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# Changes in insect populations in the field in relation to preceding weather conditions

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An attempt has been made to measure changes in a mixed insect population under natural conditions in the field, and to see to what extent they are quantitatively related to previous weather conditions.

To obtain a measure of the population, insects were caught in a light-trap at Harpenden, about 25 miles north of London, every night for four years from 1933 to 1937, and again for four years from 1946 to 1950. In all about 1,440,000 insects, mostly Diptera, were captured on about 2850 nights.

The measure of population level in any one month was the geometric mean catch per night, obtained by calculating the arithmetic mean of log $(n+1)$, where $n$ is the number of insects caught in one night. This figure has to be corrected for the effect of prevailing weather conditions on activity.

The departure of each month, on the logarithmic scale, from the average value for all repetitions of the same month gives a measure of how the population in this particular month is differing from the level to be expected for that time of the year.

These departures were then made the basis of six-factor multiple regressions, in which the population change was the dependent variable, and the rainfall and minimum temperature departures from normal in each of the three preceding months were the independent variables.

It is shown that a very high proportion of the mean changes of the population in the field can be accounted for by the effect of rainfall and minimum temperature in the three previous months.

An examination of the regressions in the different seasons shows that rainfall has a high positive effect in the summer and autumn but little or no effect in the winter. Minimum temperature, on the contrary, has its lowest effect in the summer, so that the relation between population and minimum temperature one month previous is negative in the summer, and with temperature two months previous is negative in the autumn.

The analysis of the available data has so far only been carried out on the total insect population, against rainfall and minimum temperature. Work is continuing on other weather conditions, other time intervals, and also on special groups of insects, but it is unlikely that the method can be applied with any great accuracy in the near future to single species of insects.

## Introduction

The problem of measuring and accounting for changes in animal populations has attracted considerable interest for many years, both from the purely ecological point of view, and also in relation to the economic aspect of outbreaks of insect pests. The problem is extremely complex and in the past has been studied chiefly by simplification—and at times perhaps over-simplification—by examining the behaviour of relatively small populations of very few species under controlled laboratory conditions. The development of statistical methods of analysis for biological data made it seem possible, however, to attack this problem direct as it occurs in the field, provided that a sufficient number of population measurements could be obtained capable of being expressed numerically.

In general short-period population changes are caused by changes either in weather conditions, or in the abundance of food supply, or in the numbers of natural enemies; that is to say by changes in the physical or in the biological environment of the animals concerned. But the change in food supply or in the number of enemies must in itself also be partly dependent on earlier weather conditions; so that either directly or indirectly previous weather conditions are likely to play a considerable part in determining the changes and level of animal populations. In the case of the relatively short-lived insects, with the rapid fluctuations resulting from their high birth-rate and high death-rate, the changes might be sufficiently definite and frequent to be amenable to statistical analysis.

It was therefore necessary to find some simple method of numerically sampling an insect population at frequent intervals over long periods in the field, and with an accuracy comparable with that of the meteorological observations already available for temperature, humidity, wind and other rapidly varying factors of the physical environment. It was decided that for practical convenience an electric light trap for catching nocturnal flying insects had considerable advantages, and a trap of this type, which had previously been successfully used for catching large numbers of insects in Egypt, was adapted for the purpose. Except for very small details, no change was made in the position or construction of the trap, or in its source of illumination (a 200 W bulb) through the whole period of observations.

It is, of course, recognized that only nocturnal phototropic insects were captured, but we have no reason to believe that because an insect is phototropic it therefore behaves differently from others in relation to weather conditions; in fact, we consider that the trap gives a sample which is 'random' for the purposes of this investigation.

A description of the trap will be found in Williams (1948). It was placed about $3\frac{1}{2}$ ft. (1 m.) above the ground in the open fields at Rothamsted Experimental Station, which is about 25 miles north of London. The immediate surroundings of the trap were unusually stable from an agricultural point of view. It was situated on a small footpath running north and south. On the whole of the east of this was an experimental field of 8 acres known as 'Barnfield', on which mangolds are grown every year; to the west and south-west was permanent grassland with an occasional group of trees and two grass tennis courts; to the north-west was a small orchard which was moderately well grown when the trap was started in 1933; but this was, unfortunately, cut down in February 1950 just three months before the trapping finished. This probably has had a disturbing effect on the catches in the last three months.

The district is undulating chalk overlaid with clay and there is very little standing water. A small artificial pond existed in the first four years about 200 yards to the east; but this was drained in the second period. The very small proportion of aquatic insects captured at any time indicates that this had probably little effect on the total captures.

Insects were caught almost every night from March 1933 to February 1937 and again from May 1946 to April 1950 inclusive.

In the first four years, about 850,000 insects were caught on 1407 nights. The number per night varied very greatly from zero on many nights to 73,000 on the night of 30 June 1935.

After a gap of nine years, trapping was resumed again in May 1946 on the same spot with the same trap, and carried on for a second period of four years, during which 582,000 insects were captured on 1440 nights, with a maximum of 17,000 in one night and one period of 48 days (from 21 January to 10 March 1947) without a single insect.

In the first four years 86·7 % of the catch was Diptera, 10·3 % Lepidoptera, and only 3 % all the other orders together. Full details will be found in Williams (1939, p. 87). In the second four years 86·0 were Diptera, 9·7 % Lepidoptera and 4·3 % all the other orders.

Since all the evidence indicates that changes in catch from night to night are of a geometric nature and not arithmetic (see Williams 1937), for statistical purposes the catches each night are expressed as logarithms, and (to avoid the difficulty over zero catches) the form log $(n+1)$ is used. The log is calculated only to the second decimal place which gives an accuracy of about 2 %, which is quite sufficient for these biological observations.

The catch each night is dependent on variations in the population and in activity. The latter is dependent on immediate weather conditions, such as maximum and minimum temperature, wind, humidity, night cloud, etc., which factors are themselves also interrelated. The catch also has a periodic change corresponding to the lunar cycle, with larger catches near new moon and smaller catches near full moon (see Williams 1936). This has, however, little effect on the monthly mean catches which form the basis of the present discussion.

Both graphical and statistical methods have shown that arithmetical changes in maximum and minimum temperature, and in wind velocity, produce geometric changes in the catch; thus by the statistical method of partial regressions the effect on log catch (i.e. the percentage effect) of unit changes in maximum and minimum temperature and in wind can be calculated. If these are called $r_1$, $r_2$ and $r_3$, then the relation between catch, population and activity is given by:

Log catch varies as log population $+r_1$ (max. temp.) $+r_2$ (min. temp.) $+r_3$ (wind group), etc.

By taking as a basis of calculation the difference between catches on successive days, the effect of population changes is reduced to a minimum, and in this way the values of the partial regressions for activity have been calculated for each month of the first four years. They show little or no evidence of any seasonal change. The results are given in table 1 (for fuller details see Williams 1940, p. 294). These regressions can be restated in the form that the catch is doubled by a rise in minimum temperature of the night of 4·3° F (2·4° C); or by a rise of 13° F (7·2° C) in the maximum temperature of the previous day; or by a fall in wind of just over two groups.

Table 1

| factor | regression as log | regression as percentage |
|---|---|---|
| min. temperature: | | |
| per ° F | +0·070 | 116 |
| per ° C | +0·126 | 134 |
| max. temperature: | | |
| per ° F | +0·023 | 105 |
| per ° C | +0·041 | 110 |
| wind per group* | −0·144 | 72 |

* Wind was divided into six somewhat arbitary groups with velocities, during the period of the working of the trap, as follows: I, dead calm; II, up to 2 m.p.h.; III, 2 to 5 m.p.h.; IV, 5 to 10 m.p.h.; V, 10 to 20 m.p.h.; and VI, over 20 m.p.h. (see Williams 1940, p. 278). Kilometre values are as follows: II, up to 3; III, 3 to 8; IV, 8 to 16; V, 16 to 32; VI, over 32 km./hr.

The independent effect of increase of population and increase of activity, and the possibility of correcting for the latter so as to estimate changes in the former, can be shown diagrammatically if one takes the simplified case in which activity is assumed to depend only on a single factor, say minimum temperature. Figure 1*A* shows as a scatter diagram an imaginary series of ten observations in which the minimum temperature for each night is plotted against the log catch. The mean catch and temperature is shown by the cross X, and the regression by the diagonal line. This particular regression line indicates that a rise of temperature of 1° F is associated with an increase of 0·07 in the log catch.

If each of the nights had been 2° F warmer, but with the same population, the log catch on each night would have been increased by 0·14 due to increased activity, and the scatter diagram under these conditions would be shown by the heavy dots in figure 1*B*. The mean will thus have moved along the regression line by the distance corresponding to a rise of 2° F.

If, on the other hand, the population had doubled without any change in temperature each night's log catch would be 0·30 higher, as shown in figure 1*C*. In this case the mean will have moved *horizontally* by a distance equal to 0·30, and the new regression line through the mean will be as shown by the heavy line.

What normally happens is that both population and activity vary, so the old mean at $M_1$ (figure 1 *D*) moves to $M_2$. In this case, if we know the regression for activity on temperature, a correction can be made bringing the mean along the regression line to $M_3$. Thus the population change is measured by the horizontal distance $M_1 M_3$, between the two regression lines.

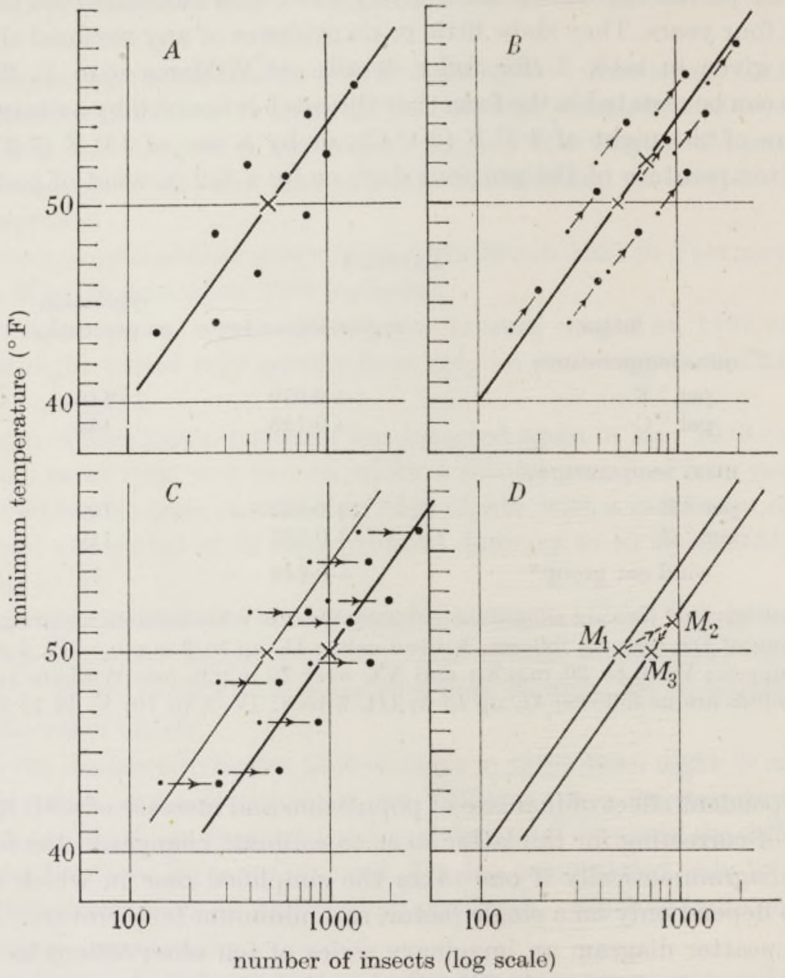



FIGURE 1. Diagrammatic representation of changes in the scatter diagram showing the relation between log catch and minimum temperature when either the temperature or the population is independently varied.

