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Studies in the Effect of Weather Conditions on the Activity and Abundance of Insect Populations

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STUDIES IN THE EFFECT OF WEATHER CONDITIONS ON THE ACTIVITY AND ABUNDANCE OF INSECT POPULATIONS

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CONTENTS

This paper is a statistical analysis of captures of insects every night for over 4 years in traps in a locality in the Scottish Highlands. It should be considered in relation to a similar account of work in south-east England (Williams 1951 *a*).

From the trap catches (on a logarithmic scale), and meteorological records taken alongside the traps, statistical analyses, chiefly by multiple regressions, were made to show (1) the relation between day to day changes in log catch and corresponding changes in temperature and wind, and (2) the relation between changes in mean log catch in the same month in different years and changes in rainfall and temperature in the three previous months. The former is an activity effect, and the latter a population effect.

Details are given for total Diptera, for the bloodsucking flies of the family Simuliidae, and for total Lepidoptera in a light trap, and for total Diptera in a suction trap, this latter for activity only.

The results show quantitatively the very high dependance, more so in some groups and at certain seasons, of the activity of insects on the current weather conditions, and of the population level on the previous weather. A fuller summary is included in the paper, pp. 367 to 369.

I. Introduction

(1) *Outline of the problem*

For many years the problem of fluctuations in insect populations has been under discussion by naturalists, with particular reference both to the causes of such changes and to their effects. From the economic point of view the study is fundamental to the understanding and prevention of insect outbreaks. From the scientific point of view the so-called 'balance of nature' is the synthesis of all the changes in populations of different species in an area, and great interest lies in the question as to whether fluctuations in numbers of species are primarily due to changes in the biological or in the physical environment.

The biological environment of any animal consists of its food supply, its enemies (parasites and predators), its competitors, and (only too few) its allies, including among these the enemies of its enemies. All these are themselves subject to continual changes in numbers, both within the annual cycle of seasons and from year to year.

The physical environment can be roughly divided into, first, those factors which are stable, or moderately so for any particular area; and secondly, those which, like the biological factors, vary almost continuously. For example, the geographical position of a habitat (in relation to latitude, height, slope, exposure, drainage, proximity to the sea, etc.), the soil texture and chemistry, and the geological structure of the area are generally stable; also the 'climate' which, in its strictest sense, has only long-term secular changes. On the other hand we have the rapidly varying 'weather' factors such as rain, temperature, cloud, sunshine and wind, which change from hour to hour, from day to day, from season to season, and from year to year: but usually vary about means which change only slowly, and which define what we call climate.

The physical environment can act not only directly on any particular species under discussion, but also indirectly by affecting (again directly or indirectly) the factors of its biological environment.

It is thus of considerable importance to get accurate measurements of the changes in numbers of insects, and to see what proportion of such changes can be accounted for by simultaneous or previous changes in weather conditions.

(2) *The method of approach to the problem*

The relation between weather conditions and the activity and abundance of insects can be studied either by experimental methods in the laboratory, or by direct measurements of weather factors and insect numbers in the field. The former method usually suffers from the dangers of over-simplification, since it is only possible to study under closely controlled conditions very few of the multitude of factors, and of the interactions of these, that are found in nearly all natural wild populations.

The direct approach to the problem in the field is, however, so complex that, until the development of statistical methods of analysis, it was impossible to separate the effect of the different factors, and to assess the effect of each quantitatively. By means of new techniques—and particularly by the use of multiple regressions—it is now possible to make a beginning in such an analysis, provided one can get a sufficient number of moderately accurate measurements of populations numbers at frequent intervals. There is little value in observing the temperatures of an environment to a fraction of a degree if the only measure of population level is some subjective estimate such as 'common' or 'rare'; the meaning of which not only varies from observer to observer, but even within observers from time to time.

To avoid such difficulties it was decided to get an impersonal objective measure of insect numbers by some carefully standardized trap. Eventually a light trap (described below) was adopted, but for some recent work in this new locality, a suction trap has been used. The light trap is a very efficient mechanism and can easily be standardized, but it only catches those nocturnal insects which are also phototropic. However, the number of such species, and the number of individuals, have proved to be more overwhelming than insufficient. We have, further, no reason to believe that, if any general laws exist for the quantitative relation of insect activity or numbers to weather conditions, they are likely to be different for those insects which happen to be active at night in the adult stage.

The suction trap has the advantage that it can be used both by day and by night but, at the time of the start of the original investigation in 1933, it was not well developed or standardized; so, as all the earlier work had been carried out by a light trap, this new study in Scotland was developed along the same lines to get comparable results.

The data available for analysis is thus the number of insects (sorted into various groups) caught each night over a period of several years, under conditions as standardized as possible so far as the efficiency of trapping is concerned, but subject to all the natural variations of biological and physical environment up to the moment of entry of the insects into the trap. To correlate with these values are the day-to-day meteorological factors, such as temperatures, wind, rainfall, cloud, barometric pressure, phases of the moon, etc., taken nearly all under standardized meteorological conditions. The statistical problem (see p. 342) is to extract from all these the maximum information about the relation of the numbers and activity of the insect to current and previous weather changes.

(3) *Previous work at Rothamsted Experimental Station, Harpenden*

I had carried out two periods of regular trapping, each of 4 years duration, at Rothamsted Experimental Station, about 25 miles north of London. The first was from March 1933 to February 1937, and the second from May 1946 to April 1950. A total of nearly 1 500 000 insects were captured on over 2900 nights, with a maximum of 73 000 insects in one night, and on many nights, under bad weather conditions, there was no catch at all. Each night's catch was divided into the different orders of insects, the numbers in each being counted separately. In some orders there was a further subdivision into families, while in the Macro-Lepidoptera nearly all were identified to species, and some to sexes. About 86·5 % of the catch were Diptera, 10 % Lepidoptera, and only about 3·5 % all other orders together. Coleoptera were only just over 0·25 %. Aquatic insects were almost completely absent owing to the absence of streams or ponds in the district.

The analysis of the results (by the method that will be discussed below) was carried out to try to answer two problems. The first was a question of insect activity: to what extent can changes from night to night in numbers of insects captured be explained quantitatively by the simultaneous changes in the weather conditions, such as maximum and minimum temperatures, amount of wind, amount of cloud, rain during the previous day and during

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the night, relative humidity, etc. The second was a population question: to what extent can differences in population level between the same months in different years be estimated from the trap results, and to what extent can they be explained (again quantitively) by changes in the preceeding weather conditions, in particular rainfall and temperature (see Williams 1936, 1939, 1940, 1951 *a*).

The results of the first half of the analysis gave a series of regression values which are, in effect, the amount of change (on a geometric scale) of the catch associated with a change of one unit in the weather factor under consideration. It would perhaps be more accurate to say that they are the best estimates of such relations that could be obtained from the data available. The following are some examples of the effect found on the total catch of all insects per night at Rothamsted. The number of insects caught in the trap was on an average doubled by a rise in the minimum temperature of 4·5 °F (2·5 °C) from one day to the next; and was reduced to one-half by a fall of the same amount. It required, however, a rise of about 13·5 °F (7·5 °C) in the maximum temperature of the previous day to double the catch. The relation to wind was approximately that the catch was halved if the wind velocity increased four times. From these three weather factors, calculated independently, it was possible in the summer months to account for nearly 60 % of the variability of the catch from night to night (for further details see Williams 1940).

For the analysis of the effects of previous weather conditions on population level, multiple regressions were calculated to show the quantitative relation between the mean log catch of insects in one particular month in a series of years, and the total rainfall and mean minimum temperature in each of the 3 previous months; all being expressed as departures from the mean values for that month. (See below p. 342 for a fuller description of the analysis.)

After the end of the first 4 years, separate regressions were calculated for the 6 winter months (November to April) and the 6 summer months (May to October). Later, when 8 years' results were available, the regressions were calculated for each of the four seasons of 3 months each. The seasonal regressions are reproduced in table 1 and figure 1. From such a set of regressions, if one is given the rainfall and temperature departures from normal of any 3 successive months, it is possible to estimate the expected departure from normal of the insect population in the fourth month. When this was done for the two periods of 4 years trapping at Rothamsted, the estimates so obtained, smoothed to a 3 months running mean, are shown in figure 2 (redrawn from Williams 1951 *a*) together with the corrected mean log catch of insects which is a measure of the actual population change. All the values are shown as departures from the 4-year monthly average.

The close resemblance between the measure of the population changes made direct from the trap catches and the estimates made from the multiple regressions on rainfall and temperatures is remarkable. In the whole of the 8 years there is only one short period, August to December 1935, in which the fit is bad. Otherwise almost every main change in population trend in the insects has been reproduced by estimates made from the changes in rainfall and temperatures of the 3 previous months.

Further, the seasonal changes in regressions for rainfall and temperatures for 1 month previous show a greater importance of temperature change in the winter, and a greater importance of rainfall in the summer and autumn. The district where the trapping was

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done had an evenly distributed moderately low rainfall (about 25 in. per year); and a cold winter, with little evaporation and transpiration, followed by a warm summer in which the rainfall is rapidly used up by high evaporation and high transpiration. The results

TABLE 1. PARTIAL REGRESSIONS SHOWING THE EFFECT OF UNIT CHANGES IN MINIMUM TEMPERATURE AND RAINFALL IN EACH OF 3 CONSECUTIVE MONTHS ON THE POPULATION OF ALL INSECTS ON A LOG SCALE, IN THE FOURTH MONTH

Data obtained in two periods of trapping, each of 4 years, at Rothamsted Experimental Station.

	spring	summer	autumn	winter
minimum temp. (per °F)				
1 month previous	+0·027	−0·049	+0·004	+0·033
2 months previous	+0·017	+0·012	−0·051	+0·018
3 months previous	−0·024	+0·007	+0·028	−0·015
rainfall (per inch)				
1 month previous	+0·059	+0·116	+0·092	+0·014
2 months previous	−0·022	+0·086	+0·071	+0·045
3 months previous	+0·009	+0·054	+0·081	+0·021
metric scale				
minimum temp. (per °C)				
1 month previous	+0·049	−0·088	+0·007	+0·059
2 months previous	+0·031	+0·022	−0·092	+0·014
3 months previous	−0·043	+0·013	+0·050	−0·027
rainfall (per cm)				
1 month previous	+0·023	+0·046	+0·036	+0·006
2 months previous	−0·009	+0·034	+0·028	+0·018
3 months previous	+0·004	+0·021	+0·032	+0·008

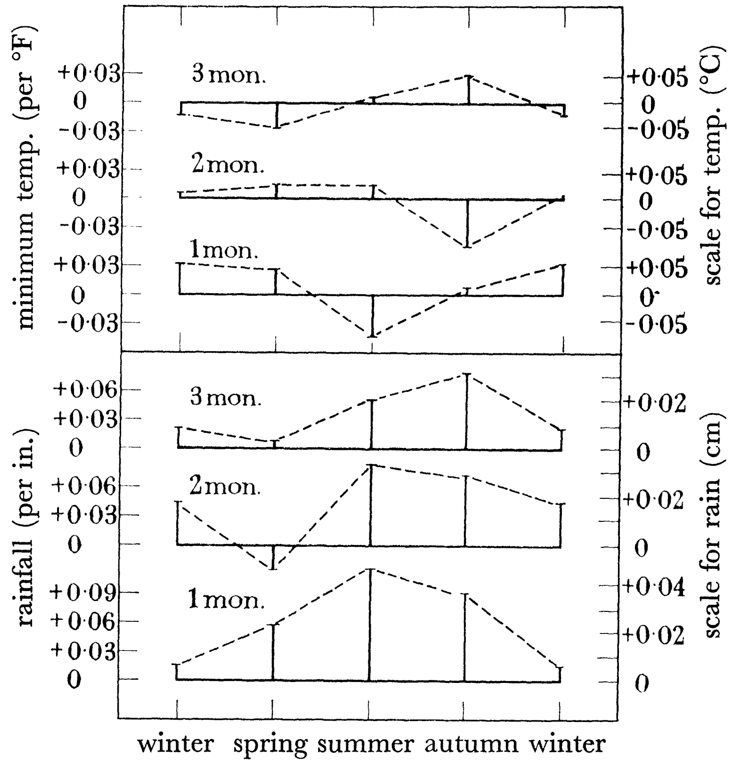


FIGURE 1. Seasonal change in regressions of rainfall and minimum temperature in 3 successive previous months on the population of all insects, as indicated by a light trap, in the following fourth month. From two 4-year periods of trapping at Rothamsted in 1933–37 and 1946–50.

obtained therefore might have been expected, at least qualititively, from purely biological reasoning.

In view of the success of the estimates of population change made in this series of investigations at Rothamsted, it was important to repeat the work—for at least one period of 4 years—in another locality, preferably in the British Isles, with climatic and environmental factors as different as possible from that of south-east England.

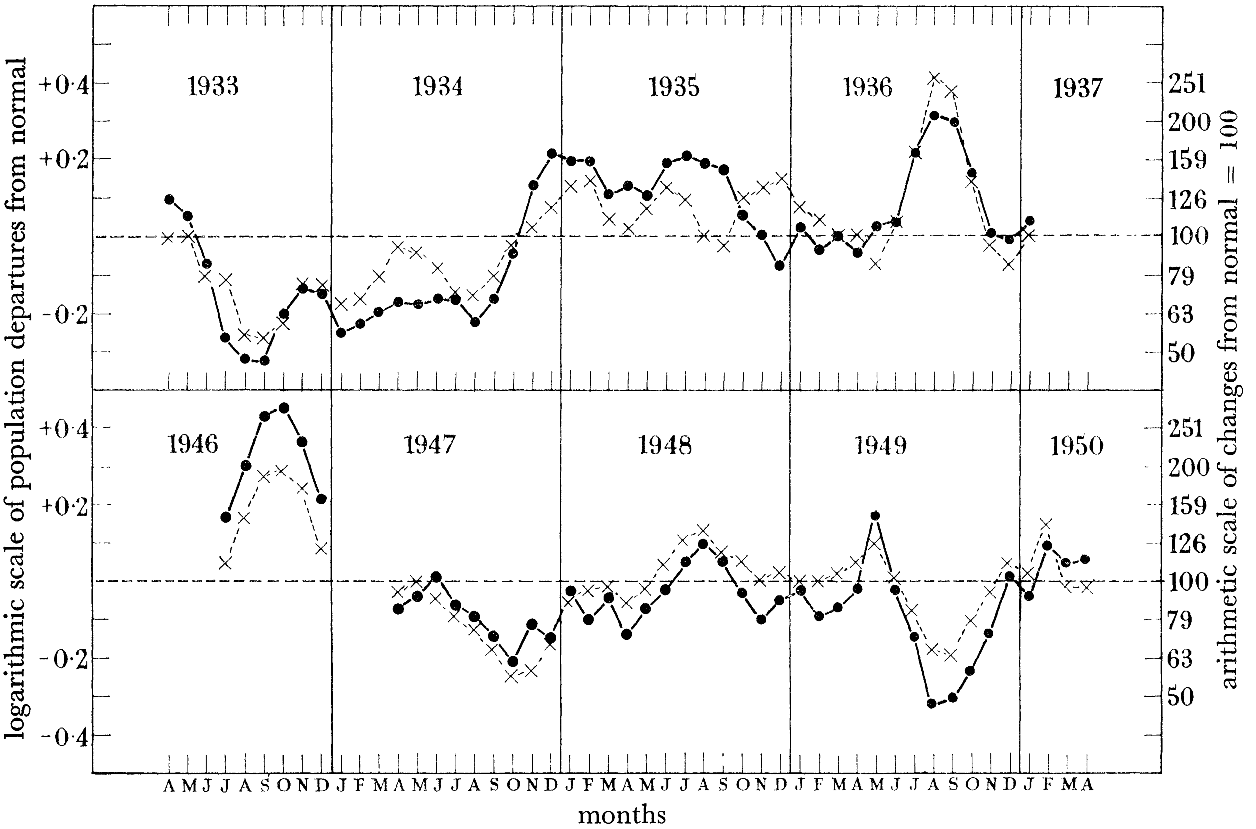


Figure 2. Changes in population of insects at Rothamsted, as departures from normal (– – –) for the time of the year. ●, estimated from the monthly mean catch per night, on a log scale; ×, calculated from the regressions on rainfall and temperature departures in the previous 3 months. Both are smoothed to a 3 months running mean.

(4) *Description of the locality for the new experiment: Kincraig, Inverness-shire, Scotland*

The village of Kincraig is at a height of about 750 ft. above sea level in south-east Inverness-shire in the valley of the River Spey—57° 08′ N; 3° 56′ W. It is just under 400 miles north-north-west of Harpenden where the first set of records were taken. The night (sunset to sunrise) is just under an hour longer at Kincraig than at Harpenden in the winter, and just under an hour shorter in the summer, but in the summer the twilight lasts considerably longer.

The valley is about a mile wide at Kincraig, the river running from south-west to north-east. On the east the ground rises rapidly to the main block of the Cairngorm mountains, with four peaks of over 4000 ft. within 10 miles, and extending for another 25 miles beyond these. On the west is the large block of the Monadliath mountains with some peaks of about 3000 ft. within 10 miles reach, and the whole extending to Loch Ness, and beyond.

The fall in the valley in the neighbourhood of Kincraig is small, only about 50 ft. in 12 miles, and as a result the flatter portions of the valley are liable to extensive flooding both in summer and in winter. A considerable amount of the land bordering the river is marshy and the Spey, normally 10 to 20 yards wide, may extend at high flood to over half a mile.

A number of small streams come down from the mountains on either side, and the river is expanded into Loch Insh, about 1 mile long and ½ mile wide, just above Kincraig. In severe winters this can be almost completely frozen over. Snow is general on the hills above the 2500 ft. level from December to April. The first falls usually occur on the hill tops in late September and patches persist till the end of June or even later on the north slopes. The air shade temperatures during the 4 years of observations ranged from a maximum of 87 °F (30·5 °C) to a minimum of −6 °F (−21 °C).

