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STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

VI. DISCUSSION ON RESULTS OF STUDIES I–V

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CONTENTS.

1. Introduction.

These studies of insect populations were designed primarily to collect information regarding periodic fluctuations as they occur in nature, and secondly, to provide hints of the factors involved (**1**). Thus it was hoped ultimately to amass sufficient knowledge to make possible the prediction of outbreaks of insect pests. The gall midges were chosen as a suitable group of insects to study on a quantitative basis. Five separate yet concurrent studies, involving six species of gall midges and each covering a period of about five years, were undertaken. Each study varied slightly in details. The first (**1**) dealt with two wheat-blossom midges, *Contarinia tritici* Kirby and *Sitodiplosis mosellana* Géhin, as they occurred on the classical field of wheat at the Rothamsted Experimental Station at Harpenden. Normally both these species are single-brooded, yet frequently there is a partial second flight of adults in the case of *Contarinia tritici*. The second study (**2**) was on one of the meadow foxtail grass midges, viz. *Dasyneura alopecuri* Reuter. On rare occasions there is a second flight in this species, but it is really single-brooded and univoltine. In this case the material came from near Aberdeen. The third study (**3**) was on the button-top midge of willows, *Rhabdophaga heterobia* H.Lw., which is multi-brooded. Only the over-wintering brood was studied, and the material was collected on one field of a commercial bed near Leicester. The fourth (**4**) was on the Arabis midge, *Dasyneura arabis* Barnes, which is also multi-brooded. In this case midges were reared in captivity for 18 generations from one original sample collected in Surrey. The fifth and final study (5) was on the leaf-curling pear midge, *Dasyneura pyri* Bouché, another multi-brooded species. Fresh material for each brood was sent from an extremely localised area in Devon.

Throughout, the insects were collected as full-grown larvae, and the samples reared in an outdoor unheated insectary at the Rothamsted Experimental Station, Harpenden. Each of the studies has now been completed for the initial period of roughly five years, and it is opportune to pause and consider.

It is proposed in this paper to state how far these studies are achieving their object or failing in it, and to discuss the results so far obtained as a whole. It is as well to state at the outset that the studies on the foxtail grass midge, the Arabis midge and the leaf-curling pear midge have been discontinued after the initial period, but that it is proposed to continue the other two studies for an indefinite period.

2. COLLECTION OF INFORMATION ABOUT PERIODIC FLUCTUATIONS OF INSECT POPULATIONS IN THE FIELD.

It is perhaps unfortunate that so much of the labour entailed in collecting data is purely routine and consequently unattractive. To ensure real success in a project such as this there should be a team of workers carrying out similar studies on a considerable number of insects, preferably pests, in various districts. Such studies should be continued over a long period. In the present case all the insects, although coming from different districts, were reared in one locality, namely Harpenden.

As a consequence of only one person doing the work it has been necessary to use simple, even crude, methods, and also to limit the number of species as well as samples of insects studied; on the other hand, an element of personal error is eliminated. As a direct result it cannot be claimed that minor fluctuations shown in the data are statistically significant; to ensure this would have entailed far too much work. In other words the methods employed are only sufficiently exact for revealing large increases or decreases in population numbers. In spite of these objections there is no doubt that these studies are proving fairly satisfactory in amassing data concerning periodic fluctuations of insect populations as they occur in the field.

The rapidity with which an insect can assume alarming numbers has been brought out on several occasions. For example, the data concerning *Contarinia tritici* and *Sitodiplosis mosellana* show that there are very considerable rises and falls in numbers from year to year. Additional figures since the publication of the first study are now available for the years 1932–5. Table 1 shows the numbers of larvae of both these species that have been present in the standard sample of 500 ears of wheat during the years 1927–35 inclusive.

Table 1. *Numbers of larvae of* Contarinia tritici (A) *and* Sitodiplosis mosellana, (B) *present in* 500 *ears of wheat on Broadbalk*, 1927–35.

