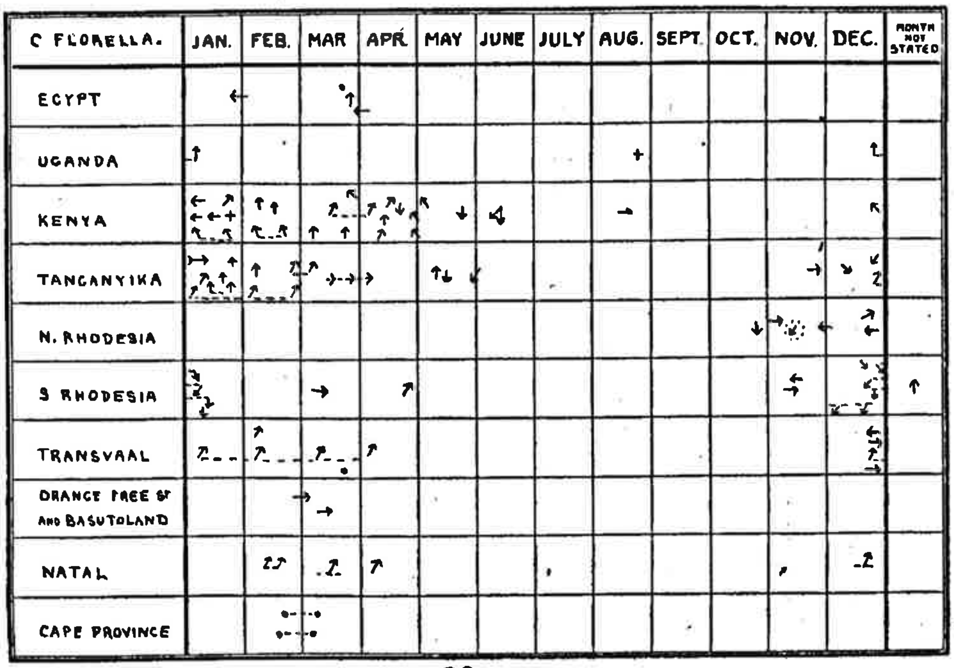

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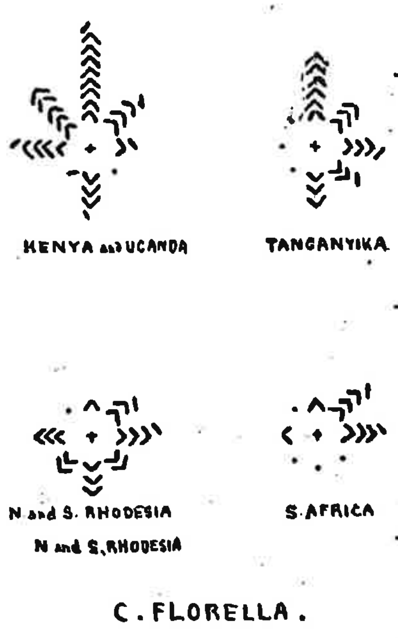
Fig. 39.—Diagram of recorded flights of *Catopsilia florella* in Africa.



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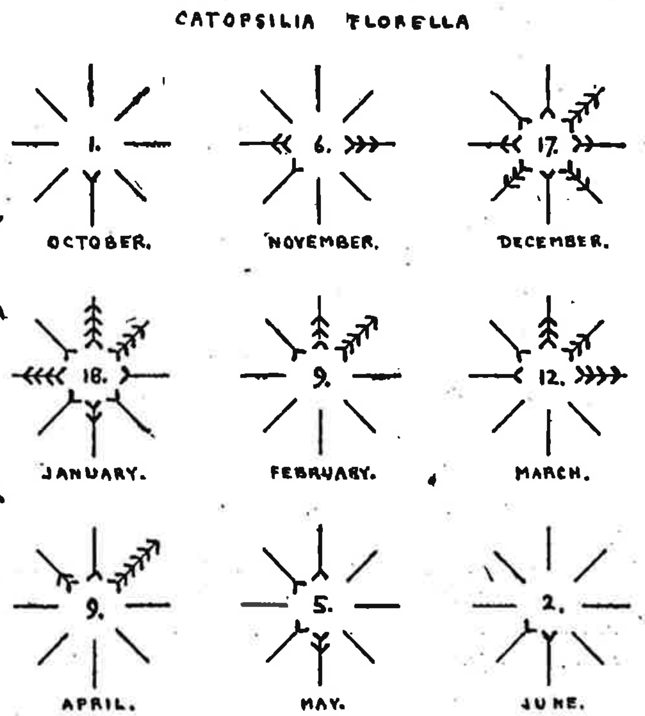

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Fig. 40.—Directions of flights of *C. florella* in different parts of Africa.

Fig. 41.—Direction of flights of *C. florella* in Africa in different months of the year.

practically no flights to the N. and N.W. (cf. Kenya and Uganda), while in S. Africa nearly all the flights are to the E. and N.E. It is difficult at the present state of our knowledge to suggest any explanation of these curious differences.

Fig. 41 shows the flights arranged according to the month. The majority are from November to April. It is interesting to note that there are no flights recorded with a southerly component during February, March and April. This may be accidental, and more records are needed from all areas before definite conclusions can be drawn.

(10) *Andronymus neander.*

New Records.

1926, March or April. Amani, Tanganyika. ?.
Big migration flying " in usual direction " (Burt mss.).

1930, March. Malindi, nr. Mombasa, Kenya. To W. by S.
Many hundreds flying more or less down the coast 8–15 feet above ground. Flying swiftly for some hours, little or no wind; about 5 p.m. smaller numbers flying in opposite direction, though still some flew in original direction. Two specimens captured. Graham (Williams 1933b).

1931, Oct. 28. Makimuga, Bwambo, Uganda. To N.
Large swarm flying at average height of 20 feet for one hour, one captured. Hazel (Williams 1933b).

1937, March. Amani, Tanganyika. To S.
Very dense migration for a week or more, 5–10 feet above ground (Nutman mss.).

1939, April. Amani, Tanganyika. To S.E.
Up to 200 per minute in narrow lanes of flight. Forty-two specimens captured (Kirkpatrick mss.).