The soil in the area is thin and sandy, much of the subsoil in the Kincraig area being a deep sand moraine with rounded stones among the sand. As a result surface drainage, except in the flood lands, is very good and there is little water lying about even after heavy rains. The rainfall is low, averaging about 30 in. a year, and drought conditions may be rapidly set up. Agriculture is mostly sheep farming with comparatively little arable cultivation. Owing to the high frequency of late spring and even summer frosts there is very little fruit growing. A continually increasing area has in recent years been planted up in conifers by the Forestry Commission. The typical semi-wild land is dominated largely by an association of birch (*Betula*), juniper, bilberry (*Vaccinium*) and various heathers (*Erica* and *Calluna*).

(5) *Methods of obtaining the data*

(*a*) *The insect numbers*

Since an important part of the object of the present investigation was to confirm (or otherwise) the results of previous work, it was necessary that as few changes as possible should be introduced into the technique of trapping.

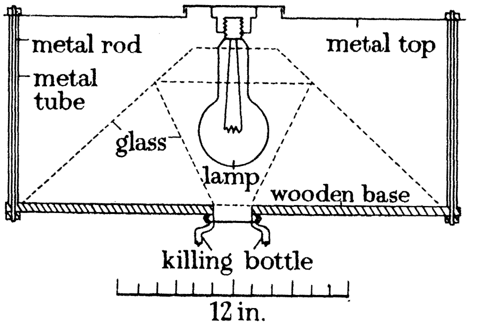
The light trap was almost identical with the one previously in use at Rothamsted, the only difference in structure being a slight cut-away in the sides of the roof to allow the light rays to rise at a higher angle, so as to be more visible to insects flying above. A difference was also made in the source of light, as instead of a 200 W filament bulb, a dual circuit 'Sieray' lamp rich in ultra-violet rays, but of the same wattage, was adopted. Both these changes were made to increase the numbers of insects captured, as it was expected that the new district, being so far north, might produce catches too small to be of use for statistical analysis. These fears turned out to be quite groundless, as in parallel observations which two exactly similar traps in the first two summers, the one at Rothamsted caught fewer *Diptera* than the one at Kincraig (see table 2).

A cross-section of the trap is shown in figure 3*a*, and a photograph in 3*b*. It is approximately 22 in. (56 cm) square and about 10 in. (25 cm) high. Fuller details can be found in Williams (1935, 1948), and a comparison of its efficiency for different orders of insects and with other types of trap in Williams (1951*b*, 1955).

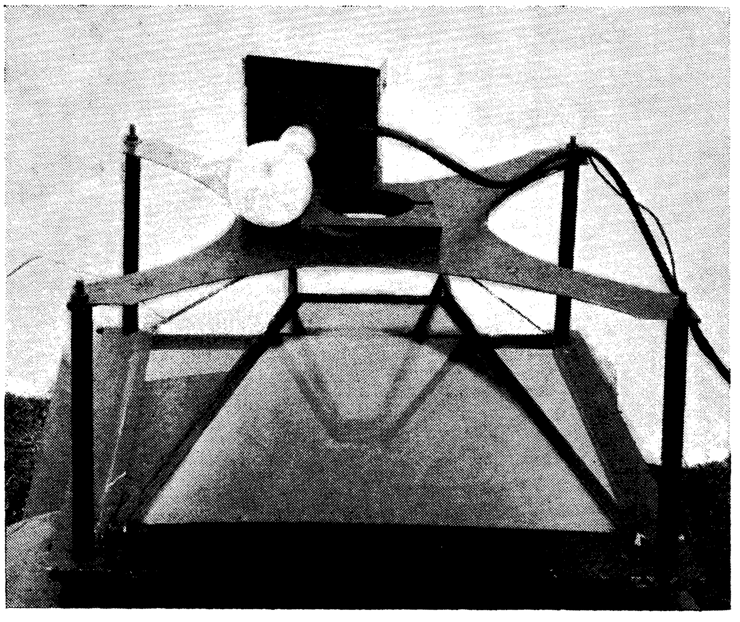
The situation of the trap was in my garden at Kincraig, at the top of a slight slope overlooking first about 20 yards of garden with flowers, some vegetables and a number of birch (*Betula*) and mountain ash (*Sorbus aucuparia*) trees, and then over a spruce hedge to open country of birch-heather association.

Table 2. Catches of Diptera and Lepidoptera in two identical light traps in 1955 and 1956, one at Rothamsted, Harpenden, Hertfordshire and the other at Kincraig, Inverness-shire

	Diptera		*Lepidoptera*	
	Rothamsted	Kincraig	Rothamsted	Kincraig
1955				
Aug.	51272	**88066**	**5336**	5104
Sept.	**15939**	13736	**2117**	590
Oct.	4802	**14680**	**893**	637
1956				
Apr.	251	**493**	102	**784**
May	**2163**	**4241**	**599**	475
June	4813	**10634**	**1314**	614
July	29567	**49285**	**4422**	2189
Aug.	20310	**60949**	3797	**3881**
Sept.	27747	**86383**	804	**3034**
Oct.	8472	**11589**	**1079**	562



(*a*)



(*b*)

Figure 3. (*a*) Diagrammatic cross-section of the light trap used in these measurements of insect numbers.

(*b*) Photograph of the light trap in use in the experiments at Kincraig, with the cap holding the light bulb removed to show the method of fitting. It also shows the cut-away edges of the roof to allow a higher angle of light. The trap is approximately 22 in. square and 10 in. high.

The suction trap was a small standard type developed by Johnson and Taylor at Rothamsted, described and illustrated by Johnson (1950). The mechanism for sorting the catches into different hours was not fitted. Instead the insects were collected into a tube of methylated spirit, fitted with a gauze-covered overflow to prevent swamping by rain. This trap was also in my garden, but to be out of sight of the light trap, it had to be in a slight hollow and near to a large cedar tree, with the result that the local environment was more enclosed and sheltered from the wind than the light trap.

Both traps were switched on and off automatically by a solar-dial switch, at $\frac{1}{2}$ h after sunset and before sunrise by suntime. The hours for trapping varied from just over 5 h in June to 16 h 15 min in December.

Trapping was started for the light trap in June 1955 but as the wind recorder was not working till August, and as it was decided to consider, for the activity analysis, only complete seasons, the period of trapping was continued till the end of August 1959, giving 4 complete years of four seasons each.

The suction trap was started a year later in June 1956.

(*b*) *Meteorological records*

The meteorological screen was about 75 yards outside my garden and in a slight hollow, which may have caused lower minimum temperatures. This was the nearest point to the trap which was not shaded either by the house or by trees. It was at a height of about 750 ft. above sea level, and about a quarter of a mile from the river Spey and the north end of Loch Insh, but these being about 50 ft. lower.

The instruments in the screen were wet and dry bulb and minimum and maximum thermometers, and also a thermograph with weekly sheets. Outside were a grass minimum thermometer and a 5-in. rain gauge. Readings were taken at 9 a.m. G.M.T.

The wind recorder—a cup anemometer with a pen and 24 h drum recorder connected electrically—was about 20 ft. above the roof of my house and about 50 ft. above the ground. It recorded the run of the wind, but not the momentary velocity of gusts.

(6) *Summary of the data obtained*

(*a*) *Insect numbers*

A summary of the catches in the light trap for the 4-year period of trapping, divided into the different orders of insects is shown in table 3. It will be seen that 93·7 % of the total number of insects caught belong to the order Diptera, as compared with the Rothamsted figure of 86·5 %. For the Lepidoptera the Kincraig value was 3·6 % (as compared with 10 % at Rothamsted) and 2·7 % all other insects. The Diptera included very large numbers of Ceratopogonidae. Owing to the large amount of running water in the district aquatic insects such as Trichoptera, Ephemeroptera, and Simuliidae came in considerable numbers, far beyond anything observed at Rothamsted.

The four tables A, B, C and D (appendix) show the total monthly catches and the mean log catch per night for the four main groups of insects which are subject to analysis below: the total Diptera, the Simuliidae, and the total Lepidoptera in the light trap, and the total Diptera in the suction trap. The latter is for 3 years only.

Figure 4 shows diagrammatically the seasonal changes in mean log catch per night for the same groups, together with 4-year means. In the Diptera the highest monthly mean

Table 3. Summary of the catches of insects in the light trap at Kincraig in 4 years trapping, 1955 to 1959, separated into Orders and some smaller groups

	1955 Sept. to Dec.	1956	1957	1958	1959 Jan. to Aug.	total 48 months	as % of total
Diptera							
Total	36216	239511	348054	312212	358408	1294401	93·66
Simuliidae	601	4220	3342	5930	2980	17073	1·23
Lepidoptera							
Noctuidae	379	6246	3182	4524	5842	20173	1·46
Geometridae	917	2595	1748	5360	2825	13445	0·97
other Macrolep.	196	431	469	524	277	1897	0·14
Microlepidoptera	113	2980	2461	4782	4269	14605	1·06
Total	1605	12252	7860	15190	13327*	50234	3·63
Trichoptera	294	7802	5851	5750	6508	26205	1·90
Hymenoptera	418	1369	1043	1095	2616	6541	0·47
Homoptera	54	229	213	650	1068	2214	0·16
Coleoptera	102	249	251	359	518	1479	0·11
Ephemeroptera	4	70	109	78	116	377	0·07 (Ephemeroptera to Mecoptera)
Heteroptera	9	80	44	74	112	319	
Neuroptera	10	22	15	9	56	112	
Plecoptera	17	22	23	24	32	118	
Psocoptera	—	10	8	10	9	37	
Mecoptera	—	1	—	2	—	3	
Total	38729	261617	363471	335453	382770	1382040	

* Includes 114 unidentifiable.

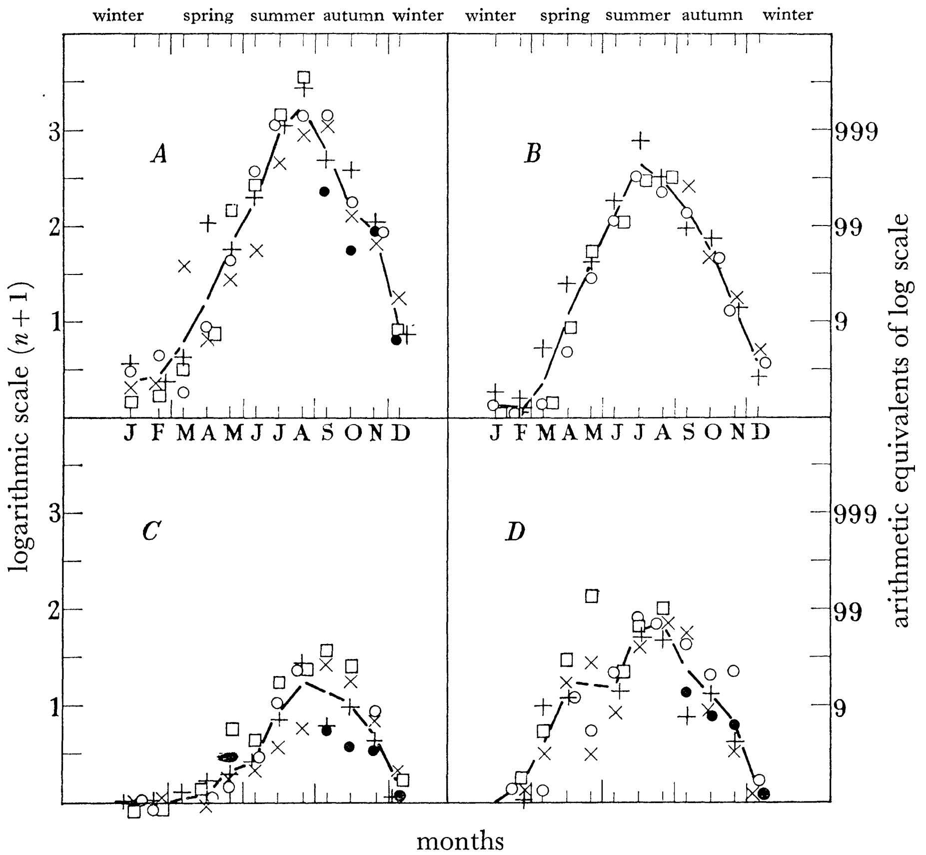


Figure 4. Monthly mean log catch per night, and 4-year means, for each month for various groups of insects captured at Kincraig. A = total Diptera in the light trap; B = total Diptera in the suction trap (3 years only); C = Simuliidae in the light trap: D = Lepidoptera in the light trap. ● 1955, × 1956, + 1957, ○ 1958, □ 1959.

log catch per night for the 4 years was in August with a value of 3·26. This is a geometric mean catch of about 1820 insects per night, and since the geometric mean has been found to be very close to the median, it implies that one night's trapping in the month of August is equally likely to be above or below 1820 Diptera.

The highest mean log (for 3 years only) for Diptera in the suction trap was 2·63 in the month of July (g.m. 427): for Simuliidae in the light trap 1·25 in August (g.m. 17): while for the Lepidoptera in the light trap the peak was 1·86, also in August (g.m. 71 insects per night). The Lepidoptera was the only group that showed a spring peak in April followed by a slow fall in the two following months before the main rise. This is due to the great abundance of a few species at this time of year.

The very slight irregularity in the autumn fall in the light trap Diptera is due to the increased abundance of winter-gnats (Trichocerinae). This was even more marked in the earlier work at Rothamsted.

(*b*) *Meteorological records*

Details of the monthly summaries of observations from May 1955 to September 1959 are shown in table *E* (appendix). The more noticeable features were as follows:

In the $4\frac{1}{2}$ years, the highest temperature was 87 °F (30·5 °C) and the lowest −6 °F (−21 °C). Air temperatures below 0 °F (−17·8 °C) occurred twice in January and once in February of 1958, and once in February of 1959. Air frosts (below 32 °F) occurred on an average on 33 % of the nights in the year, with no single month, except August, without a frost in at least 1 year. All months from October to May inclusive, had some air frosts every year. Ground frost (below 31 °F) occurred on an average on 47 % of the nights of the year, with no months without at least one ground frost except in July and September 1955. January, February and March had usually over twenty ground frosts per month. On the 10 June 1956 the early morning minimum was 30 °F and the maximum was 80 °F, a rise of 50 °F in less than 12 h.

The rainfall, considering the height above sea level and the proximity to the mountains is low: 29·4 to 37 in., with an average of 32·6 per annum for the 3 complete years 1956–58, but both 1955 and 1959 were very much drier in the months when rainfall was recorded. This is probably due to the great extent of the mountains to both east and west. Rain clouds from the south-west break on the mountains stretching practically to the coast, and rain clouds from the east break on the Cairngorms. The position of the Spey Valley is thus in the lee of the mountains for the two main directions of rain-bearing winds. The greatest rainfall in 1 month was 6·06 in. in December 1955, and the lowest 0·35 in. in July 1955. In the 3 summer months, June, July and August of 1955 the total rainfall was only 1·90 in., with temperatures reaching 80° F or above on 16 days. Drought conditions were very serious, and most of the smaller streams dried up. Conditions of drought were also severe in 1959 with only 14·33 in. in the 8 months up to the end of August, the last month of records.

The highest average run of wind per day was 196 miles in December 1956, and 195 in January 1957. Both these months were exceptionally warm, especially January 1957 when the absolute minimum was 19 °F as compared with −1, −6 and +1 °F, in the other three Januaries. Winds averaging below 100 miles per day occurred in three Augusts, two Junes, two Julys and two Novembers and in one September and one October. The only 2 months with averages below 85 miles per day were October and November 1955, with 60 and 64 miles per day, respectively.

There is a strong positive correlation between wind and temperature, especially in the winter. Really low temperatures almost always occur in calm weather and an increase of wind—often quite sudden—is associated with a rapid rise in temperature, except in the rather rare cases of north-east gales, which are cold.

The average wind per hour during the night period of trapping was highest in December and January at 6·3 m.p.h. and lowest in June at 3·3 m.p.h. (see table 4).

TABLE 4. NIGHT WIND, IN MILES PER HOUR, FOR EACH MONTH DURING THE 4 YEARS TRAPPING AT KINCRAIG

	1955	1956	1957	1958	1959	average 4 years
Jan.	—	5·9	7·8	6·4	5·2	6·3
Feb.	—	4·4	5·5	5·2	5·7	5·2
Mar.	—	5·0	5·5	6·1	5·4	5·5
Apr.	—	3·5	4·3	4·6	4·0	4·1
May	—	5·6	3·5	3·2	2·7	3·7
June	—	3·4	2·8	2·3	4·7	3·3
July	—	4·1	3·0	3·1	3·8	3·5
Aug.	—	3·1	3·8	2·8	4·5	3·5
Sept.	4·7	3·6	4·1	4·2	—	4·1
Oct.	4·4	5·2	5·7	4·5	—	4·9
Nov.	4·1	6·2	4·9	3·8	—	4·7
Dec.	5·8	7·9	6·4	4·9	—	6·3
whole year	—	4·8	4·8	4·3	—	4·6

(7) *The analysis of the data*

The statistical problem is to extract, from a long series of measurements, as much information as possible about the relations between the numbers captured each night in larger or smaller groups of insects, as the dependent variants, and the values for as many as possible of the relevant meteorological factors as the independent variants.

It has been found that the variations in catch from night to night, and the frequency distribution of catches over a long period, show evidence of a geometrical and not an arithmetic variation. For example, in the previous work at Rothamsted it was shown that an increase of temperature of 1 °F from one night to another was associated, not with the addition of a certain number of insects to the catch, but in the multiplication of the catch by a certain fraction or percentage. In other words there would be a straight line relationship between the increase of temperature and the increase of the log catch. Thus it is necessary to convert all catches to a logarithmic scale in order that normal statistical formulae based on linear relationships can be applied.

Since, however, rarely in the summer, but more frequently in the winter, zero catches are obtained, it has been found a necessary and useful compromise to consider, as the basic figure for analysis, the logarithm of the observed capture increased by 1, i.e. log $(n+1)$. For all practical purposes this value to two decimal places (being correct to about 1·5 %) is as accurate as the data will allow. The best method of obtaining a measure of the mean catch during any period is to find the mean value of log $(n+1)$, which is of course the logarithm of the geometric mean. Owing to the geometric nature of the variation this is very close to the median, so that any one night's catch in a particular month is equally likely to be above or below the geometric mean, and not the arithmetic mean catch. Fuller details, and evidence of the reliability of this method, will be found in Williams (1937, 1940, 1951 *a*).