An actual example is shown in figure 2, which gives the log catch and minimum temperatures on each night in May 1934 and May 1936, together with the means and regressions. It will be seen that, considering other factors as 'error', the mean log population in 1936 was about 0·30 above 1934, or about double in numbers.

It is not possible to show diagrammatically the simultaneous correction for several factors affecting activity, but essentially the process is a repetition of the above.

The method adopted is as follows:

For each month the successive night's catches ($n$) are converted to log $(n+1)$, and the mean log $(n+1)$ per night is calculated. This is (except for the complication of the added 1) the logarithm of the geometric mean.

For any one month of the year, say March, the four values of the mean log catch per night in the four years are tabulated (table 2, line 1).

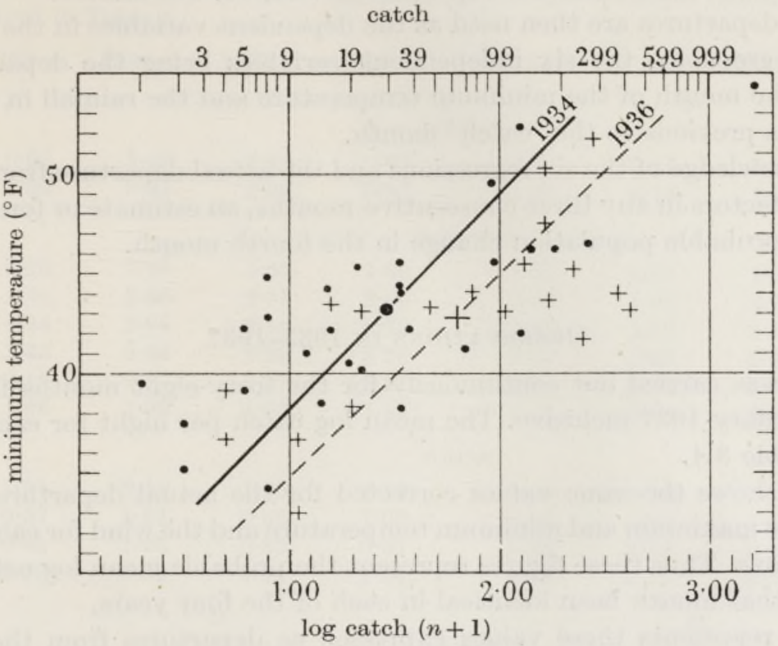



FIGURE 2. Scatter diagram showing the relation between minimum temperature and log catch for the month of May in the years 1934 (●) and 1936 (+). The horizontal shift of the regression lines indicates a population change.

TABLE 2. PROCESS OF CALCULATING DIFFERENCES IN POPULATION LEVEL IN MARCH OF THE FOUR YEARS 1933–1936

| | | 1933 | 1934 | 1935 | 1936 |
|---|---|---|---|---|---|
| (1) mean log catch per night | | 0·97 | 0·56 | 1·13 | 0·87 |
| Expected activity departure due to: | | | | | |
| (2) minimum temperature | $+0\cdot1 \times +0\cdot070 =$ | $+0\cdot007$ | — | — | — |
| (3) maximum temperature | $+3\cdot3 \times +0\cdot023 =$ | $+0\cdot076$ | — | — | — |
| (4) wind | $-0\cdot27 \times -0\cdot144 =$ | $+0\cdot039$ | — | — | — |
| (5) total expected departure | | +0·122 | −0·29 | −0·01 | +0·16 |
| (6) log catch corrected for activity, i.e. (1) − (5) | | 0·85 | 0·85 | 1·14 | 0·71 |
| (7) departure of (6) from 4-year average (0·88) | | −0·03 | −0·03 | +0·26 | −0·17 |

The expected departures from the normal for that month, due to the activity effect of departures from the normal of maximum and minimum temperatures and wind (lines 2, 3 and 4), are added together (line 5), giving a correction factor which, when subtracted from the mean log catch, gives the value that the mean catch would have been had these weather conditions been average in that month (line 6). These corrected values of mean catch are then expressed as departures from their normal (line 7). These residual departures are assumed to be chiefly due to population changes.

Thus if the mean population for March is considered to be 100, then in the four successive years this month had populations expressed on the log scale as 1·97, 1·97, 2·26 and 1·83—or in terms of percentage: 94, 94, 182 and 68.

These log departures are then used as the dependent variables in the calculation of partial regressions, the six independent variables being the departures from normal for the month of the minimum temperature and the rainfall in each of the three months previous to the 'catch' month.

From a knowledge of the six regressions and the actual departure from normal of the weather factors in any three consecutive months, an estimate or forecast can be made of the probable population change in the fourth month.

## Observations in 1933–1937

Trapping was carried out continuously for the forty-eight months from March 1933 to February 1937 inclusive. The mean log catch per night for each month is shown in Table 3*A*.

Table 3*B* shows the same values corrected for the actual departures from the average of the maximum and minimum temperature and the wind for each month as described above. Thus these figures represent the probable mean log catch had the weather for that month been identical in each of the four years.

Table 3 *C* represents these values expressed as departures from the four-year average for each month. These are presumed to represent the population changes that have occurred between the same month in different years, or in other words the departure of the population from the normal for that time of the year.

These 48 values, divided as shown into 24 summer months (May to October) and 24 winter months (November to April), formed the basis of two multiple regression calculations with the minimum temperature and the rainfall of each of the three previous months (expressed also as departures from the 4-year mean) as the independent variables.

As a result of these calculations the partial regressions of table 4 were obtained. These logarithmic values can be expressed in multiplication factors as in table 5.

From these regressions and the actual departures of the rainfall and minimum temperature in each successive three months, the expected departure—or population change—in the fourth month can be calculated. These values are shown in table 3*D*.

Thus table 3*C* is a measure of population departures from normal obtained directly from the trap catches, while 3*D* is an estimate of the same changes obtained by calculation from the regressions and the weather conditions of the three previous months. Assuming the regressions to be known, the values in 3*D* can be calculated on the first day of the month for which the population change is estimated, that is, one month before the actual log catch can be known.

Table 3. Data for the catch in the first four years (1933–1935)

*A*. Mean log catch of all insects per night for each month of the four years.

*B*. The same values corrected, as shown in table 2, for the departures from the normal of maximum and minimum temperature and wind force for the same month; that is to say, corrected as far as possible for the effects of activity.

*C*. The corrected values in *B* expressed as departures from the average value for each month in the four successive years.

*D*. Estimates of expected departures from the mean for each month calculated from the regressions given in Table 4.

| | 1933–4 | 1934–5 | 1935–6 | 1936–7 | 1933–4 | 1934–5 | 1935–6 | 1936–7 |
|---|---|---|---|---|---|---|---|---|
| | | *A* | | | | *B* | | |
| | | | | winter | | | | |
| Mar. | 0·97 | 0·56 | 1·13 | 0·87 | 0·85 | 0·85 | 1·14 | 0·71 |
| Apr. | 1·23 | 0·91 | 1·00 | 0·87 | 1·11 | 0·78 | 1·01 | 1·11 |
| | | | | summer | | | | |
| May | 2·24 | 1·47 | 1·62 | 1·80 | 1·98 | 1·51 | 1·92 | 1·72 |
| June | 2·36 | 2·36 | 2·71 | 2·60 | 2·34 | 1·45 | 2·72 | 2·51 |
| July | 2·74 | 2·78 | 3·15 | 2·78 | 2·62 | 2·70 | 3·11 | 3·04 |
| Aug. | 2·46 | 2·24 | 2·99 | 3·25 | 2·31 | 2·45 | 2·89 | 3·28 |
| Sept. | 2·19 | 2·17 | 2·37 | 2·81 | 2·09 | 2·16 | 2·55 | 2·73 |
| Oct. | 1·66 | 1·99 | 1·96 | 1·84 | 1·57 | 1·88 | 2·06 | 1·94 |
| | | | | winter | | | | |
| Nov. | 1·91 | 2·18 | 1·73 | 1·79 | 1·90 | 2·02 | 1·72 | 1·96 |
| Dec. | 0·57 | 1·94 | 0·88 | 1·02 | 0·98 | 1·38 | 1·07 | 0·98 |
| Jan. | 0·41 | 1·25 | 0·85 | 0·97 | 0·53 | 1·12 | 0·92 | 0·90 |
| Feb. | 0·30 | 0·92 | 0·51 | 1·14 | 0·41 | 0·77 | 0·77 | 0·98 |

| | 1933–4 | 1934–5 | 1935–6 | 1936–7 | 1933–4 | 1934–5 | 1935–6 | 1936–7 |
|---|---|---|---|---|---|---|---|---|
| | | | *C* | | | *D* | | |
| | | | | winter | | | | |
| Mar. | −0·03 | −0·03 | +0·26 | −0·17 | −0·15 | −0·16 | +0·09 | −0·11 |
| Apr. | +0·11 | −0·22 | +0·01 | +0·11 | +0·04 | −0·15 | −0·02 | +0·08 |
| | | | | summer | | | | |
| May | +0·20 | −0·27 | +0·12 | −0·06 | −0·04 | −0·14 | +0·12 | −0·10 |
| June | −0·17 | −0·06 | +0·21 | ± 0 | +0·04 | −0·05 | +0·22 | −0·13 |
| July | −0·24 | −0·16 | +0·25 | +0·18 | −0·17 | −0·16 | +0·18 | +0·15 |
| Aug. | −0·41 | −0·29 | +0·15 | +0·48 | −0·25 | −0·23 | −0·08 | +0·56 |
| Sept. | −0·30 | −0·23 | +0·16 | +0·34 | −0·28 | −0·09 | −0·07 | +0·45 |
| Oct. | −0·29 | +0·02 | +0·20 | +0·08 | −0·17 | −0·13 | +0·10 | +0·08 |
| | | | | winter | | | | |
| Nov. | ± 0 | +0·12 | −0·18 | +0·06 | +0·01 | +0·09 | −0·05 | −0·07 |
| Dec. | −0·12 | +0·27 | −0·03 | −0·12 | −0·01 | +0·5 | +0·09 | −0·14 |
| Jan. | −0·34 | +0·25 | +0·4 | +0·03 | −0·29 | +0·34 | −0·06 | −0·02 |
| Feb. | −0·31 | +0·05 | +0·05 | +0·21 | −0·23 | +0·14 | −0·01 | +0·10 |

