A possible method of wind orientation in migrating butterflies

by

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Introduction

In 1952 I gave the hypothesis that Chaffinches (*Fringilla coelebs* L.) take their initial direction in the early morning from the sun and can keep this direction by subsequently orientating themselves to the wind, as long as its direction remains unaltered.

In 1959 I discussed several possible methods which could be used by birds to maintain a straight course in migration by reference to the direction of the wind.

At the International Entomological Congress in Vienna (1960) I applied the hypothesis of wind orientation to the migration of butterflies and gave some evidence that migrating butterflies could also use this method of maintaining a straight course. From several possible methods of wind orientation I selected one as being the most probable in my 1959 paper. In the paper I read at the Congress I discussed the matter of wind orientation in English, but I described the probable method of wind orientation in German, because the terminology in English was incomplete and less up to date. Now I will try to describe in English my theory for migrating butterflies, and discuss several questions related to it at the same time.

Description of the method

When a butterfly is heading in a direction which is previously fixed in relation to the direction of the sun, it is only in calm air that the direction of its body-axis and the direction of its migration are the same. This is also true when the butterfly is migrating in a wind that is precisely a headwind or a tailwind. In all other wind-directions the butterfly flies with an angle between the direction of its body-axis and the direction of its migration. This angle becomes larger as the wind blows more from the side, *i.e.* when the angle between the direction of migration and the direction of the wind becomes nearer to 90°. It is necessary to give here an example with a figure. To draw this figure we need to know the speed of migrating butterflies. We shall therefore choose as an example the Large White (*Pieris brassicae*) which has been studied to some extent in this respect. BLUNCK (1954, p. 487) wrote as follows: "Bei ruhiger Luft legt *P. brassicae* in der Sekunde cirka 2 m zurück, an kühlen Tagen sogar noch etwas weniger. Umgekehrt sah ich die Tiere bei warmem Wetter 3 und 4 m je Sekunde schaffen. An einem besonders freundlichen Tag (22.8.32) legten einzelne Stücke bei 25° C. in einer windstillen Zone sogar vorübergehend bis zu 6 m je Sekunde zurück. Das entspricht einer Stundenleistung von 21½ km. Gewöhnlich bringen sie es aber nur auf 7 bis 14 km/Stunde."

In the case illustrated by Figure 1, the air-speed of the Whites is 12 km/h (vector AF; the wind AW is ± SW with a speed of about 7 km/h. AF is the heading and AM the resultant of (a) the butterflies' course (heading, axis of body) and air-speed and (b) the velocity of the wind. For the terminology I have studied YAPP (1956), WILLIAMS (1958) and LACK & WILLIAMSON (1959). The best terminology is evidently that given by YAPP, who used the terms in the sense which they have in dynamics and air navigation. LACK & WILLIAMSON (l.c.) used the term 'heading' instead of 'course', because the latter word has been used in different senses. I think that this is not necessary, because 'course' has a definite sense in dynamics and air navigation according to YAPP (l.c.). WILLIAMS (l.c.) used the word course in the same sense as YAPP.

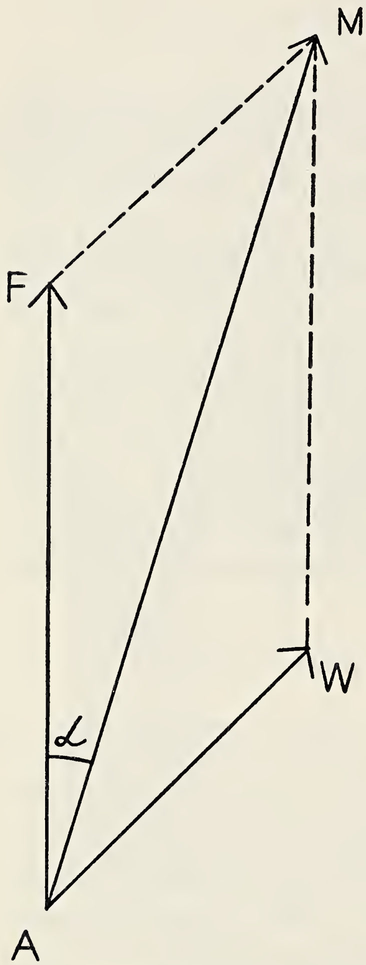

Fig. 1. Example of a parallelogram of velocities in Butterfly Migration. The air-speed of the Whites is 12 km/h, the wind AW is SW with a speed of 7 km/h. AF is the course and AM the track, the resultant of (a) the butterfly's course (heading, axis of body) and air-speed and (b) the velocity of the wind. $< \alpha = \pm 17°$.