The catch in any period is a function of the total number of insects in the population and the activity which causes them to fly within range of the trap. If on one night 1000 insects are caught in the trap and on another night 2000, the difference (doubling, not adding 1000) might be due to a population of the same size being twice as active, or to a population of twice the size having the same activity; or, more usually, to a mixture of both changes. It is important to separate these two effects as far as possible, as the activity effect is very largely a result of the immediate weather changes, while the population change is largely a result of previous conditions.

The activity of insects on any one night is very largely determined by temperature and wind, and if r_1, r_2, r_3, etc., are the effects on the log catch of unit changes in different weather factors, we get that

$$\text{log catch} \equiv \text{log population} + r_1 \text{ (maximum temp.)} + r_2 \text{ (minimum temp.)} + r_3 \text{ (wind)} \ldots, \text{ etc.}$$

The first problem in planning the analysis is to separate as far as possible the population effect from the activity effect. Since activity changes are rapid—sometimes a matter of only hours or minutes—and population changes are slower, it is possible to reduce the population effect to a minimum and emphasize the activity effect by taking as a basis for the first calculations the difference between two successive nights, both for the catches and for the weather factors. By this method estimates have been obtained for the partial regressions on insect activity of different weather factors such as maximum, minimum and sunset temperatures (this latter being the approximate temperature at the start of trapping) and night wind for each month over 4 years with moderately consistent results. These will be discussed in section II of this report.

The study of the population changes has been approached by the following method. The mean log catch per night for each month is largely independent of night-to-night changes in activity, and is determined chiefly by the population level. It is, however, slightly dependent on departures from the normal of the average temperature, wind, etc., for the whole month. But from the partial regressions for activity already obtained in the first half of the analysis corrections for these departures can be made, bringing the mean log approximately to what it would have been had the weather conditions under consideration been normal for that month. (One can compare with this the physicist who brings the volume of a gas to standard temperature and pressure before proceeding with a calculation.) Thus if the mean log catch in the month of May in 4 successive years had been M_1, M_2, M_3 and M_4, they can be corrected to M_1', M_2', M_3' and M_4' for the weather departures of each of the Mays from the average of the four. These values are a close estimate of population levels, since the variation due to activity has largely been eliminated. The final stage of the analysis is to study the departures of M_1', M_2', M_3' and M_4' from their own mean (e.g. the departure of the population each May from the normal for that time of the year) in relation to previous weather conditions by means of multiple regressions (see also Williams 1951 *a*). This is the basis of section III of the present report.

II. The relation of insect activity to weather conditions prevailing at the moment

(1) *General*

It has been explained above that, in order to minimize the effect of population changes and to emphasize as far as possible the activity factor, the basis data used for this calculation of activity regressions has been the difference between successive days, both for insect numbers and for weather conditions.

Table 5. Catch and weather conditions for the first 10 days of July 1956, to show the method of conversion of the data to the logarithmic scale, when necessary, and to the difference between successive days, which is the basis of the analysis for the effect of weather on activity

	total diptera				minimum temperature (following a.m.)		
			difference from previous day			difference	
1956	observed catch	log $(n+1)$	−	+	observed	−	+
30 June	2032	3·31	—	—	52	—	—
1 July	382	2·58	0·73	—	47	5	—
2	290	2·46	0·12	—	51	—	4
3	57	1·76	0·70	—	37	14	—
4	2784	3·34	—	1·68	51	—	14
5	434	2·61	1·83	—	51	0	0
6	47	1·68	0·93	—	34	14	—
7	321	2·51	—	0·83	38	—	1
8	8	0·95	1·56	—	50	—	12
9	15	1·20	—	0·25	35	15	—
10	20	1·32	—	0·41	32	3	—
	night wind				sunset temperature		
			difference from previous day			difference	
	observed miles	log	−	+	observed	−	+
30 June	13	1·11	—	—	55	—	—
1 July	8	0·90	0·21	—	49	6	—
2	13	1·11	—	0·21	56	—	7
3	8	0·90	0·21	—	46	10	—
4	7·5	0·88	0·02	—	55	—	9
5	30	1·48	—	0·60	54	1	—
6	7	0·85	0·63	—	48	6	—
7	2·5	0·40	0·45	—	52	—	4
8	43	1·63	—	1·25	61	—	9
9	8	0·95	0·68	—	49	12	—
10	3	0·48	0·47	—	45	4	—

Table 5 shows the preliminary layout of the data for the first 10 days of July 1956 for the order Diptera. In order to show the first difference the last day of June has been included. The column in each of the four sections shows the original data for the catch, the minimum and sunset temperatures, and the night wind. The second column, in the case of catch and night wind, shows the conversion to a log scale to two decimal places. The last column shows the difference (fall −, rise +) each day from the previous one. These are the figures from which the multiple regressions have been calculated.

At first regressions were calculated (as previously done at Rothamsted) for each separate month, but as it was found that the significance of regressions from only 30 days was low, these were replaced by calculations for each season of 3 months, approximately 90 days. Owing, however, to the number of nights without catch in the winter, the number of comparisons of successive nights was generally much lower in this season. Any two successive nights both with zero catch were removed from this calculation for both catch and weather. Some of the groups of insects studied did not occur in all seasons. The seasons were taken as:

spring:	March, April, May
summer:	June, July, August
autumn:	September, October, November
winter:	December, January, February

In addition to the weather factors shown in table 6, calculations were also made to include the maximum temperatures of the previous day (as was done with the earlier calculations at Rothamsted), and the wind from sunset to midnight only, instead of that of the whole night. It was argued that as most of the catch occurs before midmight, the wind in this portion of the night might be of greater significance. Later, however, it was found that if the wind dropped after midnight, quite large catches could be obtained; and also, that the residual variance was nearly always lower when the total night wind was used. The wind was measured as the total run during the catching period. To get the mean speed of the wind in miles per hour (see table 4) it is necessary to divide the total run by the number of hours trapping, which is of course short in summer (minimum 5 hr 7 min) and long in winter (maximum 16 h 15 min). As however the wind readings were only used in the form of differences between successive nights, when the time changes would be only 2 or 3 min at a maximum, the log of the total night wind was used as the basis. Multiple regressions for the 90 (or less) values for each season were worked out on the electronic calculator at Rothamsted, together with their error, and the original and residual variance (mean square) for various combinations of one to five weather factors. It was found that in nearly every case the three factors of sunset temperature (at the time of starting the trap) the minimum temperature next morning (usually close to the end of the trapping period) and the total run of the wind, on a log scale, during the night period of trapping, gave the lowest residual variance.

(2) *Activity of Diptera based on captures in the light trap*

The Diptera in the light trap gave a total of approximately 1 294 400 individuals, or 93·7% of the total catch. The regressions for these on the three weather factors for each of the sixteen seasons in the 4 years, together with the number of observations, the original variance of the catch, and the residual variance, are shown on table F, in the appendix, with a summary in table 6 and figure 5*A*.

It will be seen that the relation of the change of the abundance of insects, on a log scale, to unit changes (1 °F) in minimum temperature varies from +0·006 to +0·092. Both these extreme values have errors higher than the regression itself and are not in any way significant: the range of significant values is only from 0·027 to 0·067 with a mean for the 4 years of 0·045. Since an increase of 0·30 in the log catch is equivalent to a doubling, this mean regression implies that an increase of minimum temperature of 6·6 °F from one night to the next, is on an average associated with a doubling of the number of insects captured. The population changes between successive nights are the lowest that it is possible to get by this technique, and we can assume that the greater part of this regression change is due to activity.

The seasonal variation for the mean rise of minimum temperature associated with doubling is 8·1 °F in the spring, 7·1 °F in the summer, 5·7 °F in the autumn, and 6·8 °F in the winter; the greatest effect is in the autumn and the least in the spring.

TABLE 6. SUMMARY OF PARTIAL REGRESSIONS ON MINIMUM TEMPERATURE, SUNSET TEMPERATURE AND NIGHT WIND ON THE ACTIVITY OF THE ORDER DIPTERA CAPTURED IN THE LIGHT TRAP AT KINCRAIG FOR EACH SEASON OF THE 4 YEARS

Full details in table F in the appendix.

	spring	summer	autumn	winter
		minimum temperature		
1955	—	—	0·067**	0·030
1956	0·027**	0·006	0·052**	0·054**
1957	0·052**	0·092	0·053**	0·049**
1958	0·030*	0·036**	0·054**	0·044**
1959	0·039**	0·031*	—	—
av. 4 years	0·037	0·042	0·057	0·044
		sunset temperature		
1955	—	—	0·052**	0·043*
1956	0·088**	0·107**	0·048**	0·055**
1957	0·065**	0·034*	0·049**	0·076**
1958	0·045**	0·061**	0·055**	0·065**
1959	0·054**	0·083**	—	—
av. 4 years	0·063	0·071	0·051	0·060
		night wind (log scale)		
1955	—	—	−1·320**	−0·613
1956	−0·859*	−1·405**	−1·120**	−1·259**
1957	−1·700**	−1·463**	−1·210**	−1·277**
1958	−1·305**	−0·495**	−0·801**	−0·523**
1959	−0·988**	−1·530**	—	—
av. 4 years	−1·213	−1·223	−1·113	−0·918

* significant, $<0·05$; ** highly significant, $<0·01$.

For the sunset temperatures the regression range is from 0·034 to 0·107 (again both extremes in the summer) with a general average of 0·061. Thus, an average rise of sunset temperature of 4·9 °F will produce a doubling of the catch, and the seasonal means are 4·8 °F for the spring, 4·2 °F for the summer, 5·9 °F for the autumn and 5·0 °F for the winter. There is considerably less seasonal variation for the effect of sunset temperature (at the beginning of the catch) than for the minimum temperature (near the end of the catch), also the effect per degree is greater.

The regression on night wind ranges from −0·49 to −1·70, with a 4-year average of −1·12. This implies that an increase of 1·0 in the log wind is associated with a decrease of 1·12 in the log catch. An increase of 0·30 in the log catch, equivalent to doubling, is therefore associated with a decrease of 0·27 in the log wind, or a reduction of 46 %, just under half. It is within the limits of error to say that doubling the wind halves the catch.

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Considering the seasons separately, the most remarkable feature is the great uniformity from year to year in the autumn regressions, particularly those relating to temperature. With the sunset temperature there is scarcely any difference, and certainly no significant difference between the regressions in the 4 years in spite of great differences in weather type and actual numbers of insects captured. Spring and winter give moderately consistent results but the summer values are very variable from year to year. It should, however, be

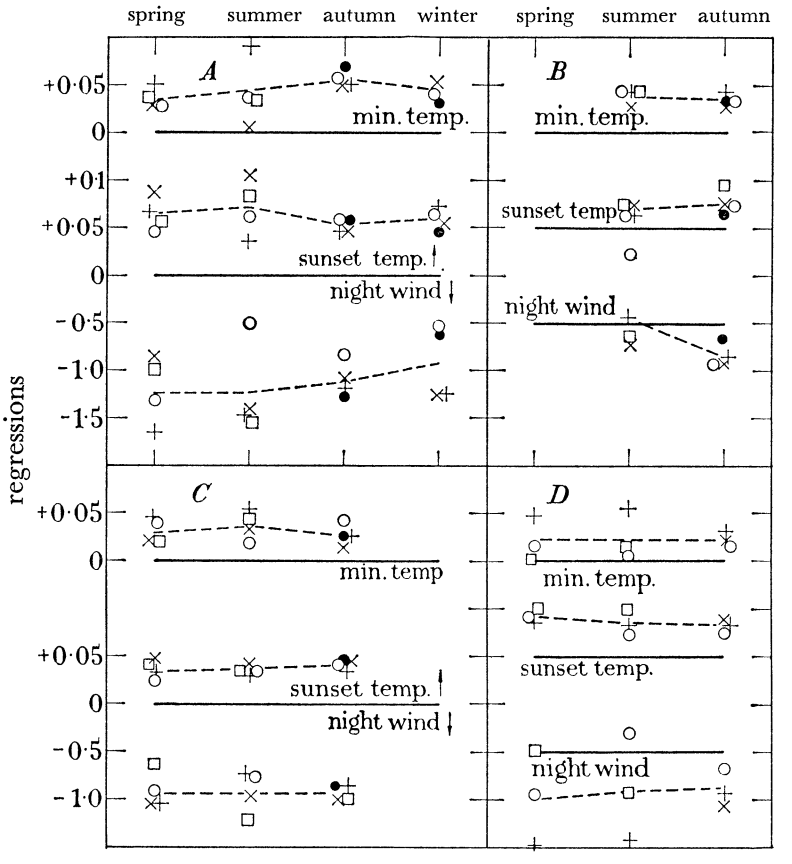

FIGURE 5. Seasonal changes in regressions for the effect of night wind and minimum and sunset temperature on different groups of insects, captured at Kincraig over a period of 4 years. *A* = Diptera in light trap; *B* = Simuliidae in light trap; *C* = Lepidoptera in light trap; *D* = Diptera in suction trap (3 years only). ● 1955, + 1956, × 1957, ○ 1958, □ 1959.

noted that in the calculation of regressions, the more closely two 'independent' variables are correlated (the 'independence' is of the dependent variable and not of each other) the more difficult it is to separate their effects and to get reliable estimates of these. Any small interference from extraneous reasons, may tend to send one regression up and the other down. In the summer months it will be noted that the very high minimum temperature regression in 1957 was associated with a very low sunset temperature regression. Similarly the very low minimum temperature regression in 1956 was associated with a very high sunset temperature regression. As these two variables are themselves highly positively correlated, this simultaneous swing in opposite directions is not unexpected. Had the two swings been in the same direction it would have been much more difficult to understand. It has already been pointed that neither of these extreme values is significant.

The efficiency of any set of partial regressions in accounting for the variation in the insect activity can be expressed by the relation between the original variance (mean square) and the residual variance after the effects of the particular independent variables have been allowed for. In table 7 (extracted from table F in the appendix) the residual variances for each each season are shown as percentages of the original. The less the percentage remaining unexplained the more likely it is that the factors studied are of importance. It will be seen that the percentage variance unexplained after allowing for the effects of minimum and sunset temperature and of night wind, ranged from 40 to 75 %. The average is lowest in the autumn and highest in winter and spring.

This residual variance includes of course, all other sources of variation and of error; such as the error of estimation from only one trap; the error due to a single unit in a small catch (in a catch of five insects an error of one is 20 % of the total); and the error due to the effect of the zero catch which is only partly reduced by the use of log $(n+1)$. That it is possible to account for 44 % of the variance of activity by three weather factor in only three months is of considerable interest.

Table 7. Residual variance, as a percentage of the original, in the analysis of the activity of Diptera captured in the light trap in relation to weather conditions

	spring	summer	autumn	winter
1955	—	—	51	70
1956	62	75	60	65
1957	53	45	50	40
1958	55	50	49	60
1959	69	59	—	—
4 years average	60	57	53	59
whole year	56			

(3) *Activity of Diptera, from 3-years catches in the suction trap*

The suction trap was not started till the end of June 1956. As winter catches were very low there are only three cycles of three seasons for analysis. The total number captured was 165000, or about 17 % of the numbers in the light trap in the same period.

This trap, to avoid interference with and by the light trap, had to be placed in a distinctly more sheltered portion of the garden, close to a large tree. Since the suction trap does not draw its catches from a long distance, the more confined outlook will not necessarily have much effect on the numbers of insects captured, but the microclimatic conditions, and particularly the wind, in the immediate neighbourhood would undoubtedly be less changeable than in the areas drawn on by the light trap.

For each season in the 3 years the partial regressions on minimum temperature, sunset temperature, and log night wind, together with their errors and the original and residual variance, are shown in table G (appendix) with a summary and average values in table 8 and figure 5*D*.

As in the analyses from the light trap the autumn regressions are much more regular from year to year than in the spring or summer. The sunset temperatures again give consistently higher regressions than the minimum temperature. The wind regressions are very variable from year to year, except in the autumn; but the lowest negative, and both positive regressions are not significant. On the other hand the mean value of the wind regressions changes little from season to season. This also applies even more to the minimum temperature regressions, where the average values for the three seasons vary only from 0·021 to 0·023.

TABLE 8. SUMMARY OF PARTIAL REGRESSIONS ON WEATHER FACTORS ON THE ACTIVITY OF DIPTERA CAPTURED IN THE SUCTION TRAP FOR EACH SEASON OF 3 YEARS

Full details in table G in the appendix.

	spring	summer	autumn
	minimum temperature		
1956	—	—	0·021**
1957	0·047**	0·057**	0·027**
1958	0·015	0·006	0·018**
1959	0·001	0·009	—
average	0·021	0·024	0·022
	sunset temperature		
1956	—	—	0·038**
1957	0·036**	0·020	0·034**
1958	0·041	0·048**	0·024**
1959	0·046**	0·040**	—
average	0·041	0·036	0·032
	night wind (log scale)		
1956	—	—	−0·533**
1957	−1·046**	−0·941**	−0·450*
1958	−0·426*	+0·176	−0·147
1959	+0·007	−0·426*	—
average	−0·488	−0·397	−0·377

* significant; ** highly significant.

TABLE 9. SUMMARY OF PERCENTAGE RESIDUAL VARIANCE IN THE ANALYSIS OF THE ACTIVITY OF DIPTERA IN THE SUCTION TRAP IN THREE SEASONS IN 3 YEARS

	spring	summer	autumn
1956	—	74	71
1957	65	54	74
1958	70	72	78
1959	83	82	—

Taking the average of the three seasons together, for the minimum temperature regression (0·022) a rise of 13·6 °F is required to double the catch; for the sunset temperature (0·036) the rise must be 8·3 °F. For the wind an increase of 1·0 in the log wind is associated with a reduction of 0·42 in the log catch. Thus a doubling of the catch is produced by a fall in the wind to approximately 20%. The positive regression for the wind in the summer of 1958 is difficult to understand; it is however not significant.

From table 9 (extracted from table G in the appendix) it will be seen that the residual variance, as a percentage of the original, is much higher in the suction trap than in the light trap (table 7).