The above new records together with those already published (Williams 1930b) indicate the very definite movement in March and April through Amani in N.E. Tanganyika, which has already been reported in eight years and probably occurs in most. However, in 1929 when I was in Amani until the 8th April, no trace of a movement had been observed up to that date in spite of a very

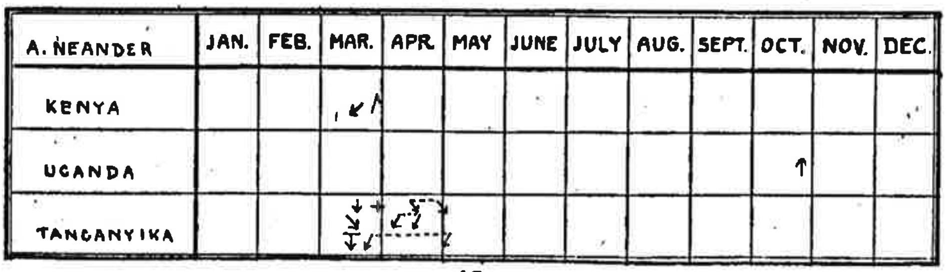

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FIG. 42.—Diagram of recorded flights of *Andronymus neander* in East Africa.

close watch. The recorded flights are shown diagrammatically in fig. 42. The only flight in March and April that is not towards the southerly quarter consisted of only a few individuals in a flight of other species; the only flight at another period of the year, in October, is towards the north.

(11) Subfamily ACRAEINAE.

In my previous summary only two species of this subfamily had been recorded as doubtful migrants; *Acraea violae*, which had twice been seen in small numbers taking part in mixed flights of other species in Ceylon; and *A. andromacha*, which had once been recorded in a flight in Queensland.

The ACRAEINAE have neither the habits nor the type of flight that one would associate with long-distance migration but several new records from Africa have now been received that put the occurrence of directional flights in the group beyond doubt, although it is not yet known over what distances they continue. The following records are new.

(1) W. Houston reported (Williams 1939b) that species of *Acraea* were taking part in a large mixed flight of many species that were moving to the east at Gatooma, Southern Rhodesia, on 7th–9th March 1934. The species were chiefly "Whites and Yellows" (including *C. florella*) with Danaines, *Atella phalantha* and others.

(2) In October 1937 at Trans-Nzoia, Kenya, Lt.-Col. Stoneham reported that *Acraea caldarena* and *A. disjuncta* were migrating in large numbers.

During the period 6th–13th October *A. caldarena* was passing in small numbers always towards the north. They were very swift on the wing and difficult to catch, although flying close to the ground. Specimens of both sexes were captured.

A. disjuncta was moving at the same time but in much larger numbers; "thousands" on the 7th, "hundreds" on the 8th, smaller numbers on the 9th and "hundreds" again on the 10th and 11th, and about 20 on the 13th. The flight direction was less constant, some days to the north and others to the west. The flight was leisurely, some low down and others high over trees. Both sexes were present.

The wind was strong from the north on the 9th, calm on the 10th and 13th and variable on the other days.

(3) A flight at about the same time was observed by Mrs. M. Tweedie at the Caves of Elgon, Kitale, Kenya. She observed a flight in mid-October 1937; not thick, but one day there were always 3–4 in sight moving steadily to the N.E. against the wind. One specimen was sent which was identified at the Natural History Museum as *Acraea jodutta*. Mrs. Tweedie adds that she had never noticed this species in the district before or after the flight.

(4) Mr. C. W. Chorley observed two flights of *Acraea bonasia*, *A. acerata* and *A. terpsichore* in S.W. Uganda in March 1940. The first flight was seen on the 14th March at Duma Point, Mawokota, Masumka District, on the west shores of Lake Victoria. The butterflies were coming across the lake from the Sesse district, flying towards the west, a distance of about 28 miles of open water. According to local fishermen they had been passing for two days in countless thousands.

On returning to the Luziro, Kyadondo, Mengo district, about 90 miles from the previous locality, he observed another migration also towards the west, which was also said to have been in progress for two days. Between the two localities no movement was noticed. A number of specimens were sent to Prof. G. D. H. Carpenter, who identified them as above.

(5) Stoneham (1934) records as migrants *Acraea melanoxantha* (in my reprint changed in mss. by the author to *oreas*) occasional; *A. terpsichore* not frequent; *A. caecilia* a strong migrant some years; *A. caldarena* very strong but irregular migrant; *A. egina* local; *A. asboloplintha* local; *A. neobule* a strong migrant some years; and *A. pharsalus* some years; but no details are given of any records in support of the above statements.

VII. Experiments in marking butterflies.

By G. F. Cockbill.

It has been realised by many workers that if migrant butterflies were suitably marked at some point on their route, and recaptured at some other point, much useful information would be forthcoming as to direction and speed of flight. Such marking experiments have been carried out with success with migrant birds, but, as yet, little progress has been made in the case of insects.

Marking experiments can yield two distinct kinds of evidence. If insects are marked and subsequently recovered at a distance from the locality of liberation, there is direct evidence of speed and direction of flight. This information is the most valuable, but the most difficult to obtain. The only case of a recovery at a distance known to the writer is that of a *V. atalanta*, marked at Stroud, Glos., by T. B. Fletcher and later believed to have been seen again at Reading, Berks. However, the observer could not get near enough to see the identification number of the insect. (Fletcher *in litt.*)

Information can also be obtained by noting the rates at which marked individuals of different species disappear from a locality. It is assumed that migrant species move away from a locality more rapidly than do non-migrants.

It is necessary to devise a method of marking the insect in such a way as to render it very noticeable, and to provide an identification number together with a well-known address to which information concerning recapture can be sent. The marking should be carried out on a large scale by a team of workers in areas where migrant species are most frequently and abundantly observed, and collectors should operate in areas situated concentrically around the area of marking.

Previous methods of marking Lepidoptera.

Various methods of marking have been used. Meder (1926) used a 0·8% alcoholic solution of ruby and scarlet dyes with a little shellac added. He marked the upper surface of the fore-wing with spots to denote the date of liberation and the under surface of the hind-wing with a mark to identify the locality of liberation. Of four to five thousand Pierid butterflies marked and liberated in July 1925, only five were recovered: four at Kiel and one at Lübeck.

Collins and Potts (1932) used aniline dyes mixed with 70% alcohol, and also artist's paints thinned with petrol, applied by means of a camel-hair brush for marking male Gipsy moths, *Lymantria dispar* L., when investigating the rate of spread of the pest in the U.S.A.

O. Querci (1936) records that in December 1929 at Cristo, near Santiago of Cuba, he marked a large number of butterflies by clipping their wings in various ways to verify that some underwent aestivation. He obtained recoveries as long after marking as June and August of the following year.

T. B. Fletcher (1936) attached small labels to the wings of butterflies by means of Canada Balsam, after removing a small patch of scales. His method of labelling was to use R for Rodborough, Stroud, Glos., England, where the insects were marked, and a series number to identify the specimen. He kept a descriptive record of each insect he marked.

During the season 1936 he marked 75 butterflies. One *V. cardui* remained at Rodborough for 10 days after marking, six *V. atalanta* for 2 or 3 days, one for 7 days and one for 12 days.

In 1938, he continued marking *V. atalanta.* His results are summarised later (p. 224).

In 1936, at Rothamsted Experimental Station, Mrs. K. Grant marked over 300 *V. urticae* by means of spots of coloured enamel paints placed on different parts of the insect. She reserved a special mark for each day when marking took place, but used no distinguishing mark for each insect.