Table 4

| | winter | summer |
|---|---|---|
| minimum temperature (° F) | | |
| 3 months previous | −0·014 | +0·013 |
| 2 months previous | +0·015 | + 0 |
| 1 month previous | +0·046 | −0·024 |
| rainfall in inches | | |
| 3 months previous | +0·019 | +0·070 |
| 2 months previous | +0·007 | +0·108 |
| 1 month previous | +0·010 | +0·092 |

Table 5

| | |
|---|---|
| summer months (May to October) | |
| In the 3rd previous month: | |
| each ° F min. temp. above normal multiplies population by | 1·031 |
| each inch of rain above normal multiplies population by | 1·174 |
| In the 2nd previous month: | |
| each ° F min. temp. above normal divides population by | 1·001 |
| each inch of rain above normal multiples the population by | 1·282 |
| In the previous month: | |
| each ° F min. temp. above normal divides population by | 1·056 |
| each inch of rain above normal multiplies population by | 1·235 |
| winter months (November to April) | |
| In the 3rd previous month: | |
| each ° F min. temp. above normal divides population by | 1·032 |
| each inch of rain above normal multiplies population by | 1·046 |
| In the 2nd previous month: | |
| each ° F min. temp. above normal multiplies the population by | 1·035 |
| each inch of rain above normal multiplies the population by | 1·016 |
| In the previous month: | |
| each ° F min. temp. above normal multiplies the population by | 1·111 |
| each inch of rain above normal multiplies the population by | 1·023 |

Figure 3 shows diagrammatically the observed and calculated values from table 3, expressed as percentage of the normal population for each month, which is taken as 100 (see also table 8, p. 142).

Taking first the observed values in figure 3 it will be seen that the first 3 months of trapping gave populations rising slightly from normal for the time of the year. Then followed a period of seventeen months (two summers and a winter) with populations nearly always well below normal. At the beginning of the winter of 1934–5 populations rose and remained above normal till the following winter, when they were mostly below normal from November till June. Then followed a spectacular increase in population with August three times normal. In this August over 105,000 insects were captured as compared with 103,500 in the whole of the year 1934–5. This increase was short-lived, and by October populations were again normal for the time of the year.

Turning to the estimates from the regressions we find that although there are a few poor estimates (particularly March 1933, and August and September 1935), on the whole every major change in population has been indicated. The long period of below-normal values is shown with only one month at the beginning and one at the end incorrect; even the temporary return to normal in November 1933 is correctly shown. The above-normal values for November 1934 to October 1935 are correctly indicated except for the two exceptions mentioned above. And, most interesting, the sudden great increase in July, August and September 1936 is shown correctly in relative value if not exactly in size, together with the return almost to normal in October.

The difference between the winter and summer regressions indicate a greater importance of rainfall in summer than in winter, and a greater importance of temperature in winter than in summer. In the Harpenden district, about 25 miles

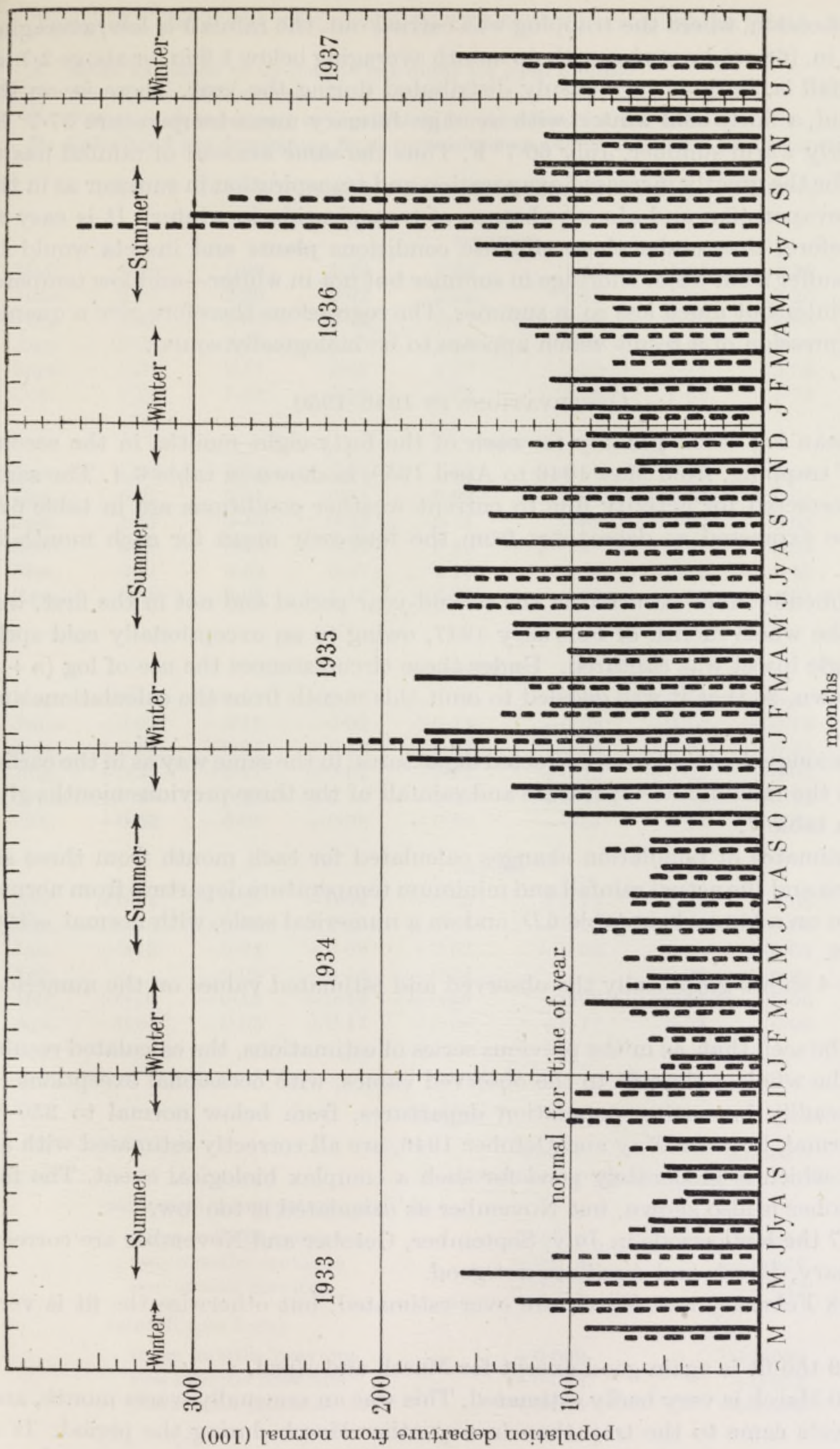



FIGURE 3. Observed and calculated departures from normal for the insect population each month from March 1933 to February 1937. Observed values = solid line; calculated values = broken line.

north of London, where the trapping was carried out, the rainfall is low, averaging about 27 in. (68 cm.) per year with no month averaging below 1·9 in. or above 2·7 in. The rainfall is, in fact, very evenly distributed during the year. There is, on the other hand, a fairly cold winter, with average January mean temperature 37·7° F; and a fairly warm summer, July 60·7° F. Thus the same amount of rainfall has to provide for the greatly increased evaporation and transpiration in summer as in the reduced evaporation and almost absence of transpiration in winter. It is easy to see, therefore, that under these climatic conditions plants and insects would be likely to suffer from water shortage in summer but not in winter—and low temperature in winter but much less so in summer. The regressions therefore give a quantitative expression of a result which appears to be biologically sound.

## Observations in 1946–1950

The mean log catch per day for each of the forty-eight months in the second period of trapping, from May 1946 to April 1950, is shown in table 6*A*. The same figures corrected for activity due to current weather conditions are in table 6*B*, and these expressed as departures from the four-year mean for each month in table 6*C*.

One difficulty, that occurred in the second-year period and not in the first, was that in the whole month of February 1947, owing to an exceptionally cold spell, not a single insect was captured. Under these circumstances the use of log $(n+1)$ breaks down, so that it was decided to omit this month from the calculations and forecasts.

Regressions calculated from corrected departures, in the same way as in the earlier series, on the minimum temperature and rainfall of the three previous months give results in table 7.

The estimates of population changes calculated for each month from these six regressions and the actual rainfall and minimum temperature departure from normal are shown on a log scale in table 6*D*, and on a numerical scale, with normal $=100$, in table 8.

Figure 4 shows graphically the observed and estimated values on the numerical scale.

It will be seen that, as in the previous series of estimations, the calculated results give on the whole a close fit to the observed values, with occasional exceptions.

The steadily increasing population departures, from below normal to 350 % above normal, between May and October 1946, are all correctly estimated with an accuracy which is moderately good for such a complex biological event. The fall after October is also shown, but November as calculated is too low.

In 1947 the low periods in July, September, October and November are correct, but January, March and April are not good.

In 1948 February and March are over-estimated, but otherwise the fit is very close.

In 1949 the fit is again good except for March and April.