Table 10 shows a comparison of the mean regressions for the three seasons and the 3 years in both light trap and suction trap. It will be seen that all the suction trap values are lower than those for the light trap. This difference may be partly explained by the sheltered position of the suction trap already mentioned. Temperature changes would be less than in the neighbourhood of the light trap; while the wind records, taken about 50 ft. above the ground, will much more closely represent the large open area drawn on by the light trap than the few yards round the suction trap. Part of the difference may also be due to the greater range of the light trap catches, up to 31 000 (log = 4·49) on a single night, as compared with only 3727 (log = 3·51) in the suction trap. This difference of range is reduced but not eliminated by the logarithmic transformation.

TABLE 10. COMPARISON OF THE REGRESSIONS FOR EACH SEASON FOR THE ORDER DIPTERA IN THE LIGHT TRAP (L.T.) AND THE SUCTION TRAP (S.T.) at KINCRAIG, FOR THE 3 YEARS IN WHICH BOTH TRAPS WERE WORKING

	spring		summer		autumn		average 3 seasons	
	L.T.	S.T.	L.T.	S.T.	L.T.	S.T.	L.T.	S.T.
minimum temp.	0·040	0·021	0·053	0·023	0·053	0·022	0·048	0·022
sunset temp.	0·055	0·041	0·059	0·036	0·051	0·032	0·055	0·036
night wind	−1·33	−0·49	−1·16	−0·39	−1·04	−0·38	−1·18	−0·42

(4) *The activity of the Lepidoptera, based on the light trap catches*

The catches of Lepidoptera in the light trap were sufficient for calculations in three seasons in 4 years. Catches in the winter months did not justify analysis. The total catch was approximately 50 000 insects, or 4·2 % of the Diptera in the same period. The highest catch in one night was 1140, log = 3·06.

TABLE 11. SUMMARY OF PARTIAL REGRESSIONS OF WEATHER FACTORS ON THE ACTIVITY OF LEPIDOPTERA CAPTURED IN THE LIGHT TRAP OVER A PERIOD OF 4 YEARS

Full details in table H in the appendix.

	spring	summer	autumn
	minimum temperature (°F)		
1955	—	—	0·029**
1956	0·022**	0·034	0·016**
1957	0·045**	0·055**	0·028**
1958	0·039**	0·017*	0·041**
1959	0·020**	0·046**	—
average	0·031	0·038	0·028
	sunset temperature (°F)		
1955	—	—	0·048**
1956	0·048**	0·044**	0·047**
1957	0·034**	0·033**	0·036**
1958	0·027*	0·036**	0·041**
1959	0·040**	0·036*	—
average	0·037	0·038	0·043
	night wind (log scale)		
1955	—	—	−0·882**
1956	−1·017**	−0·967**	−0·985**
1957	−1·140**	−0·719**	−0·872**
1958	−0·889**	−0·766	−1·000**
1959	−0·663**	−1·261**	—
average	−0·927	−0·928	−0·935

* significant; ** highly significant.

Table H in the appendix, shows the partial regressions on minimum and sunset temperatures, and on night wind, together with their errors, and the original and residual variances. Table 11 and figure 5*C* show the mean values in a condensed form.

All the sunset temperature regressions are significant, and all except one in the minimum temperatures and in the wind.

For the minimum temperatures the highest regression in any season was 0·055 and the lowest 0·016, with a mean over the whole period of 0·032, indicating that the catch would be doubled by a rise of 9·4 °F. For the sunset temperature the range is only from 0·027 to 0·048, with a mean of 0·039, requiring a rise of 7·7 °F to double the catch. The night wind regressions range from −0·66 to −1·26 with a mean of −0·94, indicating that the catch is doubled by a fall in the wind to 48 %. The most striking feature of the analysis is the great uniformity in all mean values, especially in the sunset temperatures and the wind. In the latter there is no significant difference between the mean values for the three seasons.

TABLE 12. SUMMARY OF PERCENTAGE RESIDUAL VARIANCE IN THE ANALYSIS OF THE ACTIVITY OF LEPIDOPTERA FOR 3 SEASONS IN 4 YEARS

	spring	summer	autumn
1955	—	—	57
1956	58	54	58
1957	56	44	70
1958	56	71	48
1959	67	47	—
4-year (seasons)	59	54	58
whole year		57	

The summary of the percentage residual variance, as in table 12, shows more uniformity, and in all three seasons just over 40 % of the variance is accounted for by the three weather factors of minimum and sunset temperatures and night wind on the nocturnal activity of the Lepidoptera.

(5) *The activity of the Simuliidae (Diptera) in the light trap*

As a fuller account of the biology and weather relations of this group of blood-sucking flies is being published separately (Williams 1962, in the press) only a summary is here included, as shown in tables 13 and 14, and figures 4*B* and 5*C*.

The analysis, for summer and autumn only, is based on the capture of approximately 17000 insects, as compared with over a million Diptera.

It will be seen that all but one of the regressions on minimum temperature are significant, but only three out of eight in each of the other two factors. The temperature regressions are moderately consistent both between seasons and between years. The effect of minimum temperature is, however, slightly larger per degree than that of sunset temperature. Unfortunately, we do not know at what period of the night the insects are active. From an average of all the data, the catch is doubled by a rise in minimum temperature of 8·6 °F and by a rise of 12·5 °F in the sunset temperature.

The effect of wind is very inconsistent, and apparently different from the other groups discussed. The summer regressions are, however, dominated by a highly significant positive value of +0·77 in 1958, which indicates much higher activity on windy nights, in spite of the partial elimination of temperature effects. The Diptera in the suction trap shows a similar, but not so high, positive regression in this particular summer. The regression in the summer of 1957 was also positive but not significantly so. In the autumns the wind effect, with a mean regression of −0·35, was comparable with that in other groups, but still on the low side. The Simuliidae, though small, are heavily built and very strong fliers. In some places abroad they have been shown to fly many miles between breeding and blood-feeding areas. This strong flight may be one of the causes of the low wind regression.

TABLE 13. SUMMARY OF REGRESSIONS OF WEATHER FACTORS ON THE ACTIVITY OF THE BLOOD-SUCKING DIPTERA OF THE FAMILY SIMULIIDAE CAPTURED IN THE LIGHT TRAP OVER 4 YEARS

	summer	autumn
minimum temperature		
1955	—	0·034
1956	0·023*	0·027**
1957	0·041**	0·037**
1958	0·043**	0·035**
1959	0·042**	—
4 yr. average	0·037	0·033
sunset temperature		
1955	—	0·017
1956	0·026	0·027*
1957	0·015	0·027**
1958	0·013	0·046**
1959	0·022	—
4 yr. average	0·019	0·029
night wind (log scale)		
1955	—	−0·152
1956	−0·208	−0·444*
1957	+0·024	−0·394*
1958	+0·772**	−0·431
1959	−0·197	—
4 yr. average	+0·098	−0·355

* significant; ** highly significant.

TABLE 14. PERCENTAGE RESIDUAL VARIANCE IN THE ANALYSIS OF THE EFFECT OF TEMPERATURE AND WIND ON THE ACTIVITY OF THE SIMULIIDAE

	summer	autumn
1955	—	75
1956	84	80
1957	51	70
1958	35	71
1959	64	—
4 years	59	74

The percentage residual variance, as shown in table 14, gives summer values, with one exception, lower than the autumn. That is to say that the summer activity is more closely related to these three weather factors than is the autumn; perhaps in the autumn some other factor, not considered here, is of greater importance.

III. Population changes in relation to previous weather conditions

(1) *Diptera in the light trap*

It has been explained above that to find the effect on population changes of weather conditions in the months previous to the trapping, the first process is to take the mean log catch per night for a particular month in each of the 4 years; correct this for any departure of that month's weather conditions from the average of the 4 years; and then to express these four corrected mean captures as departures from their own mean.

Table 15. The layout for data to study population changes for the months of May in 4 successive years, showing the correction of the observed mean log catch for departures from the normal of the weather factors

	1956			1957		
	departure	correction		departure	correction	
mean log catch	—	—	1·45	—	—	1·79
dept. and corrections						
min. temp.	+3·3	−0·122	—	−2·6	+0·096	—
sunset temp.	+1·6	−0·101	—	−1·4	+0·088	—
night wind	+0·23	+0·279	—	−0·02	−0·024	—
total correction	—	—	+0·056	—	—	+0·160
corrected mean	—	—	1·51	—	—	1·95
as dept. from 4-year mean	—	—	−0·26	—	—	+0·18

	1958			1959		
	departure	correction		departure	correction	
mean log catch	—	—	1·69	—	—	2·17
dept. and corrections						
min. temp.	−2·6	+0·096	—	+2·0	−0·074	—
sunset temp.	−2·7	+0·170	—	+2·6	−0·164	—
night wind	−0·6	−0·073	—	−0·14	−0·170	—
total correction	—	—	+0·193	—	—	−0·408
corrected mean	—	—	1·88	—	—	1·76
as dept. from 4-year mean	—	—	+0·11	—	—	−0·01

Regressions: min $T = +0{\cdot}0369$; sunset $T = +0{\cdot}0630$; night wind $= -1{\cdot}2129$.

As an example table 15 shows the calculations for the month of May in 1956–59. The first line shows the mean log catch for the month for the total Diptera. The next three lines show how temperatures and night wind of each of these months differed from their own mean, and the necessary corrections required from the regressions for activity (given beneath the table) as already calculated. The fifth line shows the total correction, and the sixth the new corrected mean log catch, which is an estimate of what the catch would have been if all four Mays had had similar average weather conditions. The last line shows the corrected means expressed as departures from their own 4-year average. These are used as the value for the dependent variables in the calculations of partial regressions, and are the best estimate of population changes that it seems possible to get from the trapping data.

For any one season of 3 months, each month is worked out, as above, to give a total of twelve values for the dependent variables. For the independent variables we have used the mean monthly minimum temperatures and the total months rainfall (each expressed as departures from their own 4-year average) for 1 month, 2 months, and 3 months previous to the month of trapping.

The observed and corrected mean catches per night for the Diptera in the light trap are shown in table 16, and the departures from the 4-year average of the corrected means are in the first column of table 20.

Partial regressions have been calculated from these data with various combinations of the independent variables up to a total of six. Table 17 shows a summary of these calculations giving the sign of the regression, an indication of its significance and (in the last column) the residual variance as a percentage of the original mean variance. This is in effect a measure of the efficiency of each particular combination of previous weather factors in accounting for the population changes observed.

Table 16. Observed and corrected mean log catch of Diptera in the light trap for each of the 48 months in which trapping was carried out at Kincraig

	1955	1956	1957	1958	1959
		A. Observed mean log catch			
Jan.	—	0·32	0·55	0·53	0·17
Feb.	—	0·36	0·38	0·65	0·25
Mar.	—	0·62	1·59	0·26	0·53
Apr.	—	0·83	2·03	0·96	0·95
May	—	1·45	1·79	1·69	2·17
June	—	1·73	2·30	2·57	2·43
July	—	2·66	3·05	3·05	3·12
Aug.	—	2·92	3·42	3·18	3·53
Sept.	2·32	3·06	2·68	3·14	—
Oct.	1·72	2·14	2·60	2·24	—
Nov.	1·98	1·81	2·03	1·98	—
Dec.	0·82	1·25	0·86	0·91	—
		B. Corrected mean log catch			
Jan.	—	0·44	0·05	0·64	0·66
Feb.	—	0·50	0·33	0·71	0·12
Mar.	—	0·56	1·13	0·85	0·47
Apr.	—	1·08	1·84	1·05	0·80
May	—	1·51	1·95	1·88	1·76
June	—	1·93	2·18	2·43	2·38
July	—	2·95	2·95	2·69	3·11
Aug.	—	3·31	3·55	2·95	3·22
Sept.	2·38	2·81	3·14	2·87	—
Oct.	1·93	2·16	2·62	1·99	—
Nov.	1·95	2·01	1·93	1·90	—
Dec.	1·05	0·93	0·81	1·01	—

It will be seen that the amount of the original variation in the insect population, within a single season from year to year that is accounted for by various combinations of the two factors considered, is high—sometimes very high—in the spring and quite good in the autumn. It was, however, very poor (except for one or two combinations) in the summer; and the residual variance was never below 75 % in the calculations for the winter months. On the whole either a four-factor analysis (rainfall and minimum temperatures of the *two* previous months) or a six-factor analysis (3 previous months) gave the best results, and the regressions calculated for these two combinations for each of the seasons is shown in table 18, together with their errors.

In the earlier work at Rothamsted only the six-factor analysis was carried out, but in this case 8 years' trapping, giving twenty-four values for each season of 3 months, was available. With only 4 years' data it is desirable to use as few independent factors as possible.

Table 17. Summary of the sign (+ and −) and the significance of a number of sets of partial regressions calculated with various combinations of rainfall and minimum temperature in the 3 previous months on the population of Diptera in the fourth month. Also the residual variance as a percentage of the original

no. of factors	T_1	T_2	T_3	R_1	R_2	R_3	res. var. (%)
			spring				
1	+ + +	.	.	.	.	.	57
2	+ +	.	.	+ + +	.	.	43
3	+ + +	+	.	+	.	.	42
4	+ + +	+	.	+	+ + ?	.	36
5	+	− − ?	+ + +	−	+	.	6
6	−	− − ?	+ + +	−	+	+	6
5	.	− −	+ + +	−	+	+	5
4	.	−	+ + +	−	+	+	5
1	.	.	.	+ +	.	.	73
2	.	.	.	+ +	+ + ?	.	58
3	.	.	.	+ +	+ +	−	63
			summer				
1	−	.	.	.	.	.	100 +
2	−	.	.	+	.	.	100 +
3	−	+	.	+	.	.	100 +
4	−	+	.	+	+	.	100 +
5	−	+	−	+	+	.	100 +
6	−	+ + +	+	+	−	− − −	51
5	.	+ + +	+	+	−	− − −	43
4	.	+ + +	+	.	−	− − −	41
1	.	.	.	+	.	.	100 +
2	.	.	.	+	+	.	100 +
3	.	.	.	+	−	− − ?	91
			autumn				
1	− − −	.	.	.	.	.	45
2	− − −	.	.	−	.	.	48
3	− − −	+	.	−	.	.	53
4	− − −	+	.	− − −	+ + +	.	31
5	− − −	+	−	− − −	+ +	.	34
6	− − −	+ +	− − ?	− − −	+ + +	− −	20
5	.	−	+	−	+	−	100 +
4	.	−	+	.	+	−	97
2	− − −	−	.	.	.	.	50
3	− − −	+ +	−	.	.	.	51
1	.	.	.	+	.	.	98
2	.	.	.	−	+ + ?	.	84
3	.	.	.	−	+	−	91
			winter				
1	−	.	.	.	.	.	95
2	−	.	.	−	.	.	89
2	−	+	.	.	.	.	100 +
3	−	+ + ?	.	−	.	.	76
4	− − ?	+ + ?	.	− − ?	+	.	75
5	−	+	+	−	+	.	75
6	−	+	+	−	+	+	88
1	.	−	.	.	.	.	100 +
2	.	−	.	.	−	.	100 +
3	.	−	+ +	.	−	.	81
4	.	−	+ +	.	−	−	91

− or + = not significant; − − or + + significant; − − − or + + + highly significant; − − ? or + + ? nearly significant.

From the known departures of rainfall and minimum temperature for each 3 consecutive months, estimates were made of the population departure in the fourth month, on the assumption of the applicability of the regressions. That is to say that, had the regression values been available before the trapping began, we would have had an estimate, or

Table 18. Summary of partial regressions for rainfall and temperature for 2 and 3 successive months on the population of Diptera as estimated from the catches in the light trap, also the percentage residual variance

months previous	spring	summer	autumn	winter
		2 months previous		
minimum temperature				
T_1	+0·0493 ± 0·0181**	−0·0051 ± 0·0315	−0·0989 ± 0·0243**	−0·0405 ± 0·0238
T_2	+0·0022 ± 0·0182	+0·0312 ± 0·0285	+0·0377 ± 0·0240	+0·0645 ± 0·0349
rainfall				
R_1	+0·1594 ± 0·0985*	+0·0390 ± 0·0751	−0·1447 ± 0·604*	−0·1408 ± 0·0750*
R_2	+0·1465 ± 0·0938*	+0·0518 ± 0·0823	+0·1300 ± 0·0503**	+0·0712 ± 0·0674
residual variance	36 %	100 %	31 %	75 %
		3 months previous		
minimum temperature				
T_1	−0·0001 ± 0·0108	−0·0059 ± 0·0214	−0·1206 ± 0·0230**	−0·0372 ± 0·0259
T_2	−0·0119 ± 0·0075	+0·0555 ± 0·0201**	+0·0609 ± 0·0287*	+0·0432 ± 0·0451
T_3	+0·1029 ± 0·0168**	+0·0199 ± 0·0204	−0·0585 ± 0·0327	+0·0378 ± 0·0826
rainfall				
R_1	−0·0700 ± 0·0614	+0·0410 ± 0·0707	−0·1895 ± 0·0521**	−0·0088 ± 0·0175
R_2	+0·0124 ± 0·0460	−0·0216 ± 0·0596	+0·1779 ± 0·0494**	+0·0027 ± 0·0149
R_3	+0·0396 ± 0·0334	−0·3024 ± 0·0887**	−0·0902 ± 0·0393*	+0·0034 ± 0·0148
residual variance	56 %	51 %	20 %	88 %

* significant; ** highly significant.

Table 19. Method of estimating population departures in a particular month from the known departures of temperature and rainfall in the three previous months and the regressions previously calculated for these factors

The month of March 1956 is taken as an example.

1 months previous	2 regression as calculated	3 known departure from 4-year mean	4 calculated population dept. (2) × (3)
	minimum temperature		
1 month	−0·0001	−2·7	+0·0003
2 months	−0·0119	−1·8	+0·0214
3 months	+0·1029	−2·1	−0·2161
	rainfall		
1 month	−0·0700	+0·65	−0·455
2 months	+0·0124	−0·24	−0·0030
3 months	+0·0396	+1·74	+0·0689

Total estimated population dept.	−0·174
Observed population dept.	−0·190

forecast, of the population departure at the beginning of the month of trapping. Table 19 shows an example of such a calculation for the month of March 1956 from the known rainfall and minimum temperature departures in December 1955 and January and February 1956. The summation of the six corrections gives an estimated departure from the normal of the Diptera population in the month of March as −0·174 on a log scale, which is equivalent to a reduction to 67 % of the normal. The observed value was −0·190 or 64 % of the normal.