As can be seen from Figure 1, the Large Whites fly in a NNE direction. To fly in this direction they have to orientate their body-axis in the direction of AF and to fly in this direction in relation to the air (the c o u r s e). Drifted to the right by the SW wind of the assumed strength, they move in a NNE direction in relation to the ground (the t r a c k). Whites have been observed to migrate in northerly directions, a few times in Holland (LEMPKE, 1956, p. 67), but more often in Great Britain (WILLIAMS, 1958, p. 123). The question now is whether the Whites can maintain this angle between course and track. To achieve this aim they have to "read" on the ground the directions of the vectors AF and AM. They can do this at the start of their flight when they adopt their (possibly fixed) angle in relation to the direction of the sun. For, as I (1960) wrote, it is now generally believed that the sun is the governing factor in the orientation of migrating birds. I (1953) have summarized several reasons for this belief (see also VAN OORDT, 1960). In my opinion the sun is probably also the governing factor in the orientation of migrating butterflies. As a rule butterflies start their daily journey in the morning (for literature see VLEUGEL, 1960). It is to be expected that this hour is more or less the same every morning, so that the direction of the sun is more or less the same every day. When the butterflies depart they can see the size of the angle FAM. If they take care in the following hours that the size of this angle remains the same, they maintain the constant direction AM which is about NNE. When changes of direction occur, the size of the angle FAM changes too and the Whites have to change the direction of their body-axis until the angle FAM becomes the same as in the beginning.

This method works only as long as the velocity of the wind remains unaltered. However, on most days the wind does not change much. Small changes in wind direction have no great influence, and because the changes on different days are as frequently to the left as to the right the resulting course will be, on average, more or less in the right direction. Changes of wind direction will only be observed easily when they are rapid. However, as a rule they are gradual, so that it will be difficult for the butterflies to observe them, as is the case for human observers. In fact we know very little in this respect; we shall need many more observations before we know what really happens. Even in the case of birds we are badly informed about their behaviour when actually migrating.

It seems easy for the butterflies to assess their course AF. Probably they extend the direction of their body-axis distad. Whether or not they then choose an aiming-point, is difficult to observe; both methods would give the same result. It does not seem so easy for the butterflies to assess their track AM. In ornithological literature there has been discussion on this point, chiefly by L. TINBERGEN and collaborators and by the present writer. There appear to be two main possibilities:

1. They look in a forward direction and determine the line in the landscape where there is no apparent lateral movement in the objects of the landscape: in other words the line where there is no change of parallax due to the shift of the position of the flying butterfly. This line must continually be extended further forward.
2. They do the same as under (1) but choose aiming-points now and then to be sure that the angle FAM remains the same.

Further, it is necessary in the example we gave in Figure 1 that the Whites take care that the wind blows from behind and from their left. They can observe this tailwind in two ways.

1. When the velocity of a tailwind suddenly and quickly becomes greater, the pressure on the frons of the butterfly's head becomes less and this can probably be observed during a very short time with the tactile sense-organs of the butterfly.
2. When the velocity of a tailwind suddenly and quickly becomes less, the pressure on the frons of the head becomes greater and this can surely be observed with the tactile senses of the butterfly during a very short time.

However, they can also see whether the direction of their track is all right: it should be to the right side of their course. Further, should their speed i.e. the rate of their change of position, that is the distance travelled per unit of time, be rather fast as compared with for instance the speed against a headwind. The reason for all this is that there are four angles of deviation (for explanation see below) equal in size with every wind-direction which is possible. It seems necessary to elucidate this latter question by a Figure. We choose only one case, that of Figure 1.

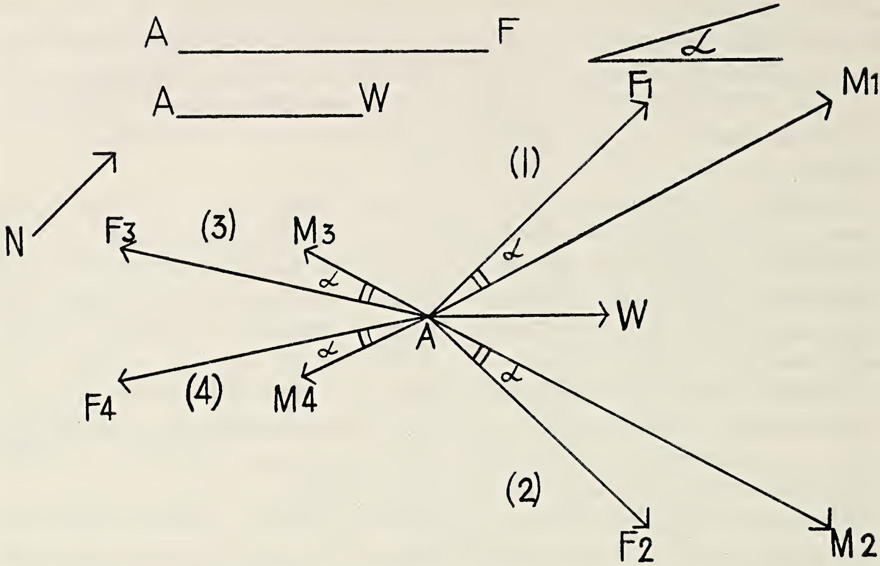

Fig. 2. The four possible headings AF_1, AF_2, AF_3 and AF_4 which give the same angle of deviation to a migrating butterfly, when as in Fig. 1: Air-speed AF = 12 km/h; wind velocity AW = 7 km/h from the SW; $< \alpha \pm 17°$. From the construction follows: Ground-speed AM_1 and AM_2 = ± 17 km/h; ground-speed AM_3 and AM_4 = ± 5,3 km/h.