Mr. D. A. Christianson of Hinckley, Minnesota, writes that during 1936 and 1937 he had marked 208 butterflies, mostly Monarchs, with serial numbers. His method was to attach to the thorax a thin cellophane label having a serial number, together with his box number and address. He says that the printing on the label was " so small as to be scarcely legible." He attached the labels by coating them with the adhesive from zinc oxide plaster.

Later he improved on his method by using as labels thin strips of metal foil in various bright colours. He was able to print on these labels in waterproof Indian Ink, or to die-stamp them. His method might be of use with the larger butterflies such as the Monarch, but we found on experiment at Rothamsted that the metal foil interfered with the flight of butterflies even as large as the Cabbage Whites.

Spots of coloured cellulose paints, arranged according to a key, were used by G. A. Brett in marking Vanessid butterflies in 1938. Each day had a special mark. He has kindly sent the results of his experiment to Rothamsted for inclusion and they will be discussed later. Here, again, individuals marked on one day were indistinguishable from one another.

W. F. Smith reports that he cut notches in the wings of several Monarch butterflies at Englewood, Fla., and recaptured four, one of which had been marked 11 days previously.

Since this section was written, Urquhart (1941) has described a method he has used in marking Monarch butterflies in Canada. A small hole, about $\frac{3}{16}$ of an inch in diameter, was punched with a paper punch, through the right forewing near the base and immediately behind the stout radial vein. The label, made of light paper gummed on one side, was bent over the front margin of the wing and glued to itself through the hole. It took only 15 seconds to punch the hole in this way and apply the label.

A further marking method.

After several tests with various labels and adhesives, the following method was found to be the most suitable for the purpose.

It was the combination of a label bearing a serial identification number and a well-known address attached to one wing with a plainly visible coloured mark on the other wing. It was considered that the address " London Zoo " was the best-known address with a conveniently short title, and the Zoological Society of London kindly agreed to its use and to co-operate in the scheme by sending us any information of recaptures that they might receive.

The address and number were written in waterproof Indian Ink, in mirror writing on labels cut from thin cellophane. The label was smeared on the written side with " Durofix " thinned with amyl acetate, and attached to one fore-wing of the insect. The other fore-wing was marked by applying with a camel-hair brush an alcoholic solution of basic fuchsin for white butterflies, and with a quick-drying white paint for the dark-winged species. An assortment of marks was obtained from the letters of the alphabet or from simple geometric designs, keeping a separate mark for each species on each day. The label and mark dried within a few seconds.

After a little practice it was possible to hold the insect with the first finger over the thorax and the thumb and second finger underneath, so that the wings were outstretched, allowing easy application of the label and mark. If the labels were written beforehand, the marking took only a few seconds for each insect.

After being marked, the insects were liberated, and the time, date, number, identification mark and species were card indexed.

All particulars of any recoveries were noted. During 1939 just over 400 butterflies were marked. Most of the butterflies were liberated at Rothamsted Experimental Station, but some batches were liberated from points situated about 1½ miles due north and due east of the Station on the chance that they would reappear in the neighbourhood of Rothamsted, thereby giving information of speed and direction of flight. However, none of these latter was recaptured.

The results of marking experiments at Rothamsted and elsewhere.

The total number of insects marked at Rothamsted in 1939 was 403, including the species *Pieris brassicae, P. rapae, P. napi, Vanessa io* and *V. urticae.* Of these 403, only 23 or 5% were recovered in the neighbourhood.

TABLE 25.

Recovery of butterflies marked at Harpenden in 1939.

Species	Total marked	Total recovered		No. recovered after days:							
		No.	%	1	2	3	4	5	6	7	8 and over
P. rapae	254	17	8	5	9	1 + (1)	1	2	0	0	1
P. brassicae	117	1	0·9	0	0	1	0	0	0	0	0
P. napi	23	1	4	0	1	0	0	0	0	0	0
N. io	6	3	50	1	2	0	0	0	0	0	0
A. urticae	3	1	33	0	0	1	0	0	0	0	0

In Table 25 the number and percentage recoveries are indicated, together with the number of recaptures after 1 to 8 days. It will be seen that there were more recoveries of *P. rapae* and *P. napi,* and far more of *V. io,* and *V. urticae* than of *P. brassicae.*

The numbers printed in brackets indicate that there is a doubt about the identity of the specimen (*e.g.* an observer noticed the mark on the insect, but not the number).

The numbers are too small to yield much real information, but if anything is shown, it is that during the experiment *P. brassicae* was moving out of the district more rapidly than *P. rapae.* This experiment, while not intended to demonstrate that *P. brassicae* was migrating, certainly lends support to this view.

Table 26A shows the results obtained by Fletcher in 1938. Here 101 *V. atalanta* were marked, and 25 different insects were recovered, *i.e.* 25%, of which more than half were not seen later than 2 days after marking. There is an indication that the butterflies were moving away from the locality of marking and that marked individuals were constantly replaced by fresh arrivals.

In the same table, the analyses of the experiments of K. Grant (B) and G. Brett (C) respectively are given. It is unfortunate that in both of these there was no provision made for identifying the individual insect. All individuals of a species marked on the same day received the same mark. This omission considerably detracts from the available information, since it leaves it an open question whether subsequent observations of insects on any particular day are to be regarded as being the same insect or as different insects.

TABLE 26.

Recovery of marked butterflies :—A, by T. B. Fletcher at Stroud in 1938. B, by K. Grant at Harpenden in 1936. C, by G. Brett at Esher in 1938.

Observer and species	Total marked	Recoveries				Recovered after days :							
		Max.		Min.									
		No.	%	No.	%	1	2	3	4	5	6	7	8 and over
(A) T. B. Fletcher													
V. atalanta .	101	25	25	25	25	10	6	6	4	4	3	2	6
(B) K. Grant													
A. urticae .	329	115	35	8	2·5	47	26	16	20	13	5	2	2+(1)
(C) G. Brett													
V. atalanta .	141	14	10	8	6	7	0	3	2	0	1	2	3
A. urticae .	77	35	45	13	17	17	9	5	3	0	1	0	3
N. io .	37	12	32	6	16	7	5	1	1	0	0	0	1
V. cardui .	6	0	—	0	—	—	—	—	—	—	—	—	—
V. c-album .	16	9	64	4	29	2	1	1	2	1	1	1	0

In the case of K. Grant's experiment on marking *V. urticae*, 32 individuals were marked on 14th September 1936 with a yellow paint spot at the base of the right fore-wing. The results show that the numbers and dates of recapture are as follows :—

On September	14th	32	marked.
,,	15th	8	recaptured and released.
,,	16th	8	,, ,,
,,	17th	6	,, ,,
,,	18th	5	,, ,,
,,	19th	3	,, ,,
,,	20th	2	,, ,,
,,	22nd	1	,, ,,

Since there was no distinction made between individuals, the records of recovery on any day may all relate to the same or to different individuals. The " maximum recoveries " would be arrived at by assuming that all records refer to different individuals, while the " minimum recoveries " would be those when it is assumed that only one individual of any batch marked was recovered. Both possibilities are considered in Table 26, where the maximum and minimum number and percentage recovery are shown.