Table 20. The corrected mean log catch of Diptera, as shown in table 16, expressed as departures for each month from the 4-year mean, as an indication of population changes; together with estimates of these changes calculated from regressions on minimum temperature and rainfall in the 2 or 3 previous months

	observed departures	calculated: 2 months	calculated: 3 months	observed departures	calculated: 2 months	calculated: 3 months
		1955			1957 (cont.)	
Sept.	−0·42	−0·28	−0·31	+0·34	+0·23	+0·33
Oct.	−0·25	−0·38	−0·34	+0·45	+0·40	+0·40
Nov.	0	+0·10	+0·13	−0·02	−0·18	−0·19
Dec.	+0·09	−0·02	−0·05	−0·12	−0·15	−0·14
		1956			1958	
Jan.	−0·01	+0·11	+0·05	+0·19	+0·20	+0·06
Feb.	+0·09	+0·09	+0·04	+0·29	+0·11	+0·09
Mar.	−0·19	−0·06	−0·17	+0·10	−0·12	+0·01
Apr.	−0·11	−0·05	−0·15	−0·14	−0·36	−0·11
May	−0·26	−0·16	−0·26	+0·11	−0·07	+0·07
June	−0·30	−0·14	−0·26	+0·20	+0·06	+0·08
July	+0·03	+0·17	+0·13	−0·23	−0·08	−0·17
Aug.	+0·05	+0·07	+0·04	−0·31	−0·04	−0·29
Sept.	+0·01	+0·13	0	+0·07	−0·07	0
Oct.	−0·01	+0·02	+0·07	−0·19	−0·05	−0·15
Nov.	+0·06	+0·05	+0·13	−0·05	+0·03	−0·09
Dec.	−0·03	−0·09	−0·04	+0·05	+0·24	+0·24
		1957			1959	
Jan.	−0·40	−0·16	−0·15	+0·21	+0·06	+0·03
Feb.	−0·09	−0·13	−0·03	−0·29	−0·08	−0·11
Mar.	+0·38	+0·37	+0·41	−0·28	−0·20	−0·24
Apr.	+0·65	+0·56	+0·67	−0·39	−0·26	−0·40
May	+0·18	+0·15	+0·13	−0·01	+0·08	+0·04
June	−0·05	−0·01	−0·09	+0·15	+0·08	+0·26
July	+0·03	−0·14	+0·05	+0·19	+0·06	−0·01
Aug.	+0·29	−0·05	+0·20	−0·04	+0·02	+0·04

Table 20 shows in the second and third columns the estimated departures of the Diptera population for each month of the 4 years based on calculations using the 2 and the 3 previous months' weather factors. In some cases the four factors estimate is closer to the observed (first column), in others the six-factor gives a better estimate. Table 21 shows comparison of the two season by season, indicating that the four-factor estimates are more frequently closer in the winter, but the six-factor estimates are better in the three other seasons.

Figures 6 and 7 show diagrammatically the observed and calculated population departures of the Diptera for weather factors of 2 and of 3 months previous, respectively Table 22 shows the same values as table 20, but smoothed to a 3-month running mean, and figure 8 shows these values diagrammatically. There is no doubt about the remarkable

Table 21. Comparison of the fit to the observed values of estimates of the population changes of Diptera, made from the minimum temperature and rainfall of 2 and 3 months previous

Equality is taken within one unit in the second decimal place.

	spring	summer	autumn	winter	year
2 months better	2	4	3	6	15
equal	1	0	2	3	6
3 months better	9	8	7	3	27

Table 22. Observed and calculated changes of population of Diptera, from table 20, smoothed to a 3 months running mean

	observed departures	calculated 2 months	calculated 3 months		observed departures	calculated 2 months	calculated 3 months
1955				**1957 (*cont.*)**			
Sept.	—	—	—		+0·36	+0·19	+0·31
Oct.	−0·22	−0·19	−0·17		+0·26	+0·15	+0·18
Nov.	−0·05	−0·10	−0·09		+0·10	+0·02	+0·02
Dec.	+0·03	+0·06	+0·04		+0·02	−0·04	−0·09
1956				**1958**			
Jan.	+0·06	+0·06	+0·01		+0·12	+0·05	0
Feb.	−0·03	+0·05	−0·03		+0·19	+0·06	+0·05
Mar.	−0·07	−0·01	−0·09		+0·08	−0·12	0
Apr.	−0·19	−0·09	−0·19		+0·02	−0·18	−0·01
May	−0·22	−0·12	−0·22		+0·06	−0·12	+0·01
June	−0·18	−0·04	−0·13		+0·03	−0·03	−0·01
July	−0·07	+0·03	+0·03		−0·11	−0·02	−0·19
Aug.	+0·03	+0·12	+0·60		−0·16	−0·06	−0·15
Sept.	+0·02	+0·07	+0·04		−0·14	−0·05	−0·15
Oct.	+0·02	+0·07	+0·07		−0·06	−0·03	−0·08
Nov.	+0·01	−0·01	+0·05		−0·06	+0·07	0
Dec.	−0·12	−0·07	−0·02		+0·07	+0·11	+0·06
1957				**1959**			
Jan.	−0·17	−0·13	−0·07		−0·01	+0·07	+0·05
Feb.	−0·04	+0·03	+0·08		−0·12	−0·07	−0·10
Mar.	+0·31	+0·27	+0·35		−0·32	−0·18	−0·24
Apr.	+0·40	+0·36	+0·40		−0·23	−0·13	−0·19
May	+0·26	+0·23	+0·24		−0·08	−0·03	−0·03
June	+0·05	0	+0·03		+0·11	+0·08	+0·99
July	+0·09	−0·07	+0·05		+0·10	+0·05	+0·10
Aug.	+0·22	+0·01	+0·19		—	—	—

fit between the observed departures and those calculated from previous weather conditions, especially when the 3 previous months are taken into consideration.

The closeness of fit of the estimate is also reflected in the amount of residual variance as shown in table 18. It will be seen that the four-factor analysis accounts for more of the variance in winter and spring but less in summer and autumn. In other words the weather of the third month previous is of less importance in the colder part of the year.

In the summer we get the curious result that, if only the 2 previous months are taken, no regression is significant and there is no reduction in the variance; but if the third month is added half the variance is accounted for, and both T_2 and R_3 are highly significant. This is again one of the difficulties arising from the high correlation between the weather factors themselves.

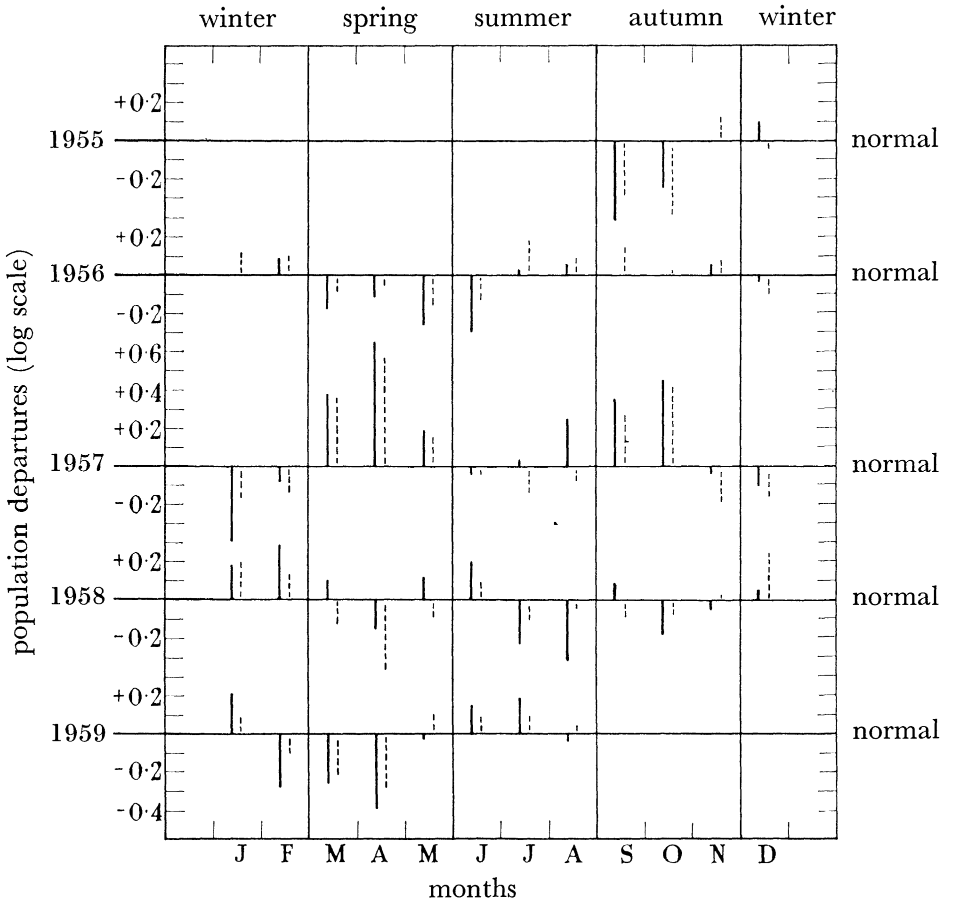

FIGURE 6. Population changes in Diptera, as departures from the four year average for each month, as shown by the mean log catch per month in the light traps (solid line), and as calculated from regressions on on rainfall and minimum temperature in the previous 2 months (dotted line).

Figures 9 and 10 show the seasonal changes in the regressions throughout the four seasons, for four and for six factors. They are not so easy to explain, from a biological point of view, as those previously obtained at Rothamsted. T_1 in both sets of analysis has a negative effect in the autumn. T_2 shows in both no relation in water and slight positive in the other seasons. R_1 in both is slightly positive in and distinctly negative in autumn. In the four factor analyses the seasonal changes are less erratic than in the six. In the latter we are straining the analysis by trying to obtain six regressions from the twelve values for each season. The Rothamsted results were based on 8 years and not 4.

(2) *Population changes in the Diptera from captures in the suction trap*

With only 3 years data for three seasons the analysis of the data from the suction trap was so unreliable as not to warrant publication. Even the 4 years available for the light trap was lower than desirable. There was also some evidence of a slow falling off in the

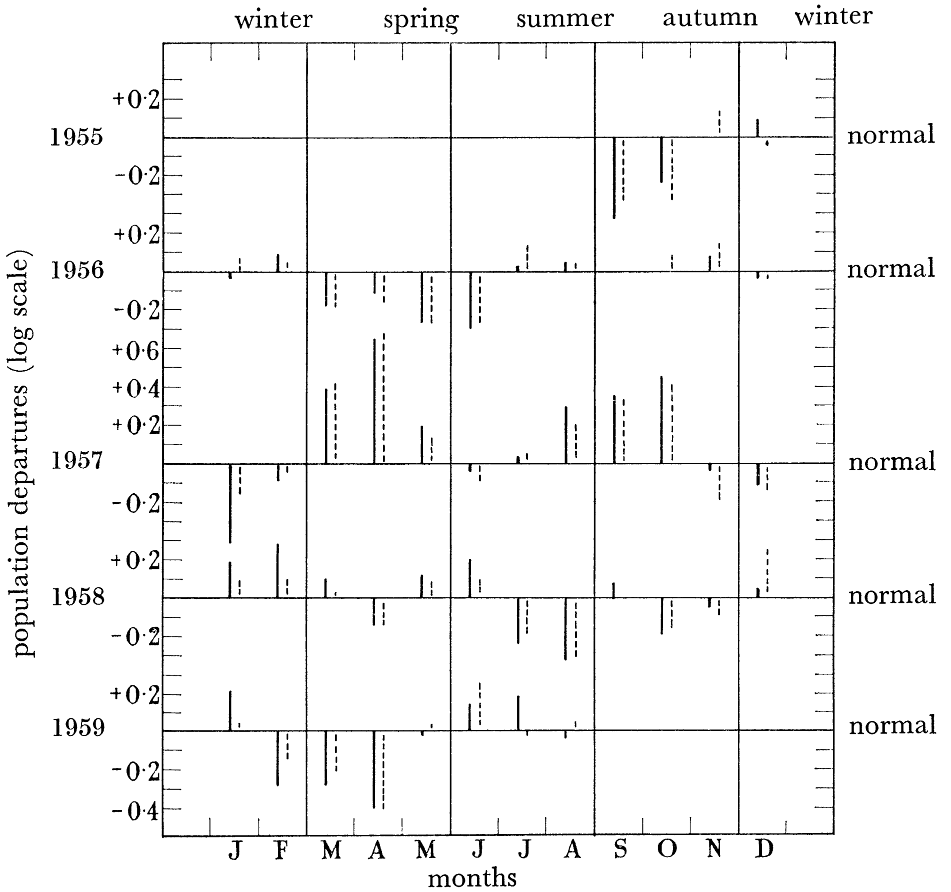

FIGURE 7. As figure 6 but calculated from regressions on rainfall and temperature in the previous 3 months.

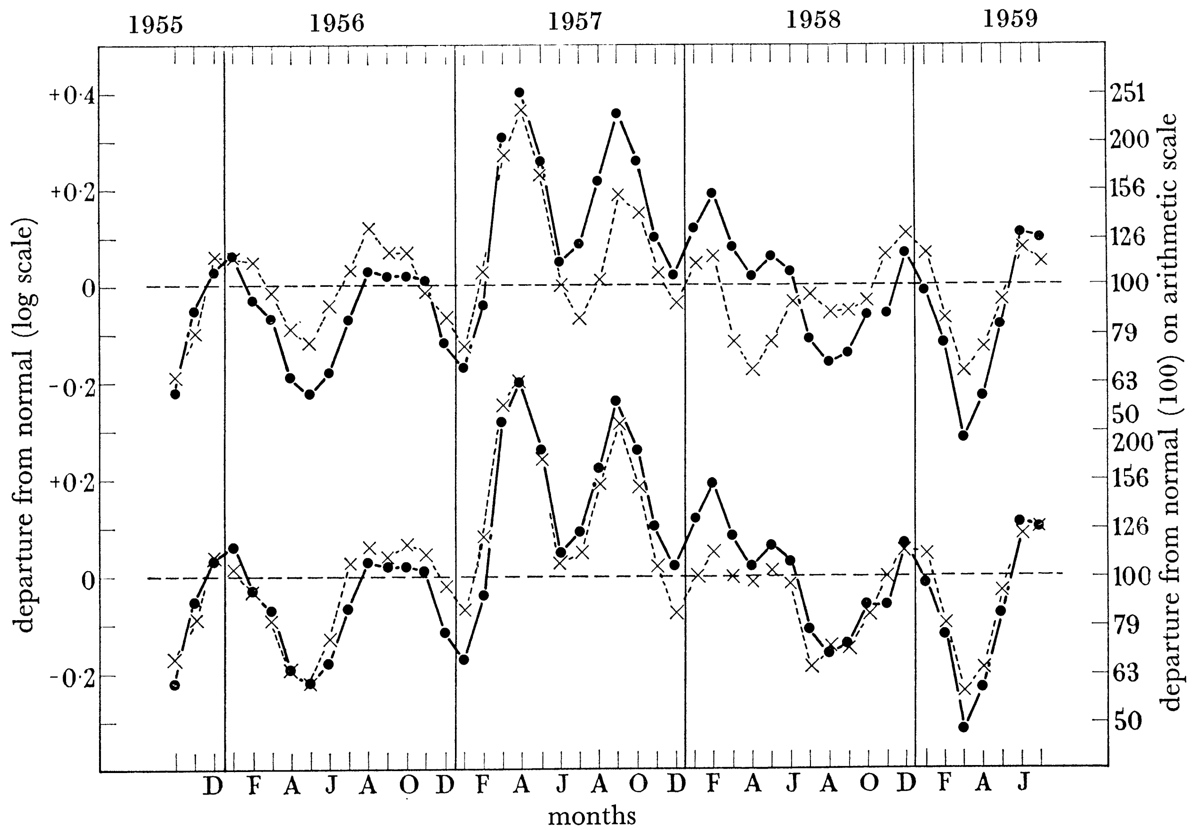

FIGURE 8. Observed (●) and calculated (×) departures from the 4-year mean of populations of Diptera, as shown in figures 7 and 8, but smoothed to a 3 months running mean for comparison with the results previously obtained at Rothamsted, see figure 2. Upper curves, 2 previous months: lower curves, 3 previous months. – – –, normal for month.

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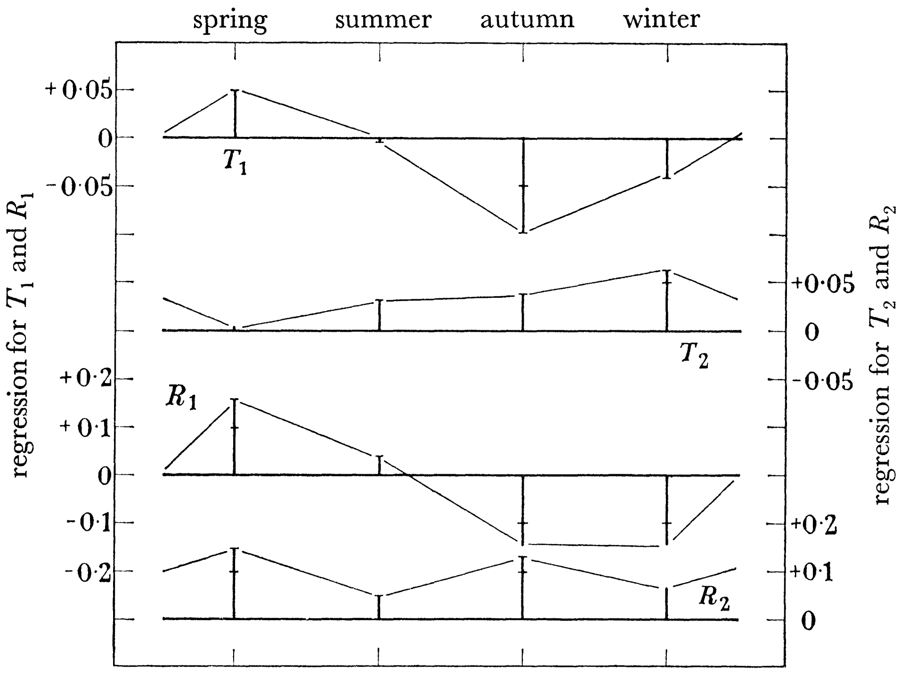

FIGURE 9. Seasonal changes of regression of minimum temperature and rainfall in the 2 previous months on population changes in Diptera, as indicated by the light trap.