In 1950 March is very badly estimated. This was an unusually warm month, and more insects came to the trap than in any other March during the period. It is

Table 6. Data for the catch in the second four years (1946–1950)

*A*. Mean log catch of all insects per night for each month.
*B*. The same values corrected for activity.
*C*. Values in *B* expressed as departures from normal for the month.
*D*. Calculated log departures from regressions on previous rainfall and temperature.

| | 1946–7 | 1947–8 | 1948–9 | 1949–50 | 1946–7 | 1947–8 | 1948–9 | 1949–50 |
|---|---|---|---|---|---|---|---|---|
| | | *A* | | | | *B* | | |
| | | | | summer | | | | |
| May | 1·25 | 1·98 | 1·28 | 1·62 | 1·43 | 1·66 | 1·31 | 1·71 |
| June | 2·03 | 2·20 | 2·02 | 2·42 | 2·15 | 1·99 | 2·20 | 2·35 |
| July | 2·85 | 2·97 | 2·73 | 2·47 | 2·47 | 2·83 | 2·85 | 2·33 |
| Aug. | 2·68 | 2·86 | 2·53 | 2·56 | 2·97 | 2·55 | 2·68 | 2·44 |
| Sept. | 2·54 | 2·17 | 2·44 | 2·46 | 2·80 | 2·17 | 2·58 | 2·08 |
| Oct. | 2·29 | 1·62 | 1·56 | 1·62 | 2·32 | 1·69 | 1·71 | 1·39 |
| | | | | winter | | | | |
| Nov. | 1·74 | 0·82 | 1·33 | 1·12 | 1·66 | 0·89 | 1·21 | 1·23 |
| Dec. | 0·35 | 0·91 | 0·74 | 0·98 | 0·85 | 0·83 | 0·55 | 0·77 |
| Jan. | 1·17 | 0·43 | 0·83 | 0·71 | 0·66 | 0·30 | 0·63 | 0·56 |
| Feb. | 0·00 | 0·46 | 0·59 | 0·40 | — | 0·27 | 0·24 | 0·02 |
| Mar. | 0·21 | 0·55 | 0·57 | 1·10 | 0·77 | 0·46 | 0·18 | 1·01 |
| Apr. | 0·63 | 0·93 | 1·17 | 0·61 | 0·77 | 0·79 | 1·01 | 0·76 |
| | | *C* | | | | *D* | | |
| | | | | summer | | | | |
| May | −0·10 | +0·13 | −0·22 | +0·18 | −0·15 | +0·10 | −0·10 | +0·15 |
| June | −0·02 | −0·18 | 0·03 | +0·18 | −0·08 | −0·14 | +0·12 | +0·11 |
| July | +0·20 | +0·07 | +0·12 | −0·43 | +0·04 | +0·04 | +0·21 | −0·30 |
| Aug. | +0·31 | −0·11 | +0·02 | −0·22 | +0·15 | +0·01 | +0·05 | −0·21 |
| Sept. | +0·40 | −0·23 | +0·18 | −0·32 | +0·43 | −0·33 | +0·10 | −0·20 |
| Oct. | +0·55 | −0·08 | −0·06 | −0·38 | +0·51 | −0·12 | +0·02 | −0·40 |
| | | | | winter | | | | |
| Nov. | +0·41 | −0·35 | −0·04 | −0·02 | +0·15 | −0·23 | +0·03 | +0·05 |
| Dec. | +0·10 | +0·08 | −0·20 | +0·02 | +0·16 | −0·15 | −0·01 | −0·01 |
| Jan. | +0·12 | −0·24 | +0·09 | +0·02 | −0·04 | −0·10 | +0·03 | +0·11 |
| Feb. | — | −0·09 | −0·12 | −0·34 | — | +0·06 | −0·05 | −0·05 |
| Mar. | +0·16 | −0·15 | −0·43 | +0·40 | −0·03 | +0·07 | −0·06 | +0·03 |
| Apr. | −0·07 | −0·05 | +0·17 | −0·08 | +0·17 | −0·05 | −0·06 | −0·06 |

Table 7

| | winter (November to April) | summer (May to October) |
|---|---|---|
| minimum temperature (per ° F) | | |
| three months previous | −0·016 | +0·014 |
| two months previous | −0·013 | +0·028 |
| one month previous | +0·011 | −0·032 |
| rainfall (per inch) | | |
| three months previous | +0·039 | +0·058 |
| two months previous | +0·038 | +0·075 |
| one month previous | +0·036 | +0·194 |

Table 8. Observed and calculated values of population departures in the two series of observations 1933–37 and 1946–50 on an arithmetic scale—Normal = 100.

1933–1937

| | 1933–4 | | 1934–5 | | 1935–6 | | 1936–7 | |
|---|---|---|---|---|---|---|---|---|
| | obs. | calc. | obs. | calc. | obs. | calc. | obs. | calc. |
| | | | | winter | | | | |
| Mar. | 93 | 71 | 93 | 69 | 182 | 123 | 68 | 78 |
| Apr. | 129 | 110 | 60 | 71 | 102 | 96 | 129 | 120 |
| | | | | summer | | | | |
| May | 159 | 91 | 54 | 72 | 132 | 132 | 87 | 79 |
| June | 68 | 110 | 87 | 89 | 162 | 166 | 100 | 74 |
| July | 58 | 68 | 69 | 69 | 178 | 151 | 152 | 141 |
| Aug. | 39 | 56 | 51 | 59 | 141 | 83 | 302 | 363 |
| Sept. | 50 | 52 | 59 | 81 | 145 | 85 | 219 | 282 |
| Oct. | 51 | 68 | 105 | 74 | 159 | 126 | 120 | 120 |
| | | | | winter | | | | |
| Nov. | 100 | 102 | 132 | 123 | 66 | 89 | 115 | 85 |
| Dec. | 76 | 98 | 186 | 112 | 93 | 123 | 76 | 72 |
| Jan. | 46 | 51 | 178 | 219 | 110 | 87 | 107 | 96 |
| Feb. | 49 | 59 | 112 | 138 | 112 | 98 | 162 | 126 |

1946–1950

| | 1946–7 | | 1947–8 | | 1948–9 | | 1949–50 | |
|---|---|---|---|---|---|---|---|---|
| | obs. | calc. | obs. | calc. | obs. | calc. | obs. | calc. |
| | | | | summer | | | | |
| May | 79 | 71 | 135 | 126 | 60 | 79 | 151 | 141 |
| June | 96 | 83 | 66 | 72 | 107 | 132 | 151 | 129 |
| July | 159 | 110 | 118 | 110 | 132 | 162 | 37 | 50 |
| Aug. | 204 | 141 | 78 | 102 | 105 | 112 | 60 | 62 |
| Sept. | 251 | 269 | 59 | 47 | 151 | 126 | 48 | 63 |
| Oct. | 355 | 324 | 83 | 76 | 87 | 105 | 42 | 40 |
| | | | | winter | | | | |
| Nov. | 247 | 242 | 45 | 59 | 91 | 107 | 96 | 112 |
| Dec. | 126 | 145 | 120 | 71 | 63 | 98 | 105 | 98 |
| Jan. | 132 | 91 | 58 | 79 | 123 | 107 | 105 | 121 |
| Feb. | — | — | 81 | 115 | 76 | 89 | 46 | 89 |
| Mar. | 145 | 93 | 71 | 118 | 37 | 87 | 251 | 107 |
| Apr. | 85 | 148 | 89 | 89 | 131 | 87 | 83 | 87 |

possible that not sufficient correction has been made for activity. Also this was just after the destruction of the orchard (mentioned above) which undoubtedly upset the environment.

It will be noticed that most of the poor estimates are in the 'winter' period, and it is possible that the January and March 1947 results are affected by the exceptional cold spell with an unusually large number of 'zero' catches.

Estimation of population changes during the summer period is more accurate, probably owing to the higher numbers caught leading to greater accuracy in the calculations, and also to the definite higher regression values in the summer period.

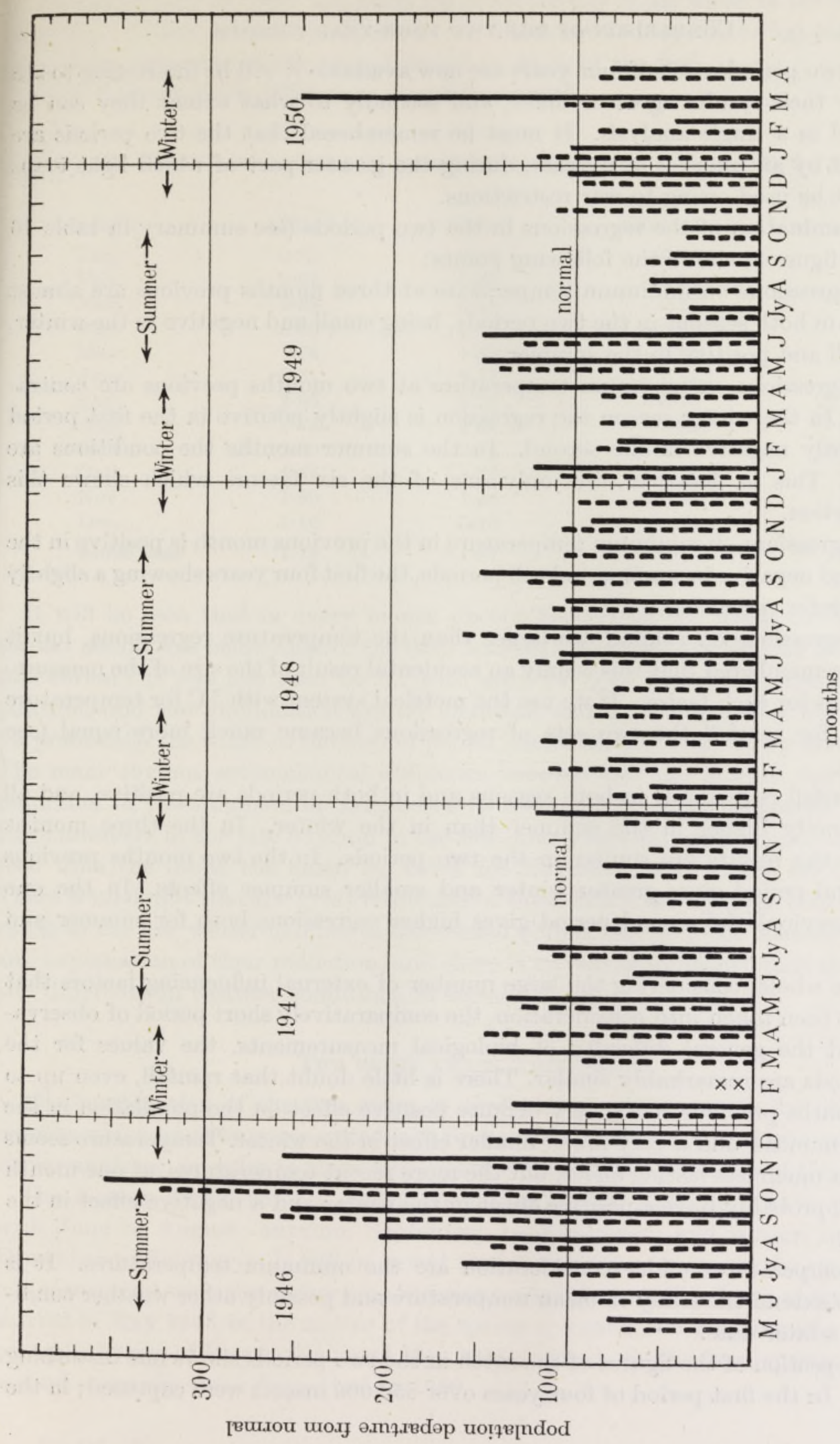



FIGURE 4. Observed and calculated departures from normal of the insect population each month from May 1946 to April 1950. Observed values = solid line; calculated values = dotted line.