It will be seen that the total recaptures from any batch marked may possibly be equal to, but cannot exceed, the number marked. Any recaptures in excess of the number marked each day have been disregarded in obtaining the "maximum recaptures," but the figures for the "recaptures after 1 to 8 days" include all recaptures. When all recoveries are regarded as being different insects, there are 35% recaptures, but when only one recapture is allowed for any day's marking, the percentage recapture is only 2·5%. The real value lies somewhere between these two, but the range is too great for the results to be of much significance.

This same wide variation between the percentage recaptures is seen in the cases of *A. urticae*, *N. io* and *V. c-album* marked by Brett (Table 26, C).

In the case of *V. atalanta*, however, there were at most only six insects which may have been seen on more than one occasion. The percentage recovery lies between 10% and 6%, and is the lowest of the species concerned.

It is doubtful whether Brett's figures are significant after allowance is made for the possibility of recapturing the same insect more than once, but if anything is shown, it is that *V. atalanta* and *V. cardui* have moved away from the area of marking faster than the other species.

VIII. The problem of orientation.

By C. B. Williams.

The problem of the method by which migrating insects determine the direction of their flights, and keep to a fixed direction over long distances and over long periods of time (sometimes many weeks) still remains unsolved and still remains one of the most fundamental questions in the study of migration.

One would expect some external guiding force or stimulus to be concerned in this direction determination, and so far the most frequently suggested possible stimuli are wind, light and the earth's magnetic field.

It is proposed to discuss the problem from the following point of view :—

(1) Is the structure of the wind such that it would be possible for an insect flying in the current to determine the direction of the wind from perception of pressure alone?

(2) If this is so, what evidence is there that insects are conscious of and allow for the influence of the wind direction?

(3) What new evidence is there on the relation of the wind to the direction of the migrating flights?

(4) Could the orientation be determined by any other method, and in particular by (*a*) sight or (*b*) the magnetic field.

Before entering on a discussion of the "wind" problem it will be interesting to bring forward an observation made by Mr. V. C. Carr on a definite double change in direction in a flight of Monarch butterflies (*D. plexippus*) with no apparent obstacle to account for it, and which appears at present quite inexplicable on any theory.

He writes, "In September 1935 I was fishing in Port Bay, a part of Lake Ontario on the south shore about 50 miles east of Rochester. On looking up I noticed a flight of Monarchs going south, flying about 60 feet above the water and 100 feet from land. A short distance to the south of me they made a sharp left turn, crossed the bay (about a quarter of a mile), then made a right turn and headed south again.

"At no time was there a massed flight nor did they extend over a space of more than 10 to 12 feet in width. At times I would say one or two thousand passed, and again only a hundred or so. Then there would be breaks in the flight for a short time. I anchored my boat under both of the turning points, and turns were made at the same two places all day. The flight stopped about an hour before dusk. The butterflies moved quite fast; I would estimate about 15 miles per hour."

Mr. Carr sent a sketch map of the locality which is reproduced in fig. 43.

The interest of the observation is great but at present it does not seem possible to suggest any reason for the change in direction or how to account for butterflies passing in the late afternoon changing direction at the same spot as those which passed many hours before.

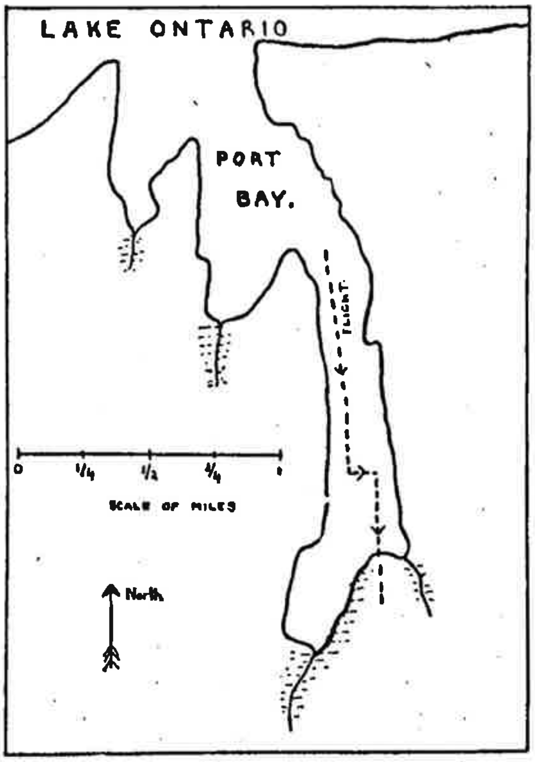

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Fig. 43.—Map of flight of *D. plexippus* in the south of Lake Ontario, with a double change of direction.

Wind structure and its possible effect on orientation and migration.

In my book on migration (Williams 1930 : 382) I discussed the problem of the effect of wind on an insect flying in a moving air current, and to what extent an insect might be able to determine the direction of the wind from the variations in pressure which it feels.

Very briefly, the conclusions I then came to were as follows:—(1) In an absolutely steady wind an insect (or bird) would be unable to determine the direction of the current. This is of theoretical interest only since winds are never steady. (2) In the practical case of an unsteady wind the insect would feel pressure on different parts of its body according to the acceleration (positive or negative) of the wind, because, owing to inertia of the insect, there would always be an appreciable time-lag between the change of velocity of the wind and that of the insect. From these pressures, however, the insect would only be able to determine the general direction of the wind if (*a*) changes in velocity of the wind (*i.e.* gusts) were more frequent in the direction of the wind than across it; and if (*b*) the gusts were asymmetrical, either rising more suddenly and dying away more gradually, or vice versa.

At the time of writing, these two ideas were contrary to the generally accepted theory of wind structure which, according to Taylor's Law, required that "excursions of the wind from uniform stream motion are similar in all directions." In other words, if one subtracted the mean velocity from a stream of air the residual motion of the particles would be backwards and forwards, up and down, and right and left, in equal proportion. There was, however, even then, a little meteorological evidence to throw doubt on the universal application of this law.

Since that time further experimental work has been carried out by the Meteorological Office, and in 1932 Giblett and Durst published a report on the wind structure as observed over flat land at Cardington in England, which shows that under certain conditions of air temperature both the conditions (*a*) and (*b*) may occur.

They came to the conclusion that, superimposed on the main stream-line motion of the wind, there are two kinds of changes :—

(1) Gusts and lulls which occur more frequently in the direction of the wind stream and which are asymmetrical, the wind rising rapidly to a maximum and falling more slowly to a lull. These are believed to be due to convectional eddies.