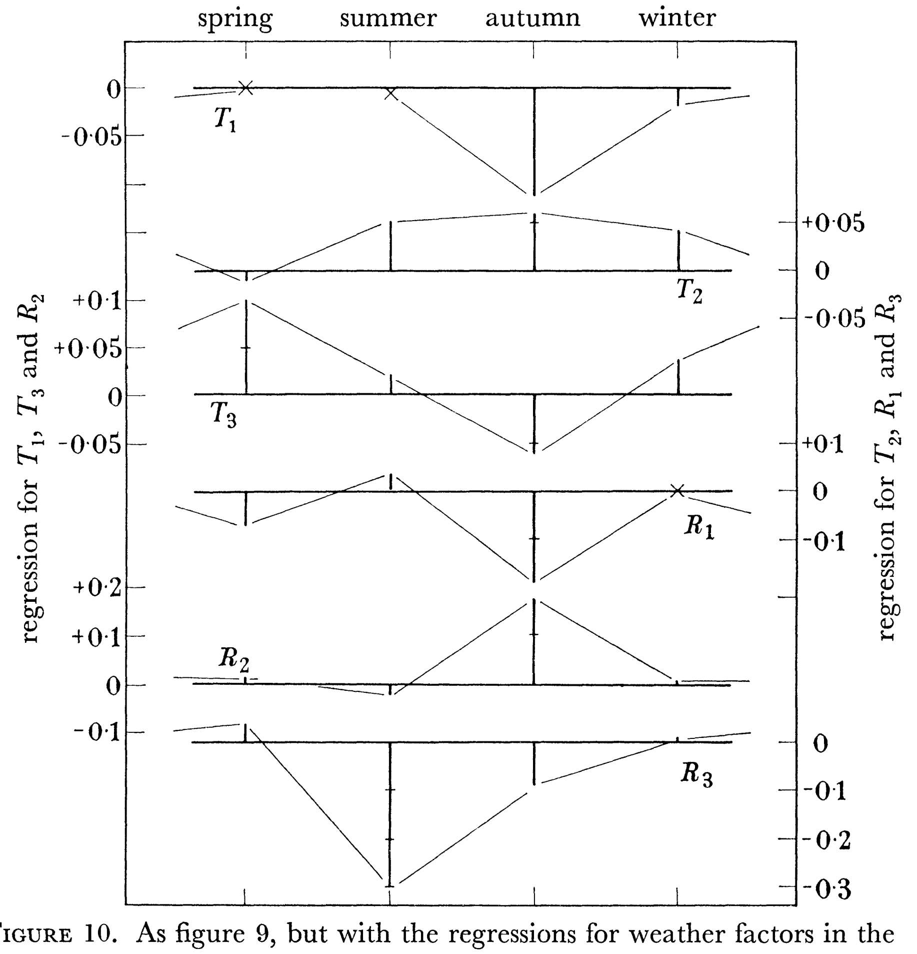

FIGURE 10. As figure 9, but with the regressions for weather factors in the 3 previous months.

efficiency of the fan in the suction trap which, while not affecting the day-to-day comparisons for activity, made the comparisons of monthly mean catches in the same month in different years very undesirable.

(3) *The effect of previous weather conditions on the abundance of Lepidoptera*

Table 23 shows in the first column the mean log catch per night (corrected for activity) for each month in spring, summer and autumn. Table 24 shows the regressions calculated for each season, one based on the temperature and rainfall of the 2 previous months, and the second on the 3 previous months. The regressions for 2 months give a very small residual

Table 23. Departures from the monthly mean populations (on a logarithmic scale) of Lepidoptera from captures in the light trap

First column as calculated directly from the mean log catch per month: second column as estimated from regressions on the minimum temperature and rainfall in each of the 2 preceding months: third column as in the second but from 3 previous months.

		estimated			estimated	
	observed	2 months	3 months	observed	2 months	3 months
		1955			1957 (*cont.*)	
Sept.	−0·26	−0·22	−0·18	−0·13	+0·09	0
Oct.	−0·03	−0·09	−0·13	+0·07	+0·02	+0·03
Nov.	−0·01	+0·11	+0·22	−0·24	−0·24	−0·21
		1956			1958	
Mar.	−0·10	+0·22	−0·10	−0·08	+0·14	+0·13
Apr.	+0·19	−0·09	+0·36	−0·07	+0·02	−0·16
May	+0·27	+0·10	+0·06	−0·28	+0·08	−0·14
June	−0·10	−0·04	−0·05	+0·05	+0·02	+0·03
July	+0·01	+0·07	+0·07	+0·08	+0·07	+0·06
Aug.	+0·25	+0·25	+0·25	−0·15	−0·17	−0·19
Sept.	+0·26	+0·04	−0·03	+0·12	+0·09	+0·21
Oct.	−0·13	+0·01	+0·03	+0·11	+0·09	+0·07
Nov.	−0·18	+0·03	−0·12	+0·43	+0·06	+0·10
		1957			1959	
Mar.	+0·08	−0·21	−0·11	+0·10	−0·15	+0·07
Apr.	−0·25	−0·02	−0·34	+0·12	+0·10	+0·13
May	−0·75	−0·34	−0·54	+0·75	+0·16	+0·61
June	−0·11	−0·08	−0·09	+0·17	+0·10	+0·11
July	−0·17	−0·20	−0·19	+0·08	+0·08	+0·07
Aug.	−0·08	−0·06	−0·04	−0·03	−0·02	−0·02

variance for the summer, but no reduction at all in the other two seasons. The 3 months calculations give good results for summer, and moderately successful ones for spring and autumn.

The second and third columns in table 23 show estimates of population changes from the regressions as previously described. Figure 11 shows diagrammatically the observed changes in population over the 4 years, as departures from the 4-year mean, together with the estimates from the 3-month (six factor) regressions. The estimates are reasonably close to the observed values.

For comparison with previous results at Rothamsted table 25 and figure 12 show the same observed and estimated changes smoothed to a 3-month running mean. In these the fit is exceptionally close.

An examination of the seasonal changes in regression (figure 13) shows moderately consistent results except in the case of T_3, in which the regression is highly negative and significant in the spring, and highly positive and significant in the autumn.

Table 24. Analysis of populations of Lepidoptera from the light trap

Regressions calculated to show the effect on population levels of minimum temperature and rainfall in 2, and in 3, previous months, with the errors of the regressions, and the original and residual variances.

	spring	summer	autumn
original variance	0·01297	0·01705	0·04330
		2 months	
T_1	−0·0149 ± 0·0404	−0·0019 ± 0·0069	−0·0155 ± 0·0401
T_2	−0·0062 ± 0·0406	0·0157 ± 0·0062*	0·0461 ± 0·0398
R_1	0·1976 ± 0·2192	0·0302 ± 0·0163*	−0·0017 ± 0·0999
R_2	−0·1852 ± 0·2090	0·1517 ± 0·0179**	0·0801 ± 0·0832
residual variance	0·01597	0·00227	0·04710
as %	no reduction	12·5 %	no reduction
		3 months	
T_1	0·0496 ± 0·0412	−0·0021 ± 0·0081	0·0311 ± 0·0335
T_2	0·0051 ± 0·0288	0·0178 ± 0·0076*	−0·0139 ± 0·0419
T_3	−0·1351 ± 0·0642*	0·0009 ± 0·0077	0·1251 ± 0·0478*
R_1	0·7269 ± 0·2334**	0·0286 ± 0·0266	0·0839 ± 0·0708
R_2	0·1237 ± 0·1766	0·1461 ± 0·0255**	0·0170 ± 0·0721
R_3	−0·3910 ± 0·1274**	−0·0249 ± 0·0334	0·1449 ± 0·0574*
residual variance	0·00734	0·00284	0·02349
as %	56·6 %	16·6 %	54·2 %

* significant; ** highly significant.

Table 25. Calculated departures from the normal of populations of Lepidoptera, as given in table 23, but smoothed to a 3-month running mean

	1955		1956		1957		1958		1959	
	obs.	est.	obs.	est.	obs.	est.	obs.	est.	obs.	est.
Apr.			+0·12	+0·11	−0·31	−0·33	−0·14	−0·06	+0·32	+0·27
May			+0·12	+0·12	−0·37	−0·32	−0·10	−0·09	+0·35	+0·28
June			+0·06	+0·03	−0·34	−0·27	−0·05	−0·02	+0·33	+0·26
July			+0·05	+0·09	−0·12	−0·11	−0·01	−0·03	+0·07	+0·05
Aug.			+0·17	+0·10	−0·13	−0·08	+0·02	+0·03		
Sept.			+0·13	+0·08	−0·05	0·00	+0·03	+0·03		
Oct.	−0·10	−0·03	−0·02	−0·04	−0·10	−0·06	+0·22	+0·13		

(4) *The relation of population changes in the Simuliidae (Diptera) to previous weather conditions*

As a fuller report on the effect of weather conditions in the Simuliidae is being published separately (Williams 1962) only a brief summary is given here for comparison with the other groups. In the 4 years over 17 000 Simuliidae belonging to ten species, were captured in the trap. The largest catch on a single night was 382 (log = 2·58) as compared with 31 000 (log = 4·49) in the total Diptera, within which the Simuliidae were included.

A number of regressions on the rainfall and minimum temperature in the previous 3 months were calculated. In the autumn months the results were very striking, leaving a residual variance frequently below 20 %, and in the case of all six factors, only 7 %.

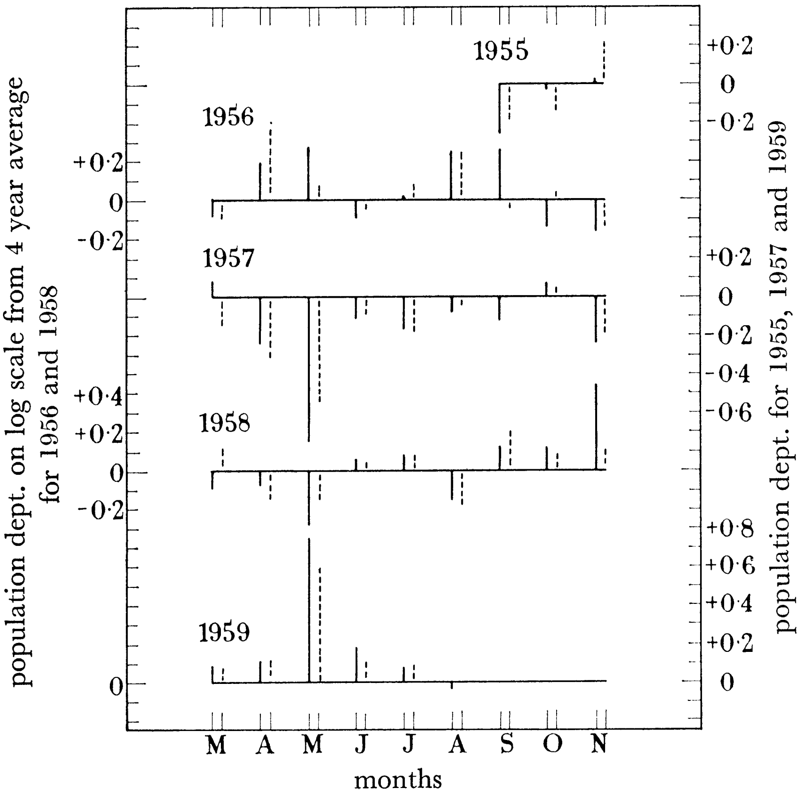

FIGURE 11. Population changes in Lepidoptera, as measured for each month from changes in the mean log catch per night in the light trap, and as estimated from regressions on the rainfall and temperature of each of the 3 previous months. ——, observed, – – –, calculated.

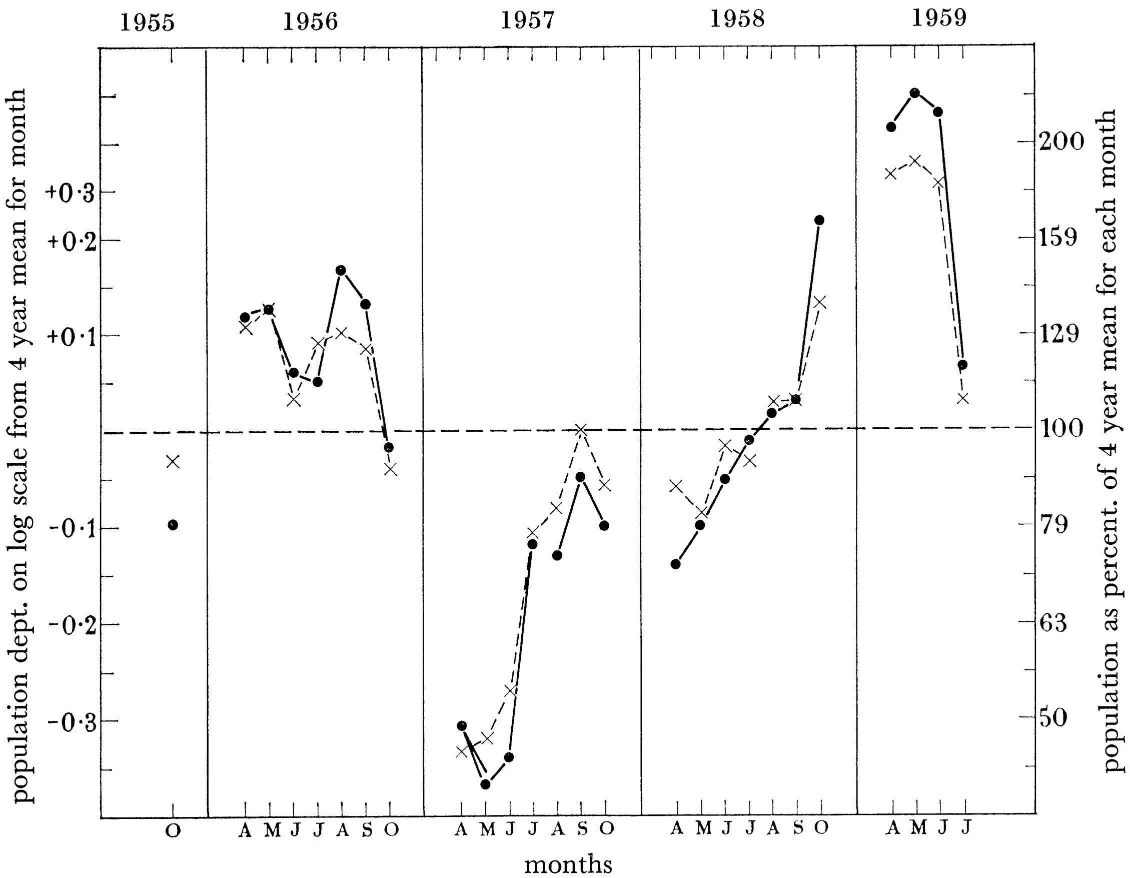

FIGURE 12. Observed (●) and estimated (×) population changes in Lepidoptera, as shown i figure 11, but smoothed to a 3 months running mean. – – –, 4 year normal for month.

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A summary of the chief autumn regressions is shown in table 26. Figure 14 shows the very close fit between the observed changes of population in this season and estimates made from the six regressions, and from that on R_2 only.

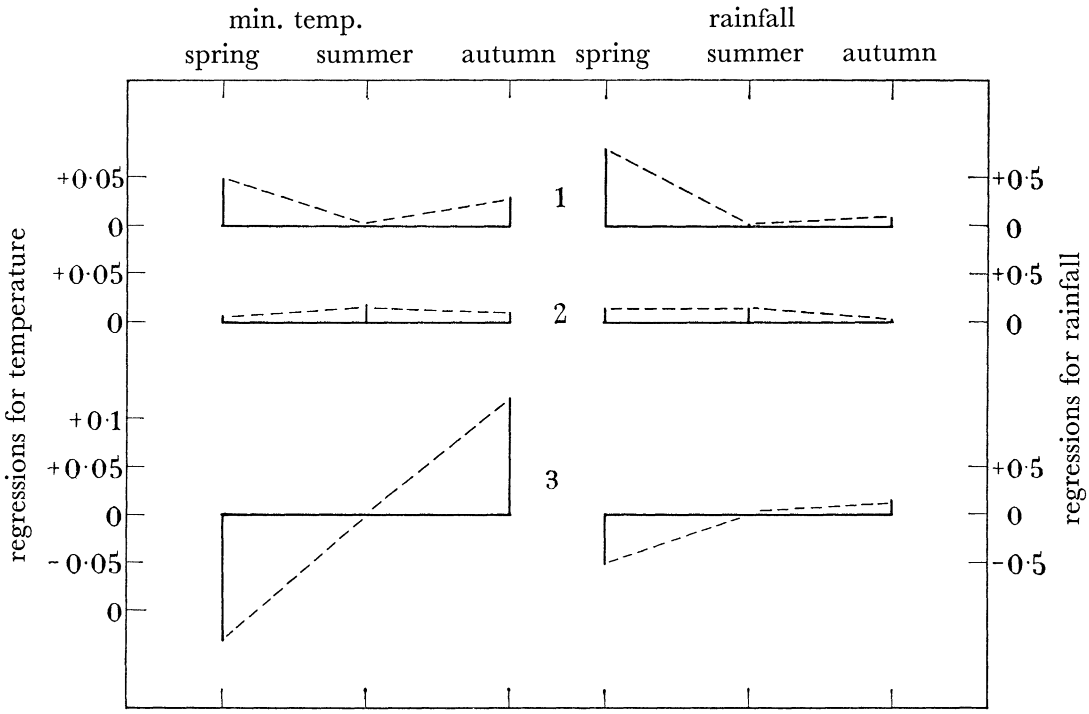

FIGURE 13. Seasonal changes in regressions showing the effect of minimum temperatures and rainfall in each of 3 previous months (1 to 3) on the population of Lepidoptera.