### Comparison of the two four-year periods

Since two periods each of four years are now available it will be interesting to see first how their results agree or differ, and secondly to what extent they can be combined in a single analysis. It must be remembered that the two periods are separated by an interval of 9 years, during the greater part of which light traps could not be used owing to war restrictions.

An examination of the regressions in the two periods (see summary in table 10 and also figure 8) shows the following points:

The regressions on minimum temperature at three months previous are almost identical in both seasons in the two periods, being small and negative in the winter, and small and positive in the summer.

The regressions on minimum temperature at two months previous are contradictory. In the winter season the regression is slightly positive in the first period and slightly negative in the second. In the summer months the conditions are reversed. This is, however, the only one of the six factors which shows this contradiction.

The regressions on minimum temperature in the previous month is positive in the winter and negative in summer in both periods, the first four years showing a slightly higher winter regression.

The regressions on rainfall are larger than the temperature regressions, but it must be remembered that this is only an accidental result of the size of the measurement units for each factor. If we use the metrical system with ° C for temperature and cm. for rainfall the two sets of regressions became much more equal (see table 10).

All rainfall regressions in both seasons and in both periods are positive, and all are distinctly higher in the summer than in the winter. In the three months previous the results are similar in the two periods. In the two months previous the second period gives greater winter and smaller summer effects. In the one month previous the second period gives higher regressions both for summer and winter.

On the whole, considering the large number of external influencing factors that have not been taken into consideration, the comparatively short period of observation, and the general difficulty of biological measurements, the values for the two periods are remarkably similar. There is little doubt that rainfall, even up to three months previous, has a very definite positive effect on the population in the summer months, and a very much smaller effect in the winter. Temperature seems to have a much less lasting effect, but the more recent temperatures, at one month previous, probably have a positive effect in the winter and a negative effect in the summer.

The temperatures under consideration are the minimum temperatures. It is hoped to extend the study to mean temperature and possibly other weather conditions at a later date.

An inspection of the figures of the catch in the two periods shows one disturbing feature. In the first period of four years over 850,000 insects were captured; in the second period only 587,000. The mean log catch per day in the whole of the first four years was 1·72 and in the second period 1·47, which is 0·25 lower in the log, indicating an average reduction of the second period to 56 % of the first.

Table 9 shows these differences month by month.

TABLE 9. MEAN LOG CATCH PER NIGHT IN EACH MONTH FOR THE TWO PERIODS

| month | 1933–6 | 1946–9 | differences | 2nd period as % of 1st |
|---|---|---|---|---|
| Jan. | 0·87 | 0·54 | −0·33 | 47 |
| Feb. | 0·72 | 0·36 | −0·36 | 44 |
| Mar. | 0·88 | 0·61 | −0·27 | 54 |
| Apr. | 1·00 | 0·84 | −0·16 | 69 |
| May | 1·78 | 1·53 | −0·25 | 56 |
| June | 2·51 | 2·17 | −0·34 | 47 |
| July | 2·86 | 2·76 | −0·10 | 79 |
| Aug. | 2·74 | 2·66 | −0·08 | 83 |
| Sept. | 2·39 | 2·44 | +0·01 | 102 |
| Oct. | 1·86 | 1·77 | −0·09 | 81 |
| Nov. | 1·90 | 1·25 | −0·65 | 23 |
| Dec. | 1·10 | 0·75 | −0·35 | 45 |
| whole year | 1·72 | 1·47 | −0·25 | 56 |

It will be seen that in every month except September the mean catch in the second period was below that of the first, and that in the winter months November to February it was less than 50 %, with only 23 % in November. The trap, its position, and the illumination are all identical, and the surrounding fields were, for practically the whole of the second period, under similar crops to the first period. The main obvious entomological difference between the two catches was a great reduction in the numbers of Trichocera (winter gnats), which appeared in very large numbers in the late autumn in the first four years and even made, as will be seen from the table, the mean log catch for November above that for October. There is no doubt that the great reduction of these flies is a very large contributing cause to the low winter catches in the second period, but it is not possible to give any explanation of their reduction, and there is no reason to believe that there was any difference in weather conditions to account for it.

## THE EIGHT YEARS COMBINED

The combination of the two series of observations gives records for ninety-six months which have been separated into four seasons, instead of the two used in the earlier analyses, in order to show any seasonal cycle in the influence of the factors.

The seasons considered are spring, including March, April and May; summer, with June to August; autumn, September to November; and winter, including December to February. It will be noted that the divisions between the seasons do not correspond with the earlier classifications. As the second series of observations started in May 1946, in the middle of the spring grouping, the trapping was carried on until the end of May in 1950, and May 1946 omitted. So the four 'springs' in the second series are those from 1947 to 1950.

Further, in view of the great difference in average catch between the first four years and the second four years, already mentioned, it was decided to express the monthly departures from normal, not from the whole eight years average, but in each group of four years from its own mean. Thus no attempt is made to explain by the regressions any difference between the two series, only the variation within the series.

Table 10 shows the regressions on rainfall and minimum temperature in the three previous months calculated from the data available from the whole eight years in four seasons. Table 11 shows the observed and calculated population departures on a logarithmic scale, and table 12 shows the same on an arithmetic scale with the normal for the time of the year as 100.

Table 10. Summary of regressions, with metric system values

| | minimum temperature | | | rainfall | | |
|---|---|---|---|---|---|---|
| | 3 months previous | 2 months previous | 1 month previous | 3 months previous | 2 months previous | 1 month previous |
| | | for 1° F | | | for 1 in. | |
| four years 1933–6: | | | | | | |
| 6 summer months | +0·014 | −0·000 | −0·024 | +0·070 | +0·108 | +0·092 |
| 6 winter months | −0·014 | +0·015 | +0·046 | +0·019 | +0·007 | +0·010 |
| four years 1946–50: | | | | | | |
| 6 summer months | +0·014 | +0·028 | −0·032 | +0·057 | +0·075 | +0·194 |
| 6 winter months | −0·016 | −0·013 | +0·011 | +0·039 | +0·038 | +0·036 |
| eight years: | | | | | | |
| 3 spring months | −0·024 | +0·017 | +0·027 | +0·009 | −0·022 | +0·059 |
| 3 summer months | +0·007 | +0·012 | −0·049 | +0·054 | +0·086 | +0·116 |
| 3 autumn months | +0·028 | −0·051 | +0·004 | +0·081 | +0·071 | +0·092 |
| 3 winter months | −0·015 | +0·008 | +0·033 | +0·021 | +0·045 | +0·014 |
| | | for 1° C | | | for 1 cm. | |
| four years 1933–6: | | | | | | |
| 6 summer months | +0·025 | −0·001 | −0·043 | +0·028 | +0·043 | +0·036 |
| 6 winter months | −0·025 | +0·027 | +0·083 | +0·007 | +0·003 | +0·004 |
| four years 1946–50: | | | | | | |
| 6 summer months | +0·025 | +0·050 | −0·058 | +0·022 | +0·030 | +0·076 |
| 6 winter months | −0·029 | −0·023 | +0·020 | +0·015 | +0·015 | +0·014 |
| eight years: | | | | | | |
| 3 spring months | −0·043 | +0·031 | +0·049 | +0·004 | −0·009 | +0·023 |
| 3 summer months | +0·013 | +0·022 | −0·088 | +0·021 | +0·034 | +0·046 |
| 3 autumn months | +0·050 | −0·092 | +0·007 | +0·032 | +0·028 | +0·036 |
| 3 winter months | −0·027 | +0·014 | +0·059 | +0·008 | +0·018 | +0·006 |

The latter figures are shown as a histogram in figure 5. It should be remembered in using this scale that it tends to exaggerate the differences between the larger populations and to minimize those in the below-normal values.

An examination of the figures and diagram shows a fit between observed and calculated not very different from the previous calculations for each series of four years separately. This is to be expected in view of the close similarity of the

TABLE 11. OBSERVED AND CALCULATED POPULATION DEPARTURES FROM NORMAL FOR THE TIME OF THE YEAR ON A LOGARITHMIC SCALE. EIGHT YEARS IN FOUR SEASONS