(2) Many smaller irregular oscillations, due apparently to frictional eddies, which are as likely to be in one direction as another, and so obey "Taylor's law."

The first type of variation occurs when the temperature gradient is adiabatic or super-adiabatic. That is to say, when the air temperature gets colder as we rise from the ground as rapidly as, or more rapidly than, can be accounted for by normal expansion (about 5·5° F. per 1000 feet).

When the temperature gradient is sub-adiabatic, and particularly when the gradient is reversed (*i.e.*, warmer air above), convectional currents cannot take place and therefore only the small irregular oscillations are found.

Adiabatic and super-adiabatic conditions most frequently occur during the daytime when the ground is heated by the sun's rays. In rough country with many obstructions, and in hilly country, the frictional eddies may greatly overshadow any convectional eddies.

The alternating development of gust and lull due to convection are of much longer duration than the small frictional eddies. The average convectional cell, the passing of which starts with the gust and ends with the lull, is, according to Durst, of the order of 3000–8000 feet, say a half to one and a half miles, in length. The passing of this may occupy several minutes. Fig. 44 shows part of one of the records from Giblet and Durst for such a gust and it will be seen that the gust occupied about twelve seconds with air accelerations up to about two feet per second^2 while the fall to the lull occupied several minutes and the retardations were of the order of 0·12 per second^2 or less than one-tenth of the force of the gust.

Given such conditions, an insect would be subjected to a pressure from the direction from which the wind is blowing during the sudden advent of a gust, and a much weaker pressure on the opposite side as the gust dies away.

It is important to note that the above discussion has only shown that it might be possible for an insect or bird to determine, from the pressure which it feels, the direction of the wind in which it is flying; but not that it does so.

Acworth (1929) has discussed at some length the effect of wind on flying birds, but his results are of little practical importance as he deals only with an absolutely uniform wind movement, and so comes to the conclusion that the

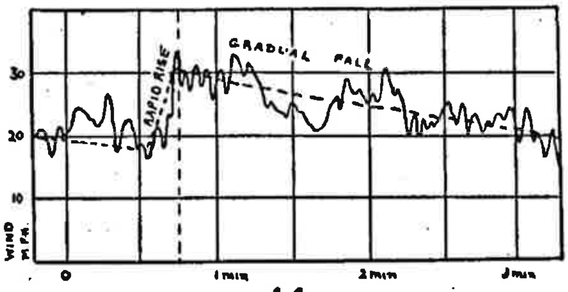

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Fig. 44.—Wind changes during the advent and passing away of a gust due to convectional eddy. After Giblett and Durst 1932.

flying bird or insect is not merely unable to tell (except by observing the drift) in which direction the wind is blowing, but even if there is a wind at all.

According to Acworth, if a bird wishes to fly from a point A to a point B with a cross wind (fig. 45), it is unable to appreciate the presence of the cross wind

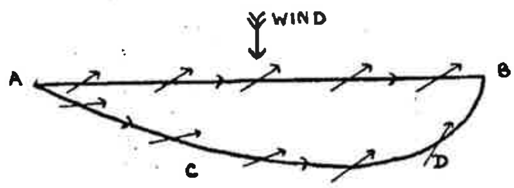

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Fig. 45.—Direction of flight of an insect across the wind from point A to point B, to illustrate Acworth's theory.

except by the fact that it is moved sideways relative to the relatively distant goal towards which it is flying and towards which it always heads in a straight line. As a result it takes a curved course A C D B and always arrives at B facing the wind. If, however, it could appreciate the wind direction it could allow for it at any moment by flying slightly skew to the desired direction, in which case the bird (or insect) would fly from A to B in a straight line.

On Acworth's theory, if a bird were flying to the north in still air and a side wind arose, the bird would be unconscious of this and would continue for some period at least to face the north and to fly through the air in the same direction and speed as before. Its speed and direction relative to the ground would therefore be the resultant of its old speed and that of the wind as shown in fig. 46, A and B, where the insect is presumed to be facing north with a wind from the west, of velocity equal to two-thirds of the speed of the insect. From an observer on the ground the insect would appear to continue to face to the north but to fly diagonally in a new direction (east of north) and also slightly faster (but this latter might be difficult to observe).

If, on the contrary, the insect were conscious of the wind direction and wished to continue to fly to the north it could do so by facing slightly to the west into the wind (fig. 46, C and D). In this case, from the point of view of an observer on the ground, the insect would on the advent of a side wind alter its body line slightly but continue to fly in exactly the same direction as before although at a slightly lower speed (though again this might be difficult to observe). In each case the insect during a wind will be moving (relative to the ground) at an angle to the line of its body, but in the first case the axis of the body will remain constant although the flight direction will alter with each change of the wind; while in the second its ground direction will remain unaltered but the axis line of the body will alter with each change of the wind.

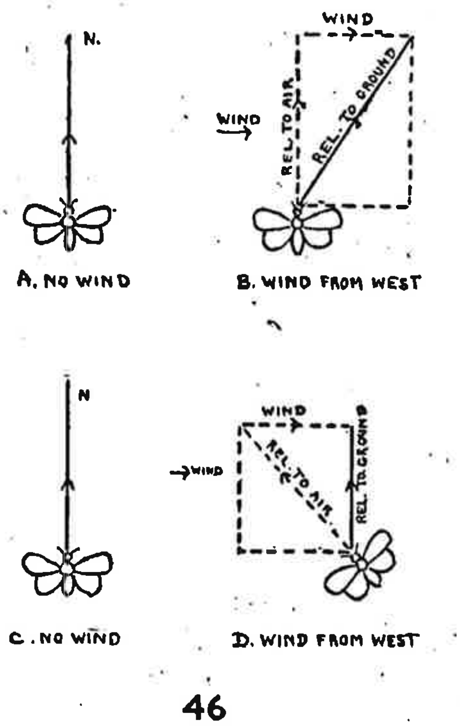

FIG. 46.—Diagram of two possible reactions of a flying insect to a side wind.

I have myself observed exactly the last condition in locusts in East Africa in 1928. In my report on the observations (Williams 1933c) I said, " At times it was obvious on close observation that the locusts were turning their bodies at an angle to the line of flight when the wind blew strongly. Thus, on 29th November at Voi [Kenya] I noted that when there was no wind the locusts were flying to the N.E. with their heads facing in this direction; when, however, the rather gusty wind blew from the S.E. the locusts' heads turned approximately to the east, although their motion relative to the ground remained the same."

In the case of these locusts it must be recognised that they were flying from 4 to 8 feet above the ground and so the possibility of visual observation of the sideways drift is not ruled out. It is difficult, however, to suggest what features of the rough ground beneath them could be used as " sighting points " to keep a constant line of flight.