	1927	1928	1929	1930	1931	1932	1933	1934	1935
A	1780	2195	19,265	18,595	19,273	7356	1511	3381	4289
B	715	2043	587	3,746	6,027	3114	319	572	4221

Similarly the population of *Dasyneura alopecuri* reared from 100 heads of meadow foxtail grass rose from 1498 in one year to 4748 in the next (1929) in locality A, and in locality B the number in this latter year was 7565. In no other year of the five during which the study was continued was the average reared population per 100 heads of grass more than slightly over 2000. Thus with the exception of the one year, 1929, when the figures were abnormally high, the average reared population of midges per 100 heads of grass was $1439 \pm 121{\cdot}4$. The figures for the numbers of parasites reared also were shown to vary, giving relative parasitism figures from 38 to 0·7 per cent. In the study of *D. alopecuri* the population numbers were based solely on the numbers of insects reared and not on direct larval counts as in the case of the first study on wheat midges. It was shown that this method of estimating populations, and more particularly damage, by emergence figures was untrustworthy as compared with direct counts. The former method masks whatever mortality occurs during the period intervening between the larval and adult stages of the insect. This possible mortality is the reason why the relative parasitism (i.e. the numbers of parasites, compared with the numbers of host, emerging after the winter) has been studied; under these circumstances there probably is differential mortality also to be considered.

In the third study which dealt with *Rhabdophaga heterobia* a similar procedure of basing population numbers on subsequent emergence figures was adopted. Here again there have been marked changes in the numbers of insects reared. It is hard to believe that such changes can be accounted for solely by mortality between the full-grown larval and adult stages. Additional figures are now available since the publication of the third study, and the figures to date are given in Table 2.

Table 2. *Average population of* 500 *galls of* Rhabdophaga heterobia, 1928–35.

Year	Midges	Parasites	Total insects
1928	1573	1607	3180
1929	1235	2204	3439
1930	341	556	897
1931	840	1323	2163
1932	1480	1662	3142
1933	2810	428	3238
1934	796	633	1429
1935	234	148	382

Both the numbers of midges and parasites have varied quite remarkably. It must be emphasised that only the over-wintering brood has been studied in this instance.

The fourth and fifth studies on the Arabis midge and the leaf-curling pear midge were not designed to show differences in actual numbers, although it is obvious from the data that changes have been taking place from year to year and also within the years, i.e. from brood to brood.

3. Possible factors involved.

Throughout these studies the vast importance of weather appears to predominate over everything else: its component physical factors, such as for example temperature and humidity, seem to underlie all fluctuations. In some cases naturally these factors act directly on the injurious insects themselves, in others they act through the host plants, and in others through their effect on the insects' enemies, e.g. their parasites.

Various hints of the way in which such factors may act have been obtained, and, as was originally intended, subsidiary studies based on these hints have been made. Actually there have been three up to date, namely one on the factors governing emergence (**6**), another on the sex ratio at the time of emergence (**7**), and the other on the segmentation of the antennae (**8**). A thorough understanding of emergence is of the utmost importance in work of this nature, and the segmentation of the antennae has been shown to be closely connected with the food supply of the larvae. Besides these aspects there remain a great many hints which must be further investigated. It is proposed in this section to outline briefly the more striking. In the following paragraphs, various lines of thought suggested by the data already accumulated will be emphasised. While in no way claiming that they are the only solutions to the problems, the view is held that they are logical partial explanations. They are given more with the idea of setting forth probable fruitful lines of research than with any intention of finality.

When the term "weather" is used, one or more of the physical factors comprising this complex is implied.