| | 1933–4 | 1934–5 | 1935–6 | 1936–7 | 1946–7 | 1947–8 | 1948–9 | 1949–50 | 1950 |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | observed | | | | |
| spring | | | | | | | | | |
| Mar. | −0·03 | −0·03 | +0·27 | −0·17 | — | +0·16 | −0·15 | −0·43 | +0·40 |
| Apr. | +0·11 | −0·22 | +0·01 | +0·11 | — | −0·07 | −0·05 | +0·17 | −0·08 |
| May | +0·20 | −0·27 | +0·12 | −0·06 | — | +0·14 | −0·21 | +0·19 | −0·15 |
| summer | | | | | | | | | |
| June | −0·17 | −0·06 | +0·21 | 0 | −0·02 | −0·18 | +0·03 | +0·18 | — |
| July | −0·24 | −0·16 | +0·25 | +0·18 | +0·20 | +0·07 | +0·12 | +0·43 | — |
| Aug. | −0·41 | −0·29 | +0·15 | +0·48 | +0·31 | −0·11 | +0·02 | −0·22 | — |
| autumn | | | | | | | | | |
| Sept. | −0·30 | −0·23 | +0·16 | +0·34 | +0·40 | −0·23 | +0·18 | −0·32 | — |
| Oct. | −0·29 | +0·02 | +0·20 | +0·08 | +0·55 | −0·08 | −0·06 | −0·38 | — |
| Nov. | 0 | +0·12 | −0·18 | +0·06 | +0·41 | −0·35 | −0·04 | −0·02 | — |
| winter | | | | | | | | | |
| Dec. | −0·12 | +0·27 | −0·03 | −0·12 | +0·10 | +0·08 | −0·20 | +0·02 | — |
| Jan. | −0·34 | +0·25 | +0·04 | +0·03 | +0·12 | −0·24 | +0·09 | +0·02 | — |
| Feb. | −0·31 | +0·05 | +0·05 | +0·21 | — | +0·09 | +0·06 | −0·16 | — |
| | | | | | estimated | | | | |
| spring | | | | | | | | | |
| Mar. | −0·07 | −0·02 | +0·07 | +0·02 | — | −0·16 | −0·05 | −0·02 | +0·30 |
| Apr. | +0·12 | −0·01 | −0·10 | −0·03 | — | +0·06 | −0·04 | +0·08 | −0·21 |
| May | −0·05 | −0·04 | +0·06 | +0·03 | — | +0·05 | −0·07 | +0·10 | −0·13 |
| summer | | | | | | | | | |
| June | −0·07 | −0·03 | +0·27 | −0·17 | −0·05 | −0·10 | +0·06 | +0·09 | — |
| July | −0·18 | +0·17 | +0·08 | +0·25 | +0·05 | −0·08 | +0·17 | −0·15 | — |
| Aug. | −0·28 | −0·21 | −0·08 | +0·58 | +0·14 | −0·09 | +0·12 | −0·18 | — |
| autumn | | | | | | | | | |
| Sept. | −0·33 | −0·09 | 0 | +0·43 | +0·25 | −0·20 | +0·13 | −0·18 | — |
| Oct. | −0·20 | 0 | +0·03 | +0·17 | +0·42 | −0·23 | 0 | −0·18 | — |
| Nov. | −0·14 | +0·03 | +0·26 | −0·14 | +0·18 | −0·33 | +0·08 | +0·07 | — |
| winter | | | | | | | | | |
| Dec. | −0·05 | +0·02 | +0·14 | −0·08 | +0·12 | −0·15 | −0·04 | +0·06 | — |
| Jan. | −0·20 | +0·21 | +0·07 | −0·02 | −0·06 | −0·05 | +0·04 | +0·06 | — |
| Feb. | −0·26 | +0·15 | +0·03 | +0·09 | — | +0·06 | 0 | −0·06 | — |

regressions in the two series of four years. Some accuracy has been lost by applying the same regressions to a longer period, and some gained by having four seasons instead of two.

The long run of below normal populations from May 1933 to November 1934 is well estimated, except for April and May of 1934. August, September and October 1936 are under-estimated and November and December over-estimated; but the sudden increase in the summer of 1937 and the rapid fall back to normal in the autumn are well covered by the calculations. In the second period January and March 1947

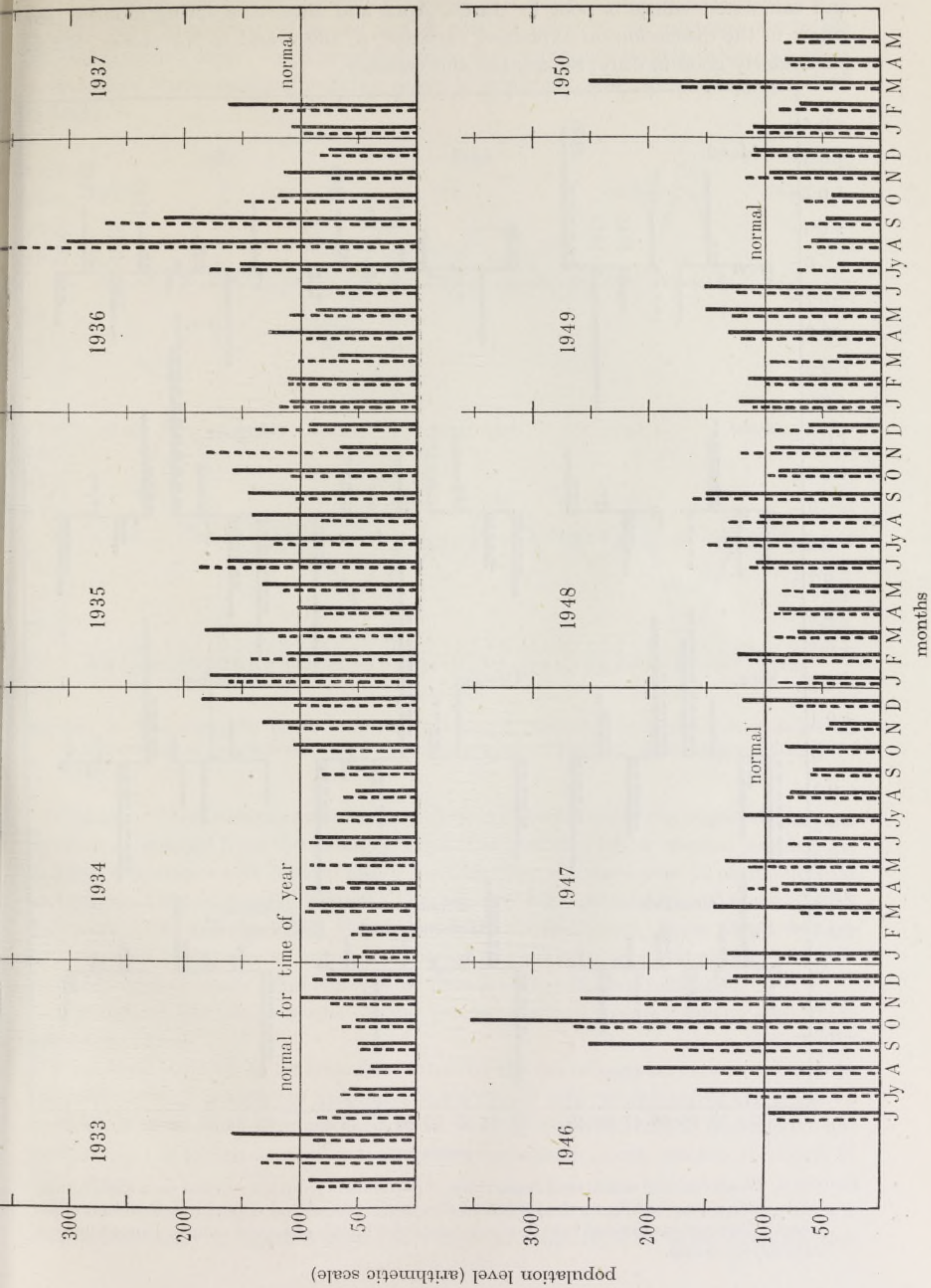
Table 12. Observed and calculated population departures from normal (= 100) for the time of the year on arithmetic scale. Eight years, four seasons.

| | 1933–4 | 1934–5 | 1935–6 | 1936–7 | 1946–7 | 1947–8 | 1948–9 | 1949–50 | 1950 |
|---|---|---|---|---|---|---|---|---|---|
| | | | | observed | | | | | |
| spring | | | | | | | | | |
| Mar. | 93 | 93 | 182 | 68 | — | 145 | 71 | 37 | 251 |
| Apr. | 129 | 60 | 102 | 129 | — | 85 | 89 | 148 | 83 |
| May | 159 | 54 | 132 | 87 | — | 138 | 62 | 155 | 71 |
| summer | | | | | | | | | |
| June | 68 | 87 | 162 | 100 | 96 | 66 | 107 | 151 | — |
| July | 58 | 69 | 178 | 151 | 159 | 118 | 132 | 37 | — |
| Aug. | 39 | 51 | 141 | 302 | 204 | 78 | 105 | 60 | — |
| autumn | | | | | | | | | |
| Sept. | 50 | 59 | 145 | 219 | 251 | 59 | 151 | 48 | — |
| Oct. | 51 | 105 | 159 | 120 | 355 | 83 | 87 | 42 | — |
| Nov. | 100 | 132 | 66 | 115 | 257 | 45 | 91 | 96 | — |
| winter | | | | | | | | | |
| Dec. | 76 | 186 | 93 | 76 | 126 | 120 | 63 | 105 | — |
| Jan. | 46 | 178 | 110 | 107 | 132 | 58 | 123 | 105 | — |
| Feb. | 49 | 112 | 112 | 162 | — | 123 | 115 | 69 | — |
| | | | | estimated | | | | | |
| spring | | | | | | | | | |
| Mar. | 85 | 96 | 117 | 104 | — | 69 | 90 | 95 | 170 |
| Apr. | 133 | 98 | 80 | 94 | — | 115 | 92 | 120 | 79 |
| May | 88 | 92 | 115 | 107 | — | 113 | 85 | 127 | 83 |
| summer | | | | | | | | | |
| June | 85 | 93 | 186 | 68 | 89 | 79 | 114 | 124 | — |
| July | 66 | 68 | 121 | 179 | 112 | 83 | 150 | 71 | — |
| Aug. | 53 | 62 | 83 | 385 | 137 | 81 | 132 | 66 | — |
| autumn | | | | | | | | | |
| Sept. | 47 | 81 | 101 | 268 | 177 | 62 | 136 | 66 | — |
| Oct. | 63 | 99 | 107 | 149 | 263 | 59 | 99 | 66 | — |
| Nov. | 72 | 107 | 181 | 72 | 151 | 47 | 121 | 118 | — |
| winter | | | | | | | | | |
| Dec. | 89 | 105 | 138 | 83 | 132 | 71 | 91 | 115 | — |
| Jan. | 63 | 162 | 118 | 96 | 87 | 89 | 110 | 115 | — |
| Feb. | 55 | 141 | 107 | 123 | — | 115 | 100 | 87 | — |

are poor fits, possibly due to the abnormally cold weather, as below a certain limit the percentage changes in catch cannot be measured. Otherwise the fit is good and all the major changes are indicated.

Figure 6 shows the results of the eight years on a logarithmic scale grouped according to the month of the year. From this it will be seen that the fit of observed

Figure 5. Observed departures of the population from the normal for each series of four years, and values calculated from regressions on minimum temperature and rainfall in the three previous months. The year divided into four seasons.


1933
1934
1935
1936
1937
normal for time of year
normal
1946
1947
1948
1949
1950
normal
normal
J Jy A S O N D J F M A M J Jy A S O N D J F M A M J Jy A S O N D J F M A M J Jy A S O N D J F M A M
months
300
200
100
50
population level (arithmetic scale)

and calculated values is poor in March, April and May—the spring months (see below in the discussion on explained variance, p. 150)—and in November; but is particularly good in July, September and October.