Mr. P. R. Gleason also has observed butterflies flying at an angle to the wind as if to allow for its influence, in a manner quite similar to my own observation on locusts, during a thin movement towards the east of an unidentified Hesperiid butterfly in New Mexico, U.S.A., in March 1940. The wind was strong and variable, sometimes from the east and at other times from the south-east or south.

He writes: "I wish to mention another peculiarity of the flight which was different from anything I have seen before. When the wind was at a maximum from the south and the insects were travelling straight across it, they faced towards the S.E. as if to avoid being blown to the north of the point they meant to reach. The forward motion, quartering against the wind, drove them straight east, *i.e.* as if they were really headed E. instead of S.E. and no wind was blowing."

The possible effect of wind direction on the density of flights and their frequency of observation.

If a flight of butterflies 2 miles long were moving at a speed of 10 miles per hour in still air it would take 12 minutes to pass any fixed observation post. If this flight passes, as at A in fig. 47, into an area of contrary wind at 5 m.p.h. (so that the insects only move forward with a ground speed of 5 m.p.h.) the front butterflies will have passed only one mile into the new area before the last

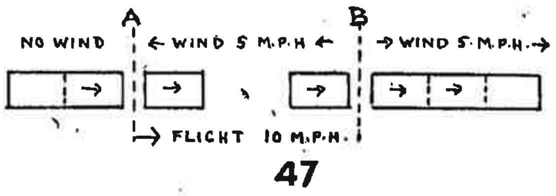

Fig. 47.—Effect of head and tail wind on the speed of a flight and the time taken to pass an observation point.

butterflies have left the old; in other words, the flight will be compressed so as to be only one mile long. But since it is only moving at half the speed it will take twelve minutes to pass an observation point.

If, as at B, it now passes into an area of following wind of 5 m.p.h. it will move forward at a ground speed of 15 m.p.h. and the first butterflies will have flown 3 miles before the rearguard has left the old area, *i.e.* the flight will now be three miles long. It will, however, still take exactly twelve minutes to pass an observation point.

In other words, unless there is deliberate spacing by the insect, the length of the flight from front to rear is directly proportional to the ground speed of the flight, in so far as this is affected by wind; but the length of time taken to pass is the same for all directions and force of the wind, and so the same number of insects will pass any observation point in the same time.

Therefore observations taken on the number of flights (or of insects) that pass a given observation line across the flight in a given period are independent on the force or direction of the wind.

If, however, an attempt is made to estimate the number of insects in a flight by counting those at any moment in a given area, or in a given line in the direction of the flight, the result will be affected by the changes in speed of the wind and will show a greater apparent density when the insects are flying slowly against the wind than when flying quickly with it.

A similar problem, and perhaps more easy to understand, arises if a number of cyclists start at regular intervals of say 15 seconds to cycle up a hill and down the other side. After a short period their distribution will be shown as in fig. 48.

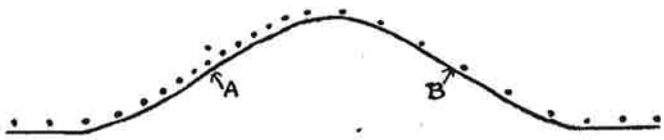

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Fig. 48.—Diagram to illustrate analogy of cyclists moving up and down hill with effect of wind on an insect migration.

The number of cyclists on any given length of road will be greater on the uphill at A and fewer on the downhill at B; but the number passing A per fixed time will be exactly the same as at B, *i.e.* four per minute.

Thus if one wishes to compare the frequency or density of different flights

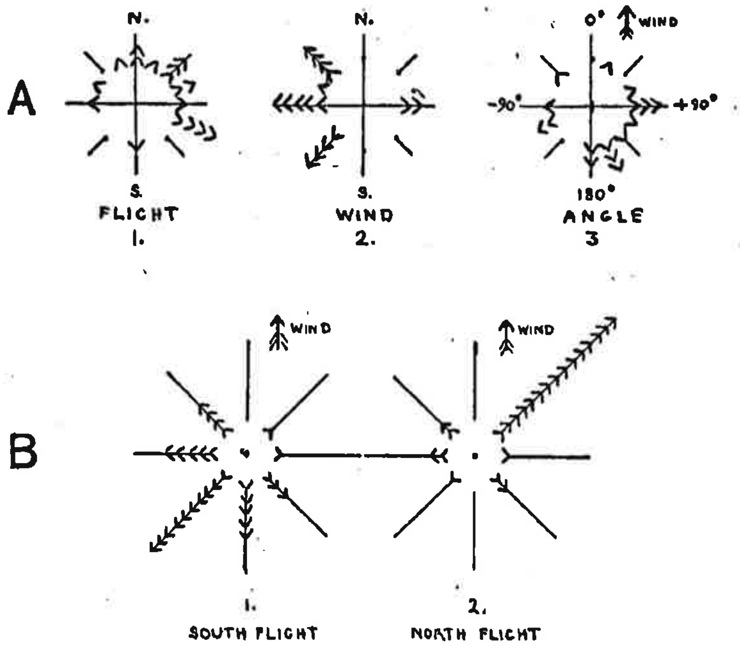

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Fig. 49.—Diagrams showing false apparent effect of wind on direction of migration:— A. Locusts in East Africa; B. *A. monuste* in Florida.

of insects it is important to measure the number crossing a fixed line, at right angles to the flight, per specified time; and not the number present on a specified area at any one moment.

It follows that in any area where there is no prevailing wind, observations of flights will be equally frequent with the wind, against it and across it in either direction, unless the insects composing the flight exert a choice. If, therefore, the records are not so distributed, the discrepancy can be explained either by (A) that there is a tendency for the insects to fly with some definite relation to the wind direction, or (B) that the records suffer from some personal error, such as a tendency for observers to be more likely to note the wind if it is against or with the flight than if it is across, as has already been discussed in a previous paper (Williams 1930b).