TABLE 26. ANALYSIS OF POPULATIONS OF SIMULIIDAE (DIPTERA) FROM CAPTURES IN THE LIGHT TRAP IN THE THREE AUTUMN MONTHS

Regressions and residual variances for various combinations of the factors of minimum temperature and rainfall in the 3 previous months

original variance = 0·06459.

no. of factors ...	6	4	4	2	3	1
T_1	0·0502**	0·0343*	—	—	—	—
T_2	−0·0245	−0·0076	0·0181	—	—	—
T_3	0·0429*	—	0·0050	—	—	—
R_1	0·0627*	0·0293	—	−0·0093	0·0082	—
R_2	0·1393**	0·1753**	0·1593**	0·1758**	0·1449**	0·1512*
R_1	0·0672*	—	0·0453	—	0·0275	—
residual variance	0·00457	0·00841	0·01080	0·01090	0·01122	0·0099
as %	7·1	13·0	16·3	16·5	16·5	15·2

* significant; ** highly significant.

A similar set of regressions for the 3 summer months gave almost no evidence of relation between weather and population. The best was that on T_1 only, the minimum temperature one month previous to the trapping. In this the regression was $0{\cdot}04111 \pm 0{\cdot}0212$ which is just on significant, but after allowing for this effect the residual variance is still 80 % of the original.

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I have suggested that this remarkable contrast between the summer and autumn population may be due to the fact that the small streams, running into the Spey from the hills and mountains on which the insects breed, are in the spring and early summer largely fed by melting snow and the drainage of bogs at high levels. Snow persists in quite distinct quantities up to the end of May on the hill tops and up to this time a warm dry spell may cause flooding. After this reservoir has dried up, however, the streams are very dependent on rainfall. In the exceptionally hot and dry summer of 1955 most of them dried up completely and it will be seen from figure 14 how low were the populations in the autumn following.

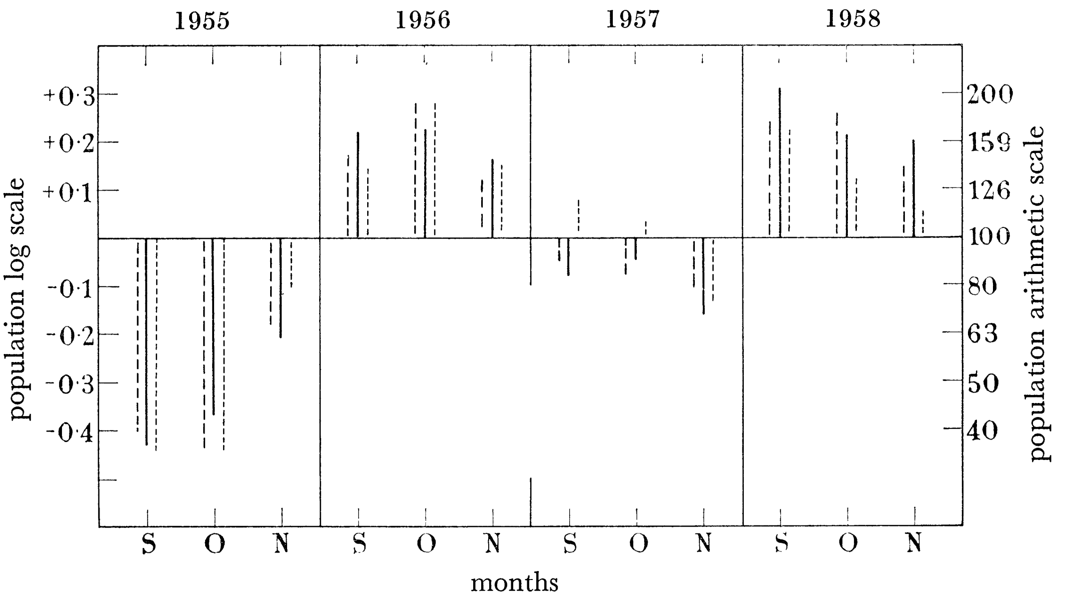

Figure 14. Population changes in the Simuliidae in the 3 autumn months as observed from the mean log catch per night in each month in the light trap (—), and as calculated from regressions on the rainfall and temperature in each of the 3 previous months (– – –), and also from the rainfall of the 2nd month previous only (-----).

IV. General discussion

As explained in the introduction, this work is a contribution to the study of the importance of weather factors in determining the fluctuations of insect populations. There have been for years discussion on the relative importance of the physical and the biological factors of the environment; and in general one may say that the density dependent factors—which are all biological—should help to prevent fluctuations, while the non-density dependent might help to increase them. A slow acting density dependent factor with a rapidly breeding injurious insect may not however have time to act beneficially (to us) before a major outbreak occurs.

In previous work at Rothamsted, over 8 years, I showed that a considerable portion of the variability of insect populations from year to year (as measured by a light trap) could be accounted for by changes in the rainfall and temperature of the three previous months (see figure 2). Not only were the estimates, made from partial regressions, fairly accurate, but the seasonal changes in regression (putting emphasis on the temperature in the winter and the rainfall in the summer and autumn) were what might be expected from purely biological reasoning.

The new work here presented was basically a check on the Rothamsted results in a new location in the British Isles, as far as possible from south-east England, and with a very different (and very severe) climate. A brief survey of the results, as far as population changes are concerned, shows that the same weather factors—rainfall and temperature in each of the 3 previous months—can account for as high a proportion, or even higher, than that found for all insects at Rothamsted. Figures 6, 7 and 8 show the observed and estimated fluctuations in the total Diptera: figures 11 and 12 for the total Lepidoptera and figure 14 for the autumn population of the blood-sucking flies, Simuliidae. In the case of the Simuliidae, which breed in small rapidly running streams, the six factors account for over 90 % of the autumn variance. In this case the connexion with the rainfall and the summer drying up of the streams is biologically satisfactory. In the other two groups, the immediate connexion of the separate factors is not so easy to determine, but more study should help to clear this up. The Rothamsted work was based on 8 years, giving more reliable calculations, than the four years at Kincraig.

It would appear therefore that this new work supports in general the previous conclusion that the weather factors of the 3 previous months play an important, and at times a dominant, part in determining the fluctuations of insect population. It is recognized that weather conditions may act directly on the insects concerned, or indirectly through their food supply or natural enemies; but in some cases we can already see the direct connexion and it is likely that any indirect effect would taken longer to develop.

If these conclusions are accepted, there is a real case for more attention to studies in the field on this branch of bioclimatics. Not only may it put into the hands of agricultural scientists a method of estimating in advance the probabilities and dangers of outbreaks but, even more important in the long run, the fact that we can estimate approximately such fluctuations indicates a beginning of understanding, and from understanding will come not merely cure, but prevention.

It is of interest to point out that with a different insect and in a different continent, Gunn & Symmons have shown (1959) highly significant negative regressions between previous rainfall (as measured by rain-gauges, or by the maximum height of a river) and outbreaks of locusts in Africa.

V. Summary

This paper describes some of the results of analyses of 4 years continuous trapping of insects at night by means of a light trap at Kincraig, in Inverness-shire, Scotland. The locality is about 800 ft. up in a wide valley in the Cairngorm mountains, which rise to over 4000 ft., and which has, for the British Isles, a severe continental type of climate. In the 4 years the air shade temperature ranged from −6 to 87 °F (−21 to 30·5 °C). The rainfall, at about 32 in., is low for this type of country.

Trapping was carried out almost every night, with a total catch of 1 382 000 insects, and a maximum on a single night of 31 000. The insects were sorted into orders (see table 3) and some smaller groups, and special studies were made on the total Diptera, the family Simuliidae, and the Lepidoptera in the light trap. A small suction trap was also run at

night for 3 years, and from it the Diptera, totalling about 165000, were studied. A small meteorological station was established close to the trap.

The analysis of the results, first by means of a logarithmic transformation, and then by partial regressions, was directed to two problems. The first was the relation between the changes in insect captures from night to night and the corresponding changes in temperatures and the night wind. The second was the changes in population level in the same month in successive years in relation to the temperature and rainfall of the 3 previous months.

A measure of the efficiency of any combination of weather factors in accounting for the changes in insect numbers was found in the relation, expressed as a percentage, between the residual variance of the trap catches after allowing for the regressions, and the original variance.

For the problem of activity in relation to current weather the three factors studied were the sunset temperature (at the beginning of the trapping period), the minimum temperature (at the end of the trapping period), and the run of the wind throughout the hours of trapping. Partial regressions were calculated for each season of three months, approximately 90 days, in each year.

For the total Diptera in the light trap most of the regressions were highly significant (see table 6), and the residual variance (table 7) varied from 53 to 60 % in the averages for each season in the 4 years. The average regressions over the 4 years indicated that the catch would be doubled by a rise of 6·6 °F in minimum temperature; of 4·9 °F in the sunset temperature; and by a reduction to one-half of the wind.

For the Diptera in the suction trap (table 7) the results, for 3 years only, were less significant, except in the autumn months, and smaller. The catch was doubled in association with a rise of 13·6 °F in the minimum temperature; of 8·3 °F in the sunset temperature; and by a fall of wind to about one-fifth. The residual variances were higher, ranging from 54 to over 80 %.

For the Lepidoptera in the light trap (table 11) the partial regressions, for spring, summer and autumn, are nearly all highly significant and the residual variance ranges from 44 to 71 %, with an overall average of 57 %, almost identical with that for the Diptera over the same seasons. The regressions indicate that the catch would be doubled by an increase of 9·4 °F in the minimum temperature, of 7·7 °F in the sunset temperature, and approximately halving the wind.

For the blood-sucking flies of the family Simuliidae, for which only summer and autumn values were available, the partial regressions (table 13) on minimum temperature were mostly highly significant; those on sunset temperatures significant in the autumn but not in the summer; and the wind regressions very irregular, only once highly significant and this a high positive value, quite abnormal and difficult to explain. The residual variance was 60 % in the summer and 74 % in the autumn. From an average of all data the doubling of the catch is associated with a rise of 8·6 °F in the minimum temperature, or 12·5 °F in the sunset temperature.

For the relation of population changes to previous weather conditions, various combinations of the six factors of minimum temperature (T_1, T_2 and T_3) and rainfall (R_1, R_2 and R_3) in each of the 3 preceding months were used in relation to the mean log catch for the month expressed as a departure from the 4-year average.

For the total Diptera the most successful combinations in accounting for variance were either T_1, T_2, R_1 and R_2, that is 1 and 2 months previous, or all six factors in the 3 months (see table 14). The residual variance was lowest in the autumn with 31 % for 2 months and 20 % for the 3 months, and in the spring with 36 and 56 %. But in the winter, when the catches are small and often zero, little variance was explained. Tables 20 and 22 and figures 6, 7 and 8 show the observed departures of the population from the normal for the time of the year, together with estimates made from the regressions for 2 and for 3 months. The fit is close and suggests a real biological relation.

With the Lepidoptera in the light trap the same two sets of regressions (see table 24) gave very successful estimates in the summer months, the percentage residual variance being only 12·5 % with four factors and 16·6 % with six; but for spring and autumn the four factors were not successful. The six factor analyses for these seasons both gave residual variances of about 55 %. Table 23 and figure 11 show the observed population departures and those calculated from the six regressions again giving a very close estimation.

With the Simuliidae the autumn changes showed a very close relation with the rainfall of 2 months previous (R_2), as seen in table 26, for which single regression the residual variance is only 15 %; while all six factors leave only 7 % of the original. Figure 14 shows the observed and calculated departures for the autumn months in the 4 years, giving an extremely close fit.

In the summer months (given in more detail in a separate report) the results were not significant, and showed no relation to previous rainfall. It is suggested that this may be due to the fact that the small hill streams in which the Simuliidae breed are fed in the spring and early summer largely from bogs and melting snow on the mountains, but by midsummer these reservoirs dry up and the streams then become very dependant on the current rainfall. In very dry summers they may dry up almost completely.

On the whole the results support completely the conclusions drawn from the earlier work at Rothamsted, that a high proportion of the changes in activity and in the abundance of insects can be associated with weather conditions at the time (in the case of activity) or in the previous months (in the case of population changes).

The investigations described in this report were carried out with the aid of a personal research grant from the Agricultural Research Council for the study of the relation of weather conditions to the activity and abundance of insects.

I am also indebted to the Statistical Department at Rothamsted Experimental Station for calculating the partial regressions on their computer and to the Meteorological Office for the loan of a screen and instruments for the weather observations.

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Appendix

Table A. Total number of Diptera captured each month in the light trap, and the mean log catch per night

	1955–56	1956–57	1957–58	1958–59	4-year average (arith. mean)
Sept.	13763	86383	34800	88520	55867
	2·32	3·06	2·68	3·14	2·80
Oct.	14680	11589	32850	12232	17838
	1·72	2·14	2·60	2·24	2·18
Nov.	6449	10089	10032	6881	8363
	1·98	1·81	2·03	1·98	1·95
autumn	34892	108061	77682	107633	82068
	2·01	2·34	2·44	2·45	2·31
Dec.	1324	4848	902	1457	2133
	0·82	1·25	0·86	0·91	0·96
Jan.	355	190	612	47	301
	0·32	0·55	0·53	0·17	0·39
Feb.	309	194	474	128	276
	0·36	0·38	0·65	0·25	0·41
winter	1968	5232	1988	1632	2710
	0·50	0·73	0·68	0·44	0·59
Mar.	336	2025	129	173	666
	0·62	1·59	0·26	0·53	0·75
Apr.	493	11523	1143	1109	3567
	0·83	2·03	0·96	0·95	1·19
May	4241	7680	2950	17372	8061
	1·45	1·79	1·69	2·17	1·77
spring	5070	21228	4222	18654	12294
	0·97	1·80	0·97	1·22	1·24
June	10634	33043	31409	39783	28717
	1·73	2·30	2·57	2·43	2·26
July	49285	61783	63839	82241	64287
	2·66	3·05	3·05	3·12	2·97
Aug.	60949	153032	102566	217555	133525
	2·92	3·42	3·18	3·53	3·26
summer	120868	247858	197814	339579	226529
	2·44	2·92	2·93	3·03	2·83

Table B. Total number of Simuliidae captured each month in the light trap, and the mean log catch per night

	1955–56	1956–57	1957–58	1958–59	4-year average
Sept.	191	1419	286	1714	903
	0·72	1·42	0·79	1·57	1·13
Oct.	214	1360	483	1093	787
	0·55	1·27	1·02	1·40	1·06
Nov.	176	557	266	653	415
	0·55	0·85	0·64	0·95	0·75
autumn	581	3336	1035	3466	2105
	0·61	1·16	0·82	1·31	0·98
Dec.	20	156	5	43	56
	0·07	0·32	0·03	0·20	0·15
Jan.	0	3	1	0	1
	0·00	0·03	0·01	0·00	0·01
Feb.	0	1	0	0	0
	0·00	0·01	0·00	0·00	0·00
winter	20	160	6	43	57
	0·02	0·12	0·01	0·07	0·05
Mar.	0	13	1	3	4
	0·00	0·11	0·01	0·03	0·04
Apr.	1	32	2	24	15
	0·01	0·21	0·02	0·13	0·09
May	30	52	31	371	121
	0·21	0·30	0·16	0·76	0·36
spring	31	97	34	398	140
	0·07	0·13	0·06	0·31	0·16
June	51	81	101	152	96
	0·32	0·35	0·47	0·65	0·45
July	155	404	804	1008	593
	0·58	0·87	1·02	1·22	0·92
Aug.	489	1716	1481	1322	1252
	0·78	1·46	1·39	1·38	1·25
summer	704	2201	2386	2482	1941
	0·56	0·86	0·96	1·08	0·87

Table C. Total number of Diptera captured each month in the suction trap, and the mean log catch per night

	1956–57	1957–58	1958–59	3-year average
Sept.	11 310	4 338	6 287	7 312
	2·40	1·99	2·12	2·17
Oct.	2 897	4 325	1 830	3 027
	1·68	1·88	1·68	1·75
Nov.	1 393	841	636	957
	1·23	1·19	1·11	1·16
autumn	15 600	9 504	8 753	11 296
	1·77	1·67	1·64	1·69
Dec.	259	108	132	166
	0·70	0·42	0·53	0·55
Jan.	52	16	1	23
	0·29	0·10	0·01	0·13
Feb.	27	4	7	13
	0·18	0·04	0·05	0·09
winter	338	128	140	202
	0·39	0·19	0·30	0·26
Mar.	184	35	21	80
	0·72	0·14	0·16	0·34
Apr.	2 126	283	580	996
	1·38	0·68	0·95	1·00
May	2 711	1 283	2 469	2 154
	1·62	1·48	1·68	1·59
spring	5021	1 601	3 070	3 230
	1·34	0·77	0·93	0·98
June	14 050	5 009	6 274	8444
	2·27	2·05	2·04	2·12
July	34 212	12 697	11 553	19 487
	2·89	2·50	2·49	2·63
Aug.	15 813	8 953	12 448	12 405
	2·50	2·36	2·50	2·45
summer	64 075	26 659	30 275	40 336
	2·55	2·30	2·34	2·50

Table D. Total number of Lepidoptera captured each month in the light trap, and the mean log catch per night

	1955–56	1956–57	1957–58	1958–59	4-year average
Sept.	590	3034	387	1937	1487
	1·11	1·79	0·90	1·64	1·36
Oct.	637	652	688	1190	792
	0·91	0·93	1·11	1·36	1·08
Nov.	371	253	259	2277	790
	0·81	0·55	0·61	1·37	0·84
autumn	1598	3936	1334	5404	3069
	0·94	1·09	0·87	1·46	1·09
Dec.	7	17	0	53	19
	0·06	0·10	0·00	0·21	0·09
Jan.	0	1	11	0	4
	0·00	0·01	0·03	0·00	0·01
Feb.	72	5	18	43	35
	0·15	0·03	0·13	0·24	0·14
winter	79	23	29	96	58
	0·07	0·05	0·05	0·15	0·08
Mar.	281	514	19	368	295
	0·52	1·00	0·10	0·73	0·59
Apr.	784	845	970	1397	999
	1·25	1·12	1·10	1·47	1·23
May	475	160	318	1162	529
	1·45	0·50	0·72	2·17	1·21
spring	1540	1519	1307	2927	1823
	1·07	0·87	0·64	1·46	1·01
June	614	708	1073	1404	950
	0·95	1·08	1·34	1·36	1·18
July	2189	2180	3990	3768	3032
	1·61	1·70	1·90	1·85	1·77
Aug.	3881	2113	3334	5185	3628
	1·88	1·69	1·87	2·01	1·86
summer	6884	5001	8397	10357	7610
	1·48	1·49	1·70	1·74	1·40