(*a*) *Effect of weather acting directly on the insect.*

(1) *Sex ratio at the time of emergence.* In the species studied there appear to be definite sex ratios for individual species, e.g. for *Contarinia merceri* Barnes it is *c.* 23 : 77; for *Dasyneura arabis c.* 27 : 73; for *D. pyri c.* 39 : 61; for *D. alopecuri*, *Contarinia tritici* and *Rhabdophaga heterobia c.* 50 : 50. It must be realised, however, that these figures do not necessarily convey the correct meaning, because they are based on large numbers of individuals from different broods and in different seasons. In fact the reverse is more true. *R. heterobia* breeds by means of unisexual families but there is no reason to suppose that *Dasyneura alopecuri* or *Contarinia tritici* does. Again it has been shown that in the case of *Dasyneura pyri* and *D. arabis* the sex ratios of their various broods are quite different. In spite of this, however, it has been possible

on occasion to record sudden departures from the normal sex ratio, e.g. in one instance that of *D. alopecuri* was 25 : 75, in another that of an over-wintering brood of *D. arabis* was 3 : 97.

Again it has been shown that delayed mating in *D. arabis* tends to result in the production of more males than is usually the case. In this connection it is interesting to note that data has been provided indicating that the sex ratios of the various broods of *D. arabis* and *D. pyri* are different. In *D. arabis* as the season advances the percentage of the males decreases; i.e. the first brood of the year has the highest percentage of males, the second brood less, and the third and over-wintering broods the least. In the case of *D. pyri* the reverse holds good: as the season advances so the percentage of males increases.

The day-to-day emergence figures show days on which the expected numbers of one sex have suddenly dropped. For example, from 13 samples of *D. alopecuri* on May 30th, 1928, 259 males and 296 females emerged; on the 31st, 257 males and 25 females emerged; on June 1st, 96 males and 301 females emerged. In this case there was a great decrease in numbers of females on May 31st, but the fall was only temporary, as on the subsequent day more females than were to be normally expected emerged.

Thus it appears probable that on some occasions weather will permanently affect the sex ratio, on others only a temporary setback is incurred. The different responses of the sexes to physical factors should be well worth investigating.

(2) *Dates of emergence and number of broods.* There appears to be little effect of season on the dates between which the majority of the over-wintering broods of a midge species may be expected to emerge. On the other hand, in an early year the insects start to emerge much sooner than in a late one. It is apparently not very wide of the mark to say that the earlier the emergence starts the longer it takes to reach the peak and *vice versa*. Further, such early emergences are not so regular in approaching the peak; there are definite minor crests if the day-to-day figures are examined (**6**).

Such observations have led one to put forward a view that the larvae require a certain more or less fixed amount of temperature to develop from fully fed larvae into adults; when such amount of temperature has been made available, then, under given favourable conditions from day to day, emergences will take place. On the other hand, although favourable day-to-day conditions may occur before such amount of requisite temperature has been received, emergences will not occur. The actual day-to-day emergences seem to depend upon day-to-day conditions to some extent, but finally when the insect is ready the urge is overwhelming, and as a result the crest of emergence is nearly constant. This suggestion of using accumulated temperatures to forecast expected dates of emergence is to receive further attention in the future.

The number of broods in multi-brooded species appears to be remarkably constant. This may be due more to the effect of the weather on the plant and so indirectly on the insects than on the insects themselves directly. It may be due to the length of the growing season of the plants.

(3) *Activity of adult midges.* Unless the weather is suitable for egg laying when the insects emerge, there is little chance of successful oviposition taking place, because the adult midges are individually so short lived (24–48 hours). Thus although large numbers of imagines may be present, unfavourable weather, such as windy days, may prevent a serious attack from developing. Data concerning day-to-day oviposition numbers over a period of four weeks are given in the study on the wheat-blossom midges. Actually virgin females have been found to live longer than impregnated ones, but it may be presumed that in a natural state there are very few virgins for any length of time. In the majority of cases oviposition starts almost directly after mating, which itself follows closely upon emergence. As there are definite times during the day for emergence in the different species, so there are definite periods during the day when oviposition normally occurs. Some details of the emergence times for several species can be found in the subsidiary study on emergence factors (**6**). Thus it will be realised that unfavourable weather conditions from hour to hour may upset a potential severe outbreak.