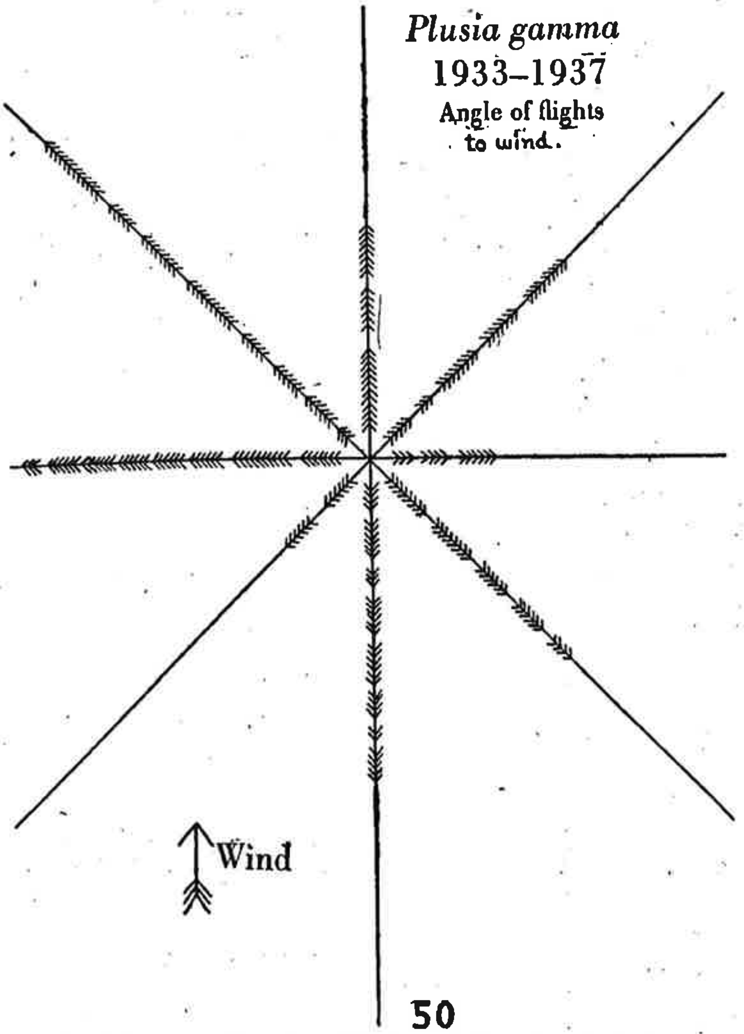

FIG. 50.—Angle between direction of flight and direction of wind on a number of flights of *Plusia gamma.*

It must be noted that if in any district there is a prevailing wind, and also a more or less regular direction of migration, an apparent relation between wind direction and flight is bound to appear although it will be no evidence of cause and effect.

One example of this has been given in connection with locust flights in East Africa in Williams (1933c) where, out of 16 flights, the wind was towards the N.W. or S.W. in fourteen, and the flights were nearly all towards the N.E., E. and

S.E. As a result (fig. 49, A) there is a preponderance of flights more or less against the wind, but as neither all possible flight directions nor all possible wind directions occurred one cannot draw any conclusion.

An even more interesting example comes from the observations of Mr. and Mrs. Hodges on the migration of *Ascia monuste* in Florida (see p. 143). At the point of observation in Melbourne, Fla., the wind was more frequently from the east and south-east than any other direction. From the 18th March to the 16th May 1938, *A. monuste* was migrating steadily to the south and the relation of these flights to the wind is shown in fig. 49, B 1, from which it might be inferred that there was a definite tendency for the insect to fly into the wind and at a slight angle to it. However, on the 18th May the insect reversed the direction of its flight and flew from that date until the end of June towards the north, and the relation of its flight direction to that of the wind is shown in fig. 49, B 2, exactly the opposite from the previous conditions. In fact, there is no possible inference from these data except that the direction of the flight of the butterfly is determined quite independently of the direction of the wind.

I have already brought forward evidence (Williams 1930b : 368) that there is little or no relation between the general direction of flights and the direction of the wind. Since then other studies have always given the same result.

In 1938 Mrs. Grant showed that in a number of flights of *Plusia gamma* in Britain from 1933 and 1937 the direction of flight was at all angles to the wind, without any preponderance either with, against or across. Her figure is reproduced in fig. 50.

Again in this report on p. 194 there is an account of a flight of *Pieris brassicae* in Harpenden, England, that lasted for three weeks. The wind on successive days ranged almost all round the compass without any alteration in the direction of the flight.

There are also, of course, many records of quite definite flights during periods of dead calm when any orientation by the wind would be impossible.

One must therefore conclude :—(1) that the structure of the wind might allow the insect to determine the wind direction from pressure alone; (2) that there is evidence from the orientation of individuals flying in a cross wind that they do appreciate and allow for wind direction, though whether this is done by vision or by pressure perception is not yet certain; (3) in spite of the above there is still no evidence that the wind direction determines the direction of any migratory flight. Very occasionally the direction may be slightly diverted by a strong side wind, but the main flight direction is quite independent of wind changes.

The possible influence of light and sight on orientation.

In my previous summary I discussed very briefly the possibility of orientation during migration being based on the direction of the light, such as the sun's rays, and came to the conclusion that this was unlikely. Firstly because migration may occur in cloudy weather with a diffuse light; secondly because it can take place at midday in the tropics when the sun is overhead, and so could not give any definite indication of horizontal direction; and thirdly because many migrations take place at night and without even the moon.

Since this was written much more has become known about the general orientation of insects by the direction of light rays, and a good summary has been recently given by Fraenkel and Gunn (1940). They call the reaction the " light-compass-reaction " and give a number of examples. All the above objections still hold, however, against it being considered as the basic determination of the direction of migration.

When one has seen a migration continue steadily in one almost compass-true direction for several weeks on end, at all times of the day and in all weathers except perhaps heavy rain, it is difficult to believe that the direction of the sun's rays can have any importance. The insect would have to allow hour by hour for the changing direction of the rays.

One point of interest here is the effect of fog which would give an almost completely diffuse illumination. The evidence is contradictory (Williams 1930b : 388). Evershed states that in south India the butterflies turned back on reaching a fog bank but returned again and again to the edge of the wall of fog. Moreau in East Africa, on the contrary, records that a migration of *G. aurota* " continued on an afternoon of thick mist when you could not see ten yards in front of you." Undoubtedly, even the presence of thick fog does not necessarily interfere with the sense of direction.

Quite recently Kennedy has carried out experiments on flying insects in relation to the apparent movement of the ground. He finds (Kennedy 1940) that mosquitoes when flying quite close to the ground tend to orientate themselves (particularly in relation to wind) so that (1) the ground never moves from back to front relative to the insect, and (2) the image moves across the retina as slowly as possible—or at least they avoid any condition that pro-produces a movement of the image above a critical velocity.

As a result of these conditions a mosquito never flies against a head wind unless it can fly faster than the wind and so make progress up wind; and it avoids flying with a strong tail wind as this increases to above the limit the velocity of its speed relative to the ground and hence the rate of movement of the image on the retina. The insect when near the ground therefore tends to fly against light winds and to alight if they become too strong for it to make headway relative to the ground.

All these experiments have been done with the mosquitoes within a few centimetres of the ground, and it is difficult to say how they would apply to an insect several feet or, still more, a hundred feet or so in the air when the movement of the image of the ground on the retina would be very much slower.

If insects are not guided by wind or by the magnetic field (see below), the most obvious thing left is vision, and this would be likely to be carried out by some form of " sighting " or by the movement of the retinal image. At the present moment, however, one is still far from being in a position to see a solution. Experiments must be carried out in the field to test such possibilities on migrating insects. Such tests might well be carried out at the Research Station at Amani in Tanganyika where flights occur quite frequently and at regular seasons. It should be noted that if an insect is flying in a wind current, the movement of the insect relative to the ground (and hence the movement of the retinal image of the ground in the insect's eye) will not be parallel to the axis of the insect's body on either of the theories of wind orientation discussed on p. 230 unless the insect is flying directly with or directly against the wind.