Table E. Summary of the main meteorological records at Kincraig during the months in which observations were taken

	temperature (Farenheit): abs. max. (°F)	mean max. (°F)	mean (°F)	mean min. (°F)	abs. min. (°F)	air frost days	grass min. extr. (°F)	ground frost days	rain: total (in.)	rain: no. of days	run of wind in 24 h (miles)
1955											
Jan	—	—	—	—	—	—	—	—	—	—	—
Feb.	—	—	—	—	—	—	—	—	—	—	—
Mar.	—	—	—	—	—	—	—	—	—	—	—
Apr.	—	—	—	—	—	—	—	—	—	—	—
May	73	54	45	36	28	7	21	11	2·23	20	—
June	72	63	53	43	27	1	22	3	0·62	12	—
July	87	74	61	48	35	0	32	0	0·35	4	—
Aug.	86	71	61	50	35	0	30	1	0·93	8	96
Sept.	75	60	53	46	38	0	33	0	2·47	19	132
Oct.	65	50	43	36	19	11	14	15	4·34	21	60
Nov.	58	47	41	34	17	9	14	16	0·58	16	64
Dec.	53	41	34	27	2	20	−4	19	6·06	21	139
year	87	—	—	—	—	—	—	—	(18·05)	—	—
1956											
Jan.	50	38	30	22	3	24	−1	26	3·01	19	146
Feb.	50	38	30	22	3	22	−1	23	2·70	21	101
Mar.	64	49	40	30	11	15	4	19	1·82	8	151
Apr.	63	52	40	28	15	17	9	23	1·67	14	113
May	80	59	49	40	21	6	14	8	1·54	19	173
June	80	61	51	41	30	4	24	9	4·00	20	114
July	75	64	54	43	29	1	23	6	3·82	17	120
Aug.	70	59	51	43	35	0	29	3	5·15	25	90
Sept.	74	62	52	42	26	4	21	6	3·88	17	98
Oct.	65	52	45	38	23	6	18	11	3·17	20	134
Nov.	51	46	40	33	18	11	14	17	2·04	17	156
Dec.	52	45	39	34	20	9	18	14	4·64	24	196
year	80	52	43	35	+3	119	−1	165	37·44	221	133
1957											
Jan.	54	43	37	30	19	14	12	24	4·62	24	195
Feb.	52	41	34	26	9	18	7	21	2·59	17	140
Mar.	66	51	44	37	25	4	21	10	2·78	18	155
Apr.	65	53	43	33	17	13	12	17	0·98	15	131
May	72	58	46	34	19	10	16	17	0·75	10	117
June	85	65	53	41	28	4	22	9	2·02	18	98
July	78	63	55	47	34	0	28	2	3·43	20	91
Aug.	77	63	54	44	33	0	28	4	3·68	20	107
Sept.	65	55	48	40	23	3	18	8	2·15	24	121
Oct.	58	52	46	39	25	7	20	14	2·37	25	145
Nov.	52	45	40	34	20	14	16	17	2·14	16	121
Dec.	51	42	36	29	10	16	6	22	3·54	20	159
year	85	53	49	45	+9	103	+6	165	31·05	227	131

TABLE E (*cont.*)

	temperature (Farenheit)								rain		
	abs. max. (°F)	mean max. (°F)	mean (°F)	mean min. (°F)	abs. min. (°F)	air frost days	grass min. extr. (°F)	ground frost days	total (in.)	no. of days	run of wind in 24 h (miles)
					1958						
Jan.	53	39	31	23	−6	23	(1)	24	2·49	19	162
Feb.	51	40	32	25	3	22	(10)	23	2·00	24	136
Mar.	49	40	33	25	−3	22	(1)	24	1·42	16	160
Apr.	63	40	41	32	15	12	13	17	1·34	21	142
May	69	56	45	34	19	9	11	18	2·75	22	115
June	74	63	52	42	32	0	27	5	1·01	14	89
July	80	64	55	46	29	2	25	3	4·26	19	95
Aug.	70	62	55	47	36	0	30	1	4·28	24	97
Sept.	74	63	54	45	29	1	24	5	3·20	14	109
Oct.	64	54	47	39	26	5	21	12	2·74	20	125
Nov.	57	47	39	30	15	18	11	25	0·91	11	99
Dec.	47	40	33	26	8	22	7	25	3·03	20	120
year	80	51	43	34·5	−6	136	+1	181	29·43	224	128
					1959						
Jan.	45	35·2	27·5	19·9	1	28	4	28	2·86	17	129
Feb.	55	45·0	35·4	25·7	0	15	−2	19	0·90	13	158
Mar.	57	49·3	40·0	30·6	16	15	12	22	1·27	16	153
Apr.	62	52·1	42·9	33·6	21	11	18	18	1·89	22	133
May	76	63·3	50·8	38·3	24	7	16	13	2·17	11	103
June	74	63·5	54·8	45·4	31	1	23	5	2·09	16	137
July	75	65·2	56·5	47·8	33	0	26	3	2·04	13	124
Aug.	80	66·9	60·1	50·3	39	0	30	1	1·11	13	128
Sept.	—	—	—	—	—	—	—	—	—	—	—
Oct.	—	—	—	—	—	—	—	—	—	—	—
Nov.	—	—	—	—	—	—	—	—	—	—	—
Dec.	—	—	—	—	—	—	—	—	—	—	—
year	—	—	—	—	—	—	—	—	(14·33)	—	—
av. of 3 complete years	(87)	52	45	38	−6	119	(−2)*	170	(32·6)†	221_1	131

* −4° occurred in December 1955.
† Both incomplete years had a rainfall below this rate for the months for which readings were available.

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Table F. Details of regressions, their errors, and the original and residual variances, in the analysis of the effect of temperature and wind on the activity of the Diptera captured in the light trap

	spring	summer	autumn	winter
year. No. of observations ...	—	—	1955 (90)	1955–56 (49)
min. temp.	—	—	0·0672 ± 0·0102	0·0296 ± 0·0169
sunset temp.	—	—	0·0522 ± 0·0121	0·0427 ± 0·0215
night wind (log scale)	—	—	−1·3200 ± 0·2508	−0·6134 ± 0·3535
variance. Orig:resid:*R* as %	—	—	0·712:0·366:51 %	0·860:0·605:70 %
year. No. of observations ...	1956 (84)	1956 (91)	1956 (90)	1956–57 (73)
min. temp.	0·0268 ± 0·0096	0·0064 ± 0·0184	0·0517 ± 0·0098	0·0544 ± 0·0155
sun temp.	0·0875 ± 0·0155	0·1065 ± 0·0275	0·0479 ± 0·0014	0·0548 ± 0·0139
night wind (log scale)	−0·8588 ± 0·3863	−1·4055 ± 0·2984	−1·1197 ± 0·2030	−1·2593 ± 0·2682
variance. Orig:resid:*R* as %	0·811:0·501:62 %	1·277:0·960:75 %	0·709:0·427:60 %	0·877:0·567:65 %
year. No. of observations ...	1957 (91)	1957 (92)	1957 (91)	1957–58 (67)
min. temp.	0·0522 ± 0·0108	0·0922 ± 0·1112	0·0535 ± 0·0109	0·0486 ± 0·0119
sunset temperature	0·0650 ± 0·0156	0·0339 ± 0·0158	0·0493 ± 0·0132	0·0760 ± 0·0165
night wind (log scale)	−1·6995 ± 0·2217	−1·4630 ± 0·2111	−1·2095 ± 0·2258	−1·2774 ± 0·3170
variance. Orig:resid:*R* as %	0·809:0·428:53 %	0·795:0·358:45 %	0·611:0·357:50 %	1·131:0·455:40 %
year. No. of observations ...	1958 (70)	1958 (92)	1958 (88)	1958–59 (49)
min. temp.	0·0298 ± 0·0112	0·0356 ± 0·0083	0·0541 ± 0·0078	0·0441 ± 0·0160
sunset temp.	0·0450 ± 0·0155	0·0611 ± 0·0132	0·0549 ± 0·0108	0·0649 ± 0·0233
night wind (log scale)	−1·3052 ± 0·2639	−0·4948 ± 0·1481	−0·8013 ± 0·1920	−0·5231 ± 0·0396
variance. Orig:resid:*R* as %	0·649:0·363:55 %	0·456:0·234:50 %	0·532:0·258:49 %	0·846:0·508:60 %
year. No. of observations ...	1959 (85)	1959 (91)	—	—
min. temp.	0·0386 ± 0·0181	0·0308 ± 0·0128	—	—
sunset temp.	0·0544 ± 0·1620	0·0832 ± 0·0173	—	—
night wind (log scale)	−0·9880 ± 0·2134	−1·5303 ± 0·2415	—	—
variance. Orig:resid:*R* as %	0·633:0·438:69 %	0·645:0·308:59 %	—	—

Table G. Details of regressions, their errors, and the original and residual variances, in the analysis of the effect of temperature and wind on the activity of the Diptera captured in the suction trap

	spring	summer	autumn
year. No. of observations ...	—	1956 (57)*	1956 (90)
min. temp.	—	0·0111 ± 0·0122	0·0214 ± 0·0066
sunset temp.	—	0·0320 ± 0·0180	0·0377 ± 0·0096
night wind (log scale)	—	−0·7769 ± 0·1680	−0·5334 ± 0·1363
variance. Orig:resid: *R* as %	—	0·315:0·233:74 %	0·273:0·193:71 %
year. No. of observations	1957 (86)	1957 (91)	1957 (86)
min. temp.	0·0467 ± 0·0093	0·0567 ± 0·0082	0·0270 ± 0·0092
sunset temp.	0·0356 ± 0·0133	0·0196 ± 0·0115	0·0342 ± 0·0109
night wind (log scale)	−1·0464 ± 0·1860	−0·9406 ± 0·1528	−0·4502 ± 0·1863
variance. Orig:resid: *R* as %	0·469:0·303:65 %	0·348:0·188:54 %	0·303:0·225:74 %
year. No. of observations	1958 (68)	1958 (88)	1958 (88)
min. temp.	0·0146 ± 0·0094	0·0064 ± 0·0074	0·0181 ± 0·0054
sunset temp.	0·0407 ± 0·0135	0·0479 ± 0·0120	0·0240 ± 0·0076
night wind (log scale)	−0·4263 ± 0·2134	+0·1763 ± 0·1388	−0·1472 ± 0·1346
variance. Orig:resid: *R* as %	0·327:0·229:70 %	0·250:0·180:72 %	0·162:0·127:78 %
year. No. of observations	1959 (77)	1959 (90)	
min. temp.	0·0014 ± 0·0078	0·0087 ± 0·0086	
sunset temp.	0·0463 ± 0·0122	0·0397 ± 0·0116	
night wind (log scale)	0·0074 ± 0·0575	−0·4263 ± 0·1624	
variance. Orig:resid: *R* as %	0·267:0·222:83 %	0·204:0·172:82 %	
3-year average			
min. temp.	0·0209	0·0239	0·0222
sunset temp.	0·0407	0·0357	0·0320
night wind (log scale)	−0·4884	−0·3969	−0·3769

* 2 months only.

Table H. Details of the regressions, their errors, and the original and residual variances, in the analysis of the effect of temperature and wind on the activity of Lepidoptera caught in the light trap

	spring	summer	autumn
year. No. of observations	—	—	1955 (86)
min. temp.	—	—	0·0285 ± 0·0079
sunset temp.	—	—	0·0477 ± 0·0093
night wind (log scale)	—	—	−0·8819 ± 0·1982
variance. Orig: resid: *R* as %	—	—	0·349 : 0·200 : 57 %
year. No. of observations	1956 (84)	1956 (91)	1956 (80)
min. temp.	0·0224 ± 0·0055	0·0343 ± 0·0821	0·0160 ± 0·0072
sunset temperature	0·0483 ± 0·0088	0·0443 ± 0·0123	0·0467 ± 0·0106
night wind (log scale)	−1·0175 ± 0·2179	−0·9669 ± 0·1332	−0·9855 ± 0·1468
variance. Total: resid: *R* as %	0·272 : 0·159 : 58 %	0·355 : 0·191 : 54 %	0·371 : 0·216 : 58 %
year. No. of observations	1957 (86)	1957 (92)	1957 (85)
min. temp.	0·0447 ± 0·0079	0·0550 ± 0·0069	0·0284 ± 0·0093
sunset temp.	0·0344 ± 0·0112	0·0328 ± 0·0098	0·0364 ± 0·0114
night wind (log scale)	−1·1402 ± 0·1624	−0·7190 ± 0·1312	−0·8722 ± 0·1963
variance. Total: resid: *R* as %	0·390 : 0·217 : 56 %	0·316 : 0·138 : 44 %	0·372 : 0·260 : 70 %
year. No. of observations	1958 (52)	1958 (88)	1958 (86)
min. temp	0·0394 ± 0·0098	0·0175 ± 0·0072	0·0406 ± 0·0060
sunset temp.	0·0273 ± 0·0145	0·0364 ± 0·0114	0·0406 ± 0·0089
night wind (log scale)	−0·8885 ± 0·2611	−0·7657 ± 1·2773	−1·0000 ± 0·1505
variance. Total: resid: *R* as %	0·469 : 0·264 : 56 %	0·245 : 0·174 : 71 %	0·318 : 0·152 : 48 %
year. No. of observations	1959 (90)	1959 (91)	—
min. temp.	0·0197 ± 0·0064	0·0464 ± 0·0079	—
sunset temp.	0·0400 ± 0·0096	0·0366 ± 0·0174	—
night wind (log scale)	−0·6633 ± 0·1267	−1·2605 ± 0·1497	—
variance. Total: resid: *R* as %	0·240 : 0·160 : 67 %	0·309 : 0·146 : 47 %	—
4 year average			
min. temp.	0·0315	0·0383	0·0284
sunset temp.	0·0375	0·0375	0·0429
night wind (log scale)	−0·9274	−0·9280	−0·9349

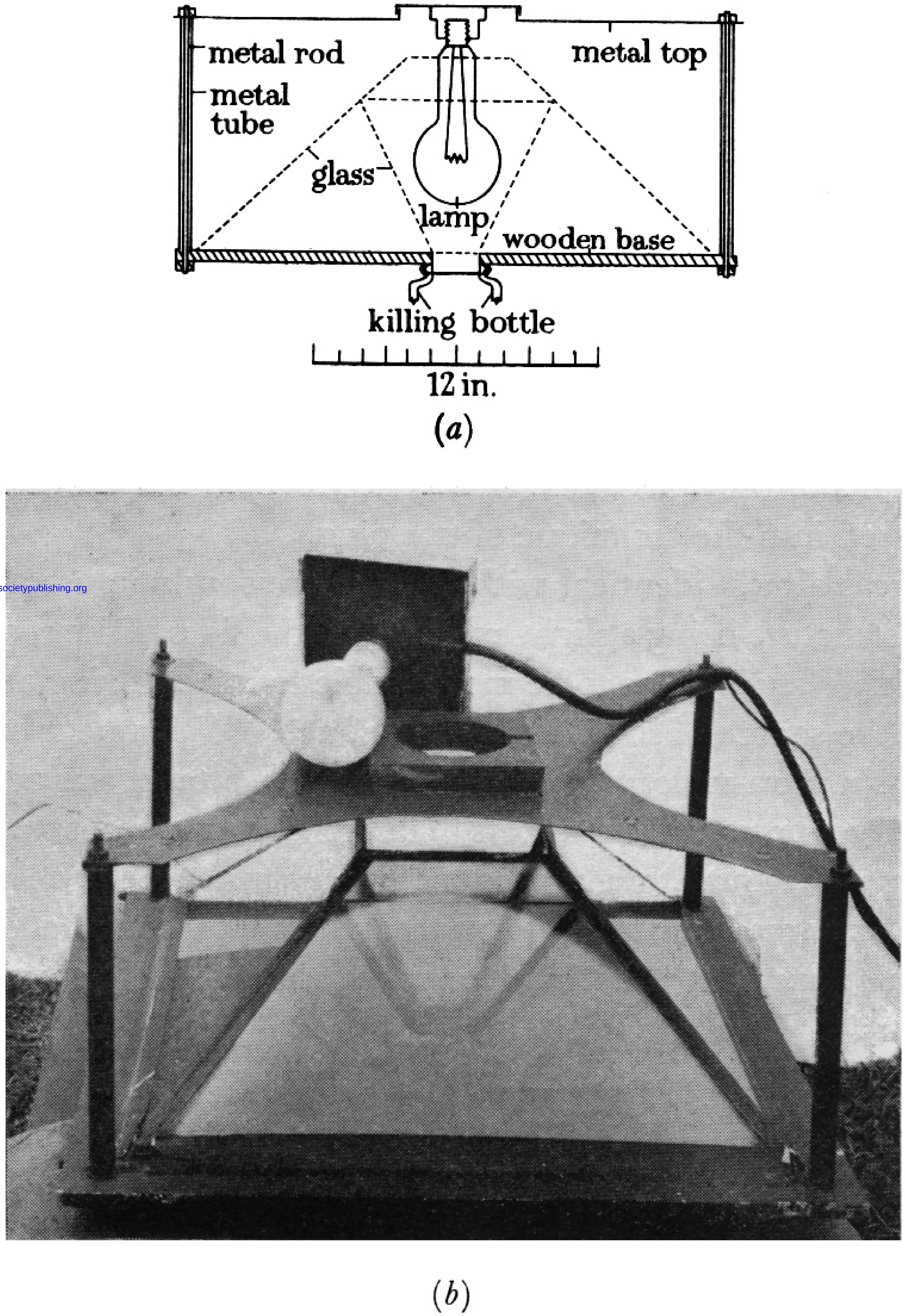

FIGURE 3. (*a*) Diagrammatic cross-section of the light trap used in these measurements of insect numbers.

(*b*) Photograph of the light trap in use in the experiments at Kincraig, with the cap holding the light bulb removed to show the method of fitting. It also shows the cut-away edges of the roof to allow a higher angle of light. The trap is approximately 22 in. square and 10 in. high.