(*b*) *Effect of weather acting through the host plant.*

(1) *Adjustment between plant condition and insect development.* The success of midge attacks depends largely on whether the plant is in the right stage of growth when the adult midges are ready to oviposit. For example, *Contarinia tritici* and *Sitodiplosis mosellana* normally emerge, oviposit and die within about 48 hours. They only lay on the wheat ears at the time when the ears are bursting from the sheaths. Normally the emergence of the wheat midges and ears coincide, but in 1933 the wheat ears burst their sheaths about a fortnight earlier than usual, and the midges emerged about three weeks before their normal date. The season had had a different effect on the wheat and the midges. The data show that in 1932 there were 7356 larvae of *Contarinia tritici* present in the sample, in 1933 only 1511; similarly in 1932 there were 3114 *Sitodiplosis mosellana* present, in 1933 only 319. Thus there was a large reduction in numbers, probably due to this lack of adjustment between plant and insect.

The state of the host plant at oviposition time also determines in some cases the form of the gall which results, and even whether the larvae succeed in establishing themselves or not. As has been shown the wheat-blossom midges oviposit successfully only at a definite period of plant growth; *Rhabdophaga heterobia*, on the other hand, makes several types of galls, e.g. lateral bud, button and catkin, depending on the stage of plant growth available (**9**). In the same way *R. terminalis* H.Lw. has been shown to cause two types of gall dependent on the state of the willow growth (**10**). Lately (**11**) it has been proved that *Macrolabis corrugans* F.Lw. seldom manages to establish itself on cultivated parsnip because of the rapidity with which the leaf buds normally uncurl; yet it scarcely ever fails to attack successfully cow parsnip whose buds uncurl slowly.

(2) *Drought.* The data given concerning *Rhabdophaga heterobia* show a remarkable fall in numbers of both midges and parasites in the year 1930. Instead of the normal 3000 insects from the sample, only about 1000 appeared. The next year there were about 2000, and not till 1932 did the insect population return to the normal 3000. The ratio between the midges and parasites remained nearly constant during this period. It is reasonable to suggest that the drought of 1929 was responsible for this diminution. The willows assumed their winter buds earlier than normal owing to the lack of sap rising sufficiently well to continue the normal autumnal growth. A natural consequence of this would be a severe shortage of food to the inhabitants, i.e. midges and parasites, in the terminal button galls. Actually the willows did not recover their normal height of year's growth until the third year (1932) after the drought.

(3) *Length of life cycle of insects.* From these fluctuation studies the view has been obtained that the first brood of the year completes its life cycle quicker than the second, the second quicker than the third, and so on. Yet this does not hold good always; for example, it was shown that the first brood of *Rhabdophaga heterobia* in 1929 reached maturity in the same time as that in 1930, but was significantly slower than the second brood in 1929 and significantly quicker than the second brood in 1930. The weather acting on the availability of food supply probably is just as much responsible for these changes as it is through its action on the insects themselves.

Further, in the Arabis midge study the methods used have revealed the unexpected fact that relatively more males pupated in the soil than in the galls. Under the circumstances of the experiment this indicated a shorter life cycle in the case of the males. Finally the different proportion from season to season of the last brood of the year emerging the same year is interesting. This occurs in both *Dasyneura arabis* and *D. pyri.*

(*c*) *Effect of weather acting through its effect on the insects' enemies, e.g. their parasites.*

(1) *Differential effect on host and parasite.* On two occasions there has been a sudden rise in numbers of midges and a corresponding fall in numbers of parasites. In 1929 the number of *Dasyneura alopecuri* was much higher than normal and there were far fewer parasites than usual. In the previous brood, i.e. in 1928, the peak emergence of the parasites was earlier than that of the midges instead of about three weeks later. There had been a different effect on the midges and their parasites. It is considered probable that this alteration from normal relative emergence times of host and parasites was directly responsible for the outbreak of midges recorded for 1929. It has also been suggested that some such reason accounts for the outbreak of *Rhabdophaga*

heterobia in 1933, there being almost double the usual number of midges present and the parasitism being about 14 per cent. instead of between 50 and 60 per cent.