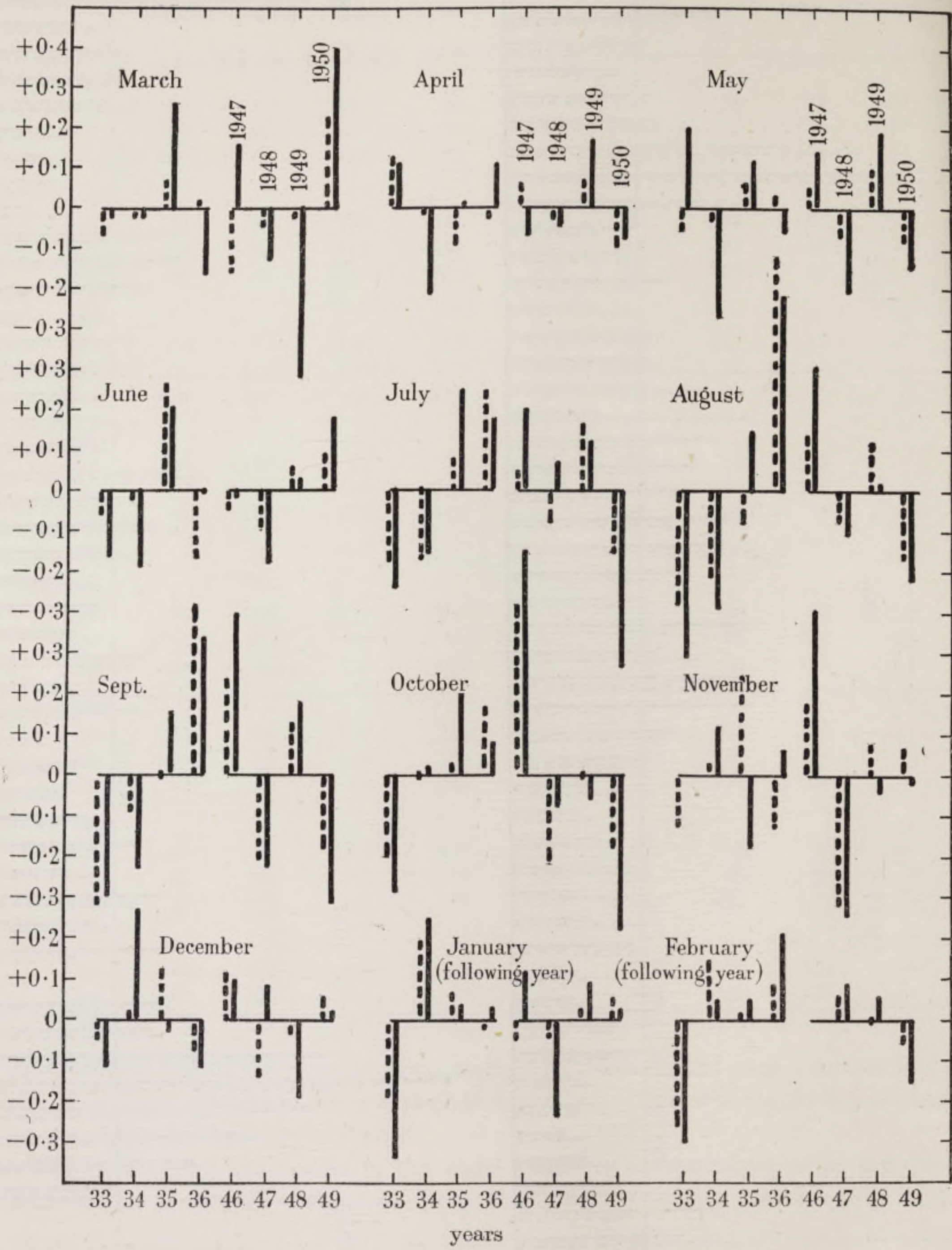



FIGURE 6. Observed and calculated departures of population from the normal on a logarithmic scale grouped according to the month of the year. Calculated departures based on eight years' observations divided into four seasons. Solid lines = observed values. Dotted lines = calculated values.

Since the population is not really changing in a series of monthly 'jumps' and as a small error in estimation in one month may be offset by an opposite one in the following month, figure 7 was prepared, from the logarithmic data in table 7, to show a smoothed three months' running mean of observed and calculated population changes.

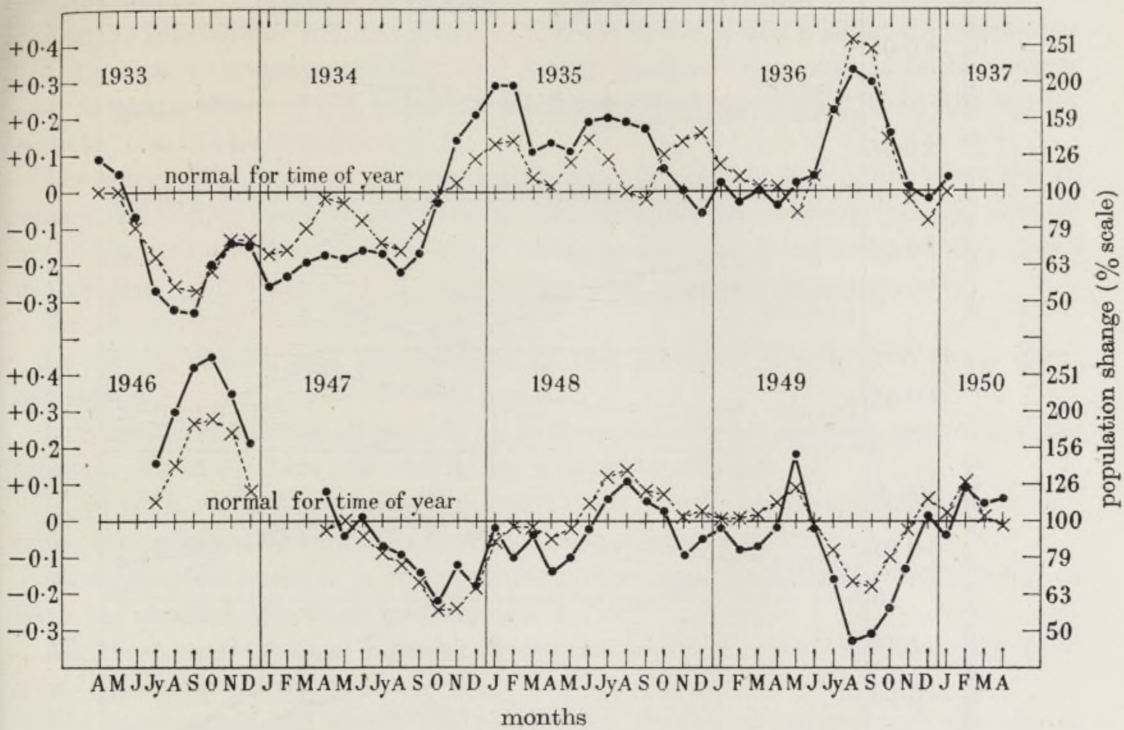



FIGURE 7. The observed (solid line) and calculated (dotted line) population changes on a logarithmic scale, shown as a three months' smoothed running mean. Original data from table 7.

This undoubtedly shows an extremely close interpretation of the observed changes by those calculated from the six regressions. The period of below-normal populations in 1933–4 is shown with its two minor fluctuations; the cross-over to above normal in October 1934 is exactly correct. The peak of high population in January and February 1935, and the fall in March and April are indicated. From about August to December 1935 there is, however, a period of definitely poor estimation, and this required further study. The changes in 1936 are very closely indicated.

Throughout the whole of the second period, the two running means are extraordinarily close.

Thus there appears to be little doubt that by the use of regressions which measure the effect of unit changes of minimum temperature and rainfall in three successive months, a very close estimate can on an average be made of the population departures in the fourth month, as measured by geometric mean catches of insects in light trap.

The seasonal changes in the regressions are of particular interest and are shown diagrammatically in figure 8 from the values in table 10. The same diagram also shows the regressions for each half of the year, summer and winter, in the two four-year periods previously discussed.

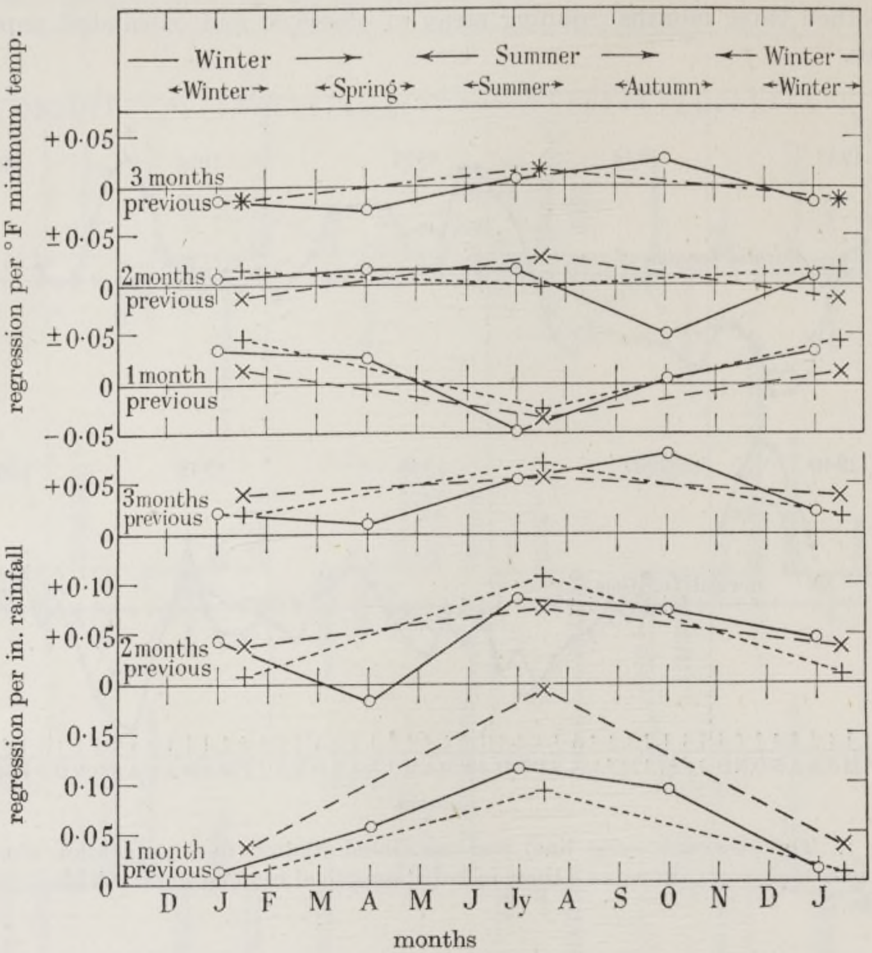



Figure 8. Seasonal changes in the regressions of population on minimum temperature and rainfall in the three previous months; based on eight years' observations divided into four seasons: spring, summer, autumn and winter (solid line). Also for two four-year periods 1933–7 (dotted line) and 1946–50 (broken line) divided into two seasons, winter and summer.

