chase, one of the plantations sampled by Ovington.

With the intention of investigating the effect of environmental factors such as precipitation, a search has been made for other areas with thin iron-pan soils similar to that encountered in parts of the Allerston Forest. A site near Bolton, Lancashire, has been sampled to ascertain the effect of the much higher rainfall prevailing in this area. Preliminary results would suggest that more attention should be paid to the relative proportions of the various layers of the raw-humus horizon. The Bolton samples have a well-developed F layer, and this may partly account for the greater biomass and faunistically richer population inhabiting this site. E. Crompton and other members of the Soil Survey team at present working in Lancashire have given generous assistance and advice.

In June P. W. Murphy received a special grant from the Forestry Commission to enable him to spend a year with Professor Kühnelt at the Zoological Institute of the University of Vienna. Professor Kühnelt is a well-known authority in the field of soil animal biology, and he and his students have carried out a considerable amount of research on the fauna of forest soils. This work includes surveys field observations and laboratory studies of the food habits and biology of individual species.

PRELIMINARY OBSERVATION ON THE EFFECT OF WEED-KILLER ON INSECT POPULATIONS

Co-operation with the Nature Conservancy and the Agricultural
Research Council

(C. G. Johnson, R. M. Dobson, T. R. E. Southwood,
J. W. Stephenson and L. R. Taylor)

The widespread use of weed-killers may have undesirable effects on some animals and on the balance of nature; because of the lack of information, experiments were planned by the Agricultural Research Council and The Nature Conservancy primarily to assess the effect on bird life of DNOC sprayed on winter-wheat. We were asked to observe the effects on the arthropod fauna.

Two fields, $\frac{1}{2}$ mile apart at Ardington, Berkshire, were among those selected; but, though superficially similar, they had different histories, weeds and insect populations. One field was sprayed, one left untreated. For some days before and for some weeks after spraying, sampling was carried out of the air above the fields by suction traps, of the herbage by sweeping and of the soil. Control soil samples were also taken from protected parts of the sprayed field.

The course of population change in both fields was similar, though the control field had a naturally higher population. The population on *both* fields declined after the date of spraying, and the effects of the DNOC were therefore difficult to detect. On the sprayed field, however, the decline set in one day earlier than on the control, and samples by sweeping suggest that the spray may have been responsible for this (Table I). No effect attributable to the spraying was noticed beyond this one day, except in the soil.

In 6-inch-deep soil samples no effects were detected on total

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population, though surface-living Collembola and Thysanoptera were fewer on sprayed land. In 2-inch-deep samples Collembola were fewer on the sprayed field than on the controls for at least 3 weeks after spraying, though this difference was not statistically significant.

TABLE 1
Daily suction trap catches

May	7	8	9	10*	11	12	13	14	15
Sprayed ..	532	631	779	4,836	4,483	2,481	3,326	694	1,080
Unsprayed	3,206	4,869	2,390	7,784	16,371	11,000	13,000	3,735	216

* Date of spraying.

Of all insects caught by trapping, only 14 per cent were definitely non-residents: this is probably a gross underestimate. The probable effect of spraying on resident populations was indicated by sweeping sprayed and unsprayed portions of the same field on the day after spraying (Table 2). A detailed analysis of groups and species showed that though most insects diminished, Frit flies and aphids increased after spraying.

TABLE 2

	Sprayed	Unsprayed
Diptera	38	129
Auchenorrhyncha	8	32
Symphyta	2	6
Collembola (Sminthurus)	7	49
Lepidoptera (larvae)	3	11
Heteroptera	2	18

A detailed report has been circulated, but this complex problem needs experiments of longer duration, with more replication and more controls, if increases and decreases associated with spraying are to be distinguished from natural population fluctuations.