It would certainly repay anyone to study under controlled conditions the possible differential effects of physical factors on host and parasite. Lund (**15**) has recently succeeded in demonstrating under laboratory conditions a differential effect of such factors upon host and parasite in some work on *Trichogramma minutum*. He found that the factors producing death of the parasite were not necessarily identical with those killing the host eggs. In the subsidiary study on emergence factors it has been shown that there seems to be a tendency for the parasites of *Rhabdophaga heterobia* to be less affected by cold than the midges themselves.

(2) *Length of life cycle of host compared with that of the parasite.* In the study on *Dasyneura pyri* it has been recorded that *Misocyclops marchali* Kieff., its parasite, occurred three years in the over-wintering generations, three years in the second generation of the particular year, but not once in the first generation. Further, it has been shown that whereas there was frequently a partial emergence of midges in the late summer only once was there a partial emergence of parasites. This delayed emergence of the parasites tends to show that the parasite's life cycle is longer than that of its host and also indicates only an incomplete adjustment of parasite to host. This may mean a recent change of host on the part of the parasite. Dumbleton (**14**) has, in New Zealand, also observed that the parasite emerges too late to parasitise the eggs which give rise to the first brood of the summer.

4. The prediction of outbreaks of insect pests.

It is much too soon to start predicting outbreaks, but in the case of the wheat-blossom midges advantage has been taken of the Ministry of Agriculture's Monthly Reports scheme, whereby its advisory officers send in observational reports on the abundance or scarcity of certain well-known pests. They used to record *Contarinia tritici* and *Sitodiplosis mosellana* as the wheat midges, and it has been possible to suggest a rhythmic periodic fluctuation (**13**). This gave a peak of abundance occurring about every fourth to sixth year. More recently (**12**), using in addition seven years' data from these studies, a prediction was made that the next peak would be about the year 1937. It remains to be seen whether this is correct or not. The data obtained in 1934 and 1935 have supported it.

5. Summary and conclusions.

It must be apparent that the only basis for such studies as these is a sound knowledge of the bionomics of the species under investigation. Time after time some detail of life history has assumed a greater importance than would have been expected. The methods used reveal the larger fluctuations in numbers and also have provided a galaxy of hints as to the factors involved. As an indicator of points needing further investigation they are ideal. As a means of collecting data for the forecasting of outbreaks of insects it is felt that these studies will, if continued over a long period, prove satisfactory. They should reveal rhythmic fluctuations, if there are any, as well as irregular ones.

It is claimed that such studies should prove more satisfactory than purely phenological observations, because, although it is possible for one person to deal with only a few species of insects, the information obtained is quantitative and throws out definite hints of the causes of fluctuations in the field instead of merely indicating rises and falls in abundance. This is also true when these studies are compared with experiments carried out under rather arbitrarily controlled conditions. The latter should follow rather than precede such studies.

One aim of the work has been to indicate that, if several workers undertook similar studies, much better and far-reaching results would be obtained. These studies need not be full-time occupations when once the details have been arranged and tried out. There could be a central research station where such studies could be planned in the first instance, as there is a large amount of research work entailed.

It is essential that the subject be chosen carefully. From an economic point of view the insect ought to be a pest, and this should not greatly detract from the ultimate value or interest of the work from wider aspects of biology. Having decided on the insect, methods should be standardised, and while not expecting them to be perfect they might well be allowed to remain constant throughout an initial period of five years or so. By this time the weaknesses in the methods would be apparent, and yet valuable data would have been collected. Then either the study could be stopped, or continued on the same basis or an improved one. This is the point at which the study could be initiated in several localities by several persons.

These studies on gall midges have now reached this stage. Only two of them are to be continued, that on the wheat-blossom midges and that on the button-top midge of willows. Several subsidiary studies suggested by this work are being taken in hand. Preparations are also being made to begin similar studies on other insects, such as the cabbage white fly and some cutworms or surface caterpillars. But before such work can be started the old point of a knowledge of the biology of the insects in question reappears. The methods to be adopted must have their foundation on this.

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