Taking first the effect of unit change in minimum temperature three months previous, it will be seen that the regressions are all small, with very slight evidence of a negative relation in winter and spring, and small positive relations in summer and autumn, slightly higher in the latter.

For the minimum temperature at two months previous there is only a very small positive regression in winter, spring and summer, but an apparent negative effect in the autumn.

For the minimum temperature one month previous the results show a small positive effect in winter and spring and a definite negative effect in summer, with autumn showing no relation.

It appears that minimum temperature has only a slight lasting effect and, except in the autumn, minimum temperatures previous to the immediately preceding month can be neglected.

With the rainfall at three months previous the regressions are all positive, at a minimum in the spring (after the plentiful moisture of winter) and a maximum in the autumn (after the deficient moisture of summer).

For the rainfall two months previous there is in the spring a slight (but probably not significant) negative relation, and a high positive regression in both summer and autumn, showing the effect of moisture deficiency sooner than the earlier months' conditions first discussed.

The effect of rainfall in the previous month is positive throughout but low in winter and high in summer and autumn. This is to be expected, as explained already in the discussion on the first four years, owing to the even distribution of the rainfall in this area, combined with the definite seasonal change in temperature.

To summarize by seasons.

In spring, rainfall and temperature in the previous month give the highest regressions.

In summer, rainfall at all periods up to three months previous is important, while temperature in the previous month has a negative relation.

In autumn, rainfall is equally important three months before as one month before, while temperature two months previous has a negative relation.

In winter, temperature in the previous month and rainfall two months previous have the greatest effect per unit change.

All these quantitative expressions appear to be justified qualitatively from a bio-climatic point of view.

We have considered above the regressions, or the effect per unit change, in minimum temperature and rainfall, but the total effect of the actual weather conditions depends on this effect per unit change multiplied by the amount of which the factor itself changes. In statistical terms the variance explained by any one of the factors considered is equal to the regression multiplied by the co-variance of this factor with the dependent variable, which in this case is the population.

Table 13 shows the total variance of the population in each of the four seasons, the variance of each of the six weather factors, and their co-variance with the population. From this information it has been possible to prepare table 14 which shows the percentage of the total population variance which can be explained in each of the four seasons, first by simple regressions on each of the six factors (neglecting their relation with each other), and secondly by the combined effect of all six factors calculated from the partial regressions already given in table 10. The results are shown diagrammatically in figure 9.

Taking first the single-factor regressions, we find that in the minimum temperature the previous months' conditions are associated with the greatest percentage of explained population variation in winter, spring and summer (and particularly in winter when it can account for 22 % of the variance), but in the autumn greater effects are associated with the temperature two months (22 %) and three months (15 %) previous.

Table 13. Total variance of population and of rainfall and minimum temperature; and co-variance of population with these weather conditions; each from twenty-four values

| | spring | summer | autumn | winter |
|---|---|---|---|---|
| variance | | | | |
| population | 0·8599 | 1·2596 | 1·5626 | 0·7038 |
| minimum temperature: | | | | |
| 3 months previous | 262·8400 | 106·6500 | 33·7000 | 45·9100 |
| 2 months previous | 207·3700 | 36·8600 | 45·6700 | 118·1500 |
| 1 month previous | 175·0700 | 42·0600 | 52·3800 | 137·7900 |
| rainfall: | | | | |
| 3 months previous | 40·0026 | 22·6307 | 37·1077 | 39·6406 |
| 2 months previous | 41·5791 | 26·7676 | 26·9398 | 52·6631 |
| 1 month previous | 31·1044 | 31·3406 | 37·6579 | 49·4604 |
| co-variance of population with | | | | |
| minimum temperature: | | | | |
| 3 months previous | +0·5400 | −0·0670 | −2·8440 | −0·0720 |
| 2 months previous | +1·0110 | +0·1690 | −4·0010 | +2·5700 |
| 1 month previous | +3·4650 | −2·2080 | −2·1110 | +4·6680 |
| rainfall: | | | | |
| 3 months previous | +0·0199 | −0·8884 | +4·6261 | +1·2294 |
| 2 months previous | −0·5938 | +3·8126 | +3·5021 | +1·8134 |
| 1 month previous | +1·5937 | +4·2090 | +3·3908 | +2·1818 |

Table 14. Percentage variance explained by regressions on previous minimum temperature and rainfall

| | spring | summer | autumn | winter |
|---|---|---|---|---|
| | simple regressions | | | |
| minimum temperature | | | | |
| 3 months previous | 0·1 | 0 | 15·6 | 0 |
| 2 months previous | 0·6 | 0·1 | 22·4 | 7·9 |
| 1 month previous | 8·0 | 9·2 | 5·4 | 22·5 |
| rainfall: | | | | |
| 3 months previous | 0 | 2·8 | 38·1 | 5·4 |
| 2 months previous | 1·0 | 43·1 | 29·1 | 8·9 |
| 1 month previous | 9·5 | 44·9 | 19·5 | 13·7 |
| | partial regressions | | | |
| all six factors | 25·2 | 69·7 | 67·3 | 44·6 |

The rainfall in the previous month and two months previous have a very high effect in summer (45 %) but in autumn, although the effect of the previous month remains high (19 %), it is overshadowed by the effect of both two months (29 %) and three months previous (38 %). The least rainfall effect is in the spring, at which season the effect of any rain before the previous month is negligible.

When we take the total effect of all six factors from the multiple regression we find that variations in rainfall and minimum temperature can explain 25 % of all the population variation in the spring; over 66 % of the variation in summer and autumn and 45 % of the variation in the winter; thus demonstrating the very important effect of weather conditions in determining the general level of insect population under the climatic and weather conditions of south-eastern England.

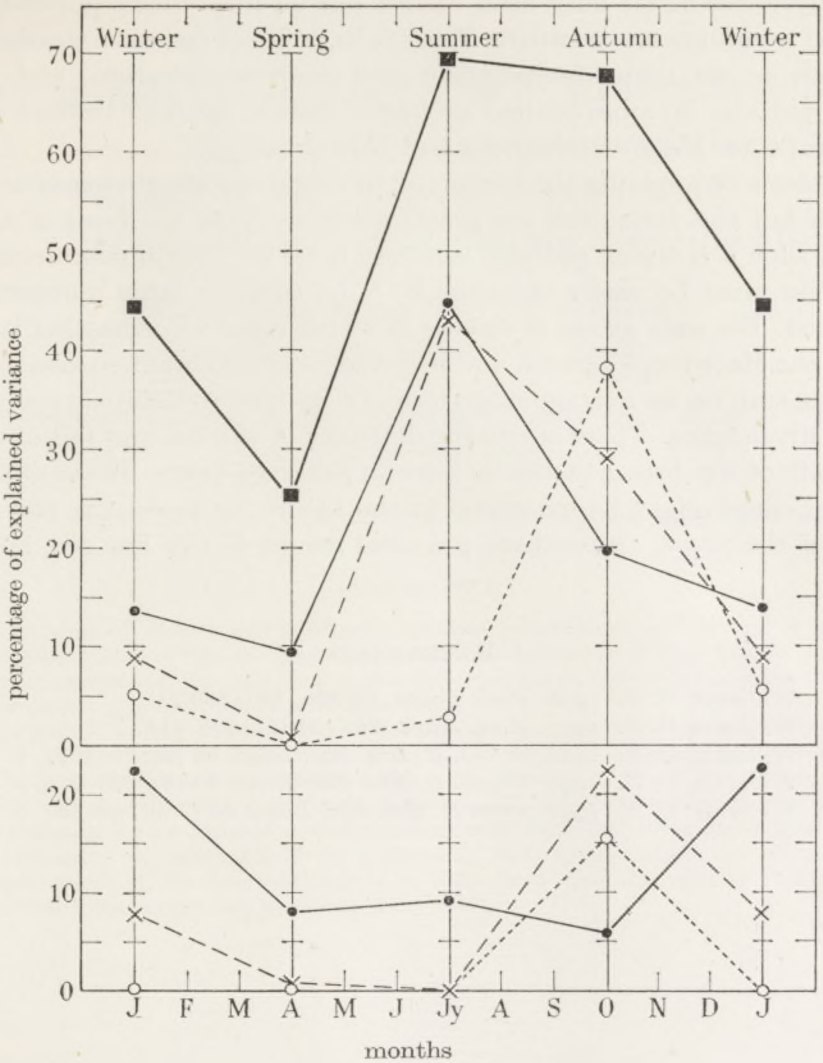



FIGURE 9. Seasonal changes in the percentage of the total variance of the population which can be explained by regressions on rainfall and temperature in the three previous months. Lower group minimum temperature. Middle group rainfall. 1 month previous = solid line. 2 months previous = broken line. 3 months previous = dotted line. Upper heavy line, percentage variance explained by all six factors as partial regression.

By means of the partial regressions the interrelation of the various climatic factors with each other is eliminated, but of course other factors which have not been considered exist and may be related to these six climatic factors. For example, parasites determine the level of an insect population but are themselves affected by similar climatic conditions. The estimations above include all effects both direct and indirect.

To sum up it appears that the departures from the normal of the minimum temperature and the rainfall in any three months—and any other factors associated with them—are capable of determining from 25 to 70 % of the total variation of the insect population according to the season of the year.

The analysis has so far only been carried out on total insect population and on rainfall and minimum temperature. Work is in progress on other weather measurements, such as maximum temperature and mean temperature, and other time intervals; and also on more limited groups of insects, such as Diptera alone, total Lepidoptera, total Macro-lepidoptera and Noctuidae.

The problems of applying the technique to single species obviously must also be undertaken but the difficulties are great, particularly as the basis of a statistical analysis of such a complex problem is a very large number of measurements. Any single species must be easily identifiable, must come in large numbers and over a long period. The only group of insects in which rapid identification is at present possible is the Macro-lepidoptera, and here the most abundant species do not come into a single trap on an average more than about 1000 individuals per year, or for more than fifty nights. There is also the difficulty of the rise and fall of the broods, and the shift of the brood earlier or later in different years. These difficulties are serious, but some might be overcome in the future by increasing the number or efficiency of the traps. Immediate practical results in this line are, however, not expected.

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