An observation of my own which might be referred to here in connection with Kennedy's work is that in East Africa in 1928 I saw locusts (recently emerged adults) flying fast with a fairly strong breeze at a height of 10–15 feet above the ground, but lower down at 1–6 feet all were flying in the opposite direction against the wind. All the time hundreds were rising from the lower layer or dropping to it, and all immediately changed their direction as they changed their level (Williams 1933c). This would undoubtedly result in the retinal image moving more slowly, as when they were near the ground their ground speed was at its minimum, and when they were farthest away it was at its maximum.

It is perhaps also worth recording again in this connection that about the same time I saw large numbers of locusts making a steady flight near the ground and all the locusts at rest on the ground were orientated in the same direction as those flying above. It is interesting to note that these locusts on the ground would see objects above them moving from rear to front. This is the condition that Kennedy says is avoided by mosquitoes, for objects below them. Is the difference in the position of the moving objects or in the behaviour of the two insects?

Experiment on the influence of the magnetic field.

By G. F. Cockbill.

Recorders of the phenomenon of prolonged unidirectional flights of butterflies have at times outlined the possible stimuli that could produce such reactions in the insect. They reasoned along the lines that a steady unidirectional flight would require a constant and prolonged stimulus, such as might be provided by the earth's magnetic field. The assumption has several times been made that the insect can appreciate and respond to this stimulus.

Such writers have either made the suggestion as an interesting speculation or have selected scant evidence to support their views. Thus Ghesquière (1932b) mentions "le sens physiologique de l'orientation magnetique" in surveying the factors concerned in insect migration; Mary (1921) suggests that the sense of magnetic orientation would be a manifestation of unilateral electrical stimulation, while Lakhovsky (1931) even invokes the cosmic rays.

On the other hand, depending on direct observation, Lenz (1931) goes so far as to suggest that the predominantly north-north-westerly flights of butterflies that he observed in northern Germany were to be explained on the grounds that as the magnetic North Pole was some distance to the west of the true North Pole, the insects were accommodating themselves to the earth's magnetic field.

The only experiments carried out on migrating animals to investigate the effect of the earth's magnetic field, as far as the writer is aware, have been those of Wodzicki, Puchalski and Liche (1939). These workers were considering the factors which determine the migration of storks. They caught twelve storks near Lwow, Poland, and sent four to Lisbon, four to Berlin and four to Harviala in Finland. In each group, three storks each had a bar magnet attached to its head, several times stronger than the earth's field "calculated according to Gauss' formula." The fourth stork of each group was used as a control. It was presumed that the presence of the bar magnet, "according to Stresemann's hypothesis, would eliminate the influence of the earth's field" on the birds.

The experiment did not give satisfactory results owing to the small numbers of birds used and also to the very unfavourable meteorological conditions in the latter part of June 1938, when the experiment took place.

No storks returned from Lisbon; three returned from Berlin, including two with the magnets attached to their heads, although their flight was slower than normal; while of the four from Finland, two died, and the remaining two stayed near the place where they were liberated.

This method of investigation would not be practical in insects. On the other hand, because of their small size, insects can be subjected to a controlled environment without much difficulty.

Although it was not thought probable that positive evidence would result, it was considered necessary to carry out some experiments.

The following experiment was designed to compare the movements of nymphal locusts when subjected to a powerful magnetic field with those under normal conditions, and to decide whether the insects under experiment possessed any mechanism for appreciating and orientating themselves in relation to the poles of a strong magnetic field.

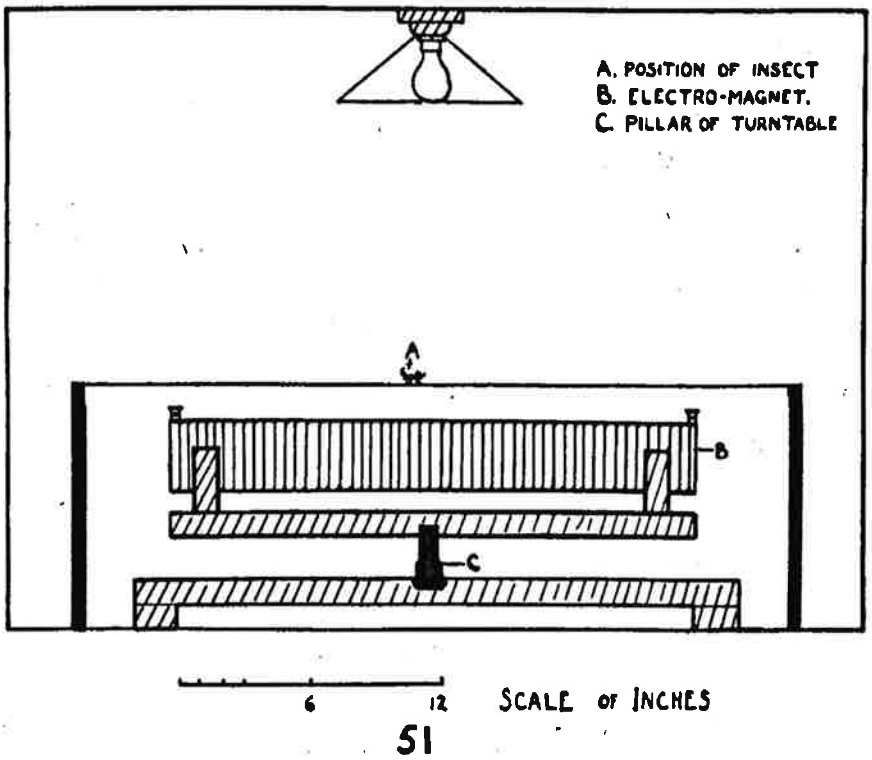

FIG. 51.—Apparatus for testing the effect of a strong magnetic field on insect orientation. Lateral view.

Apparatus and method.

The apparatus, fig. 51, consisted essentially of an electromagnet made from a transformer coil, supplied with 100 volts D.C., and placed centrally beneath a circular paper platform on which the insects were liberated.

The electromagnet was supported on a turntable which allowed it to be rotated through 180°. A reversing switch was included in the circuit, so that by rotating the magnet through 180° and using the switch, the poles of the magnet could be made to take up any position in the circle.

The entire apparatus was enclosed within an almost lightproof chamber, made of wood laths and brown paper. A flap was left in one side to allow the insects to be deposited on and taken from the platform. From the roof of the chamber hung a 60-watt electric lamp which evenly illuminated the paper platform beneath.

The room in which the experiment was conducted had a northern aspect,