The four possible headings which give the same angle of deviation when the wind velocity is the same are given in Figure 2. In case (1) and (3) the deviation is to the right; in cases (2) and (4) the deviation is to the left. The butterflies have to distinguish between deviation to the right and deviation to the left. Also, it should be possible for them to distinguish between (1) and (3), because in case (1) their ground-speed is much higher than in case (3); there is the same difference between (2) and (4). This method would always work unless the wind-speed is much less than the air-speed of the butterflies.

The "angle of deviation"

It is necessary to give a name to the angle FAM (Figs. 1 and 2). In accordance with the German name given to it (cf. Vleugel, 1959), "Abweichungswinkel", we choose "angle of deviation".

According to Drever (1952) deviation is the variation from some line, norm, or standard of reference; used in a number of technical senses: (1) visually, of one eye failing to assume its position in coordination with the other in fixation of an object, or of an irregularity between the two eyes, especially with respect to the vertical axis or meridian, in either case producing double vision.

In our case we also assume that there is double vision. The left eye of the butterfly could concentrate upon the course AF in our example (see Fig. 1). The right eye, on the other hand, could concentrate upon the track AM. In some way or other these two lines are coordinated to form an angle FAM which can be assessed by the butterfly.

Even when the butterflies have lost the direction of their migration altogether for a short time, they should be able to regain their former track if they form again the same angle FAM, provided the wind has remained blowing from the same direction. As I (1960) have said before, there is evidence that butterflies seldom migrate in variable winds or calm weather. It has also been observed that they alter the direction of their migration in conformity with an alteration in the direction of the wind (cf. VLEUGEL, l.c.). But in this respect, of course, many more observations are needed.

After having made drawings of all sorts of possibilities as regards direction and velocity of the wind and the direction of migration, it became clear that there is an endless variation in the size of the angles of deviation, the place of the "course" (in Fig. 1 AF) relative to the "track" (in Fig. 1 AM), the direction of the wind (headwind or tailwind, all sorts of sidewinds, beamwinds, crosswinds). There are many possible cases here. For this reason, the "method of projection" (translation of "Projektionsmethode" as I (1959) called it in German) is a valid one. I use here the term projection in the sense of DREVER (1952): "Projection, optical: the formation of an image by any optical system". My hypothesis is that the image of the angle of deviation can be retained for some time, and can be reproduced later on the same day after the butterfly has lost its correct direction. By means of the projection method the butterfly can shift its heading to reproduce the angle of deviation it observed at the beginning of its day's migrational flight.

Naturally it is possible that the migrating butterflies may make mistakes in orientation with the method of projection. In my opinion these mistakes will be smaller than with other possible methods. If this is so, other methods which possibly existed in the past should have been more or less ruled out in the course of evolution. At the moment I see only one other possible method of orientation: another form of sun-orientation, which seems a good alternative to the method of wind orientation. In this method we assume that migrating butterflies take their initial direction in relation to the direction of the sun, and later compensate for the daily sun-movement with the help of a kind of internal clock. Most ornithologists now believe that birds use this method (e.g. KRAMER, 1952, etc.). As I have not yet given a comparison of the accuracy of the two methods, even for the migration of birds about which we are so much better informed, it would be premature to try to make this comparison for butterflies now. I shall only mention that the eminent entomologist Dr. C. B. WILLIAMS (1958, p. 126) rejected the method of compensating for the daily sun-movement for migrating insects. In fact it seems to have been proved that honey-bees use this method on their daily flights to and from their hives (cf. BUTLER, 1958, BAERENDS, 1959, BUDEL & HEROLD, 1960). However, the behaviour of honey-bees and of Starlings (*Sturnus vulgaris* L.) in experimental situations is quite different from that which is required to maintain a straight line of flight in migration under a moving sun. Perhaps it will suffice to say here only that so far we do not know anything with certainty in this respect about migrating birds and nothing about migrating insects. We need far more information before we can decide what is really happening.

Night Migration

At night orientation by means of the direction of the wind seems possible too. I (1954) have given evidence that this type of orientation is used by birds, at least by thrushes (Turdidae). Probably another type of wind orientation is used by birds migrating during the night, because it seems difficult for them to distinguish their course and their track on the dark ground above which they are flying. But migrating birds and butterflies will be able to assess the direction of the wind by means of its changing strength (gustiness). When I expressed this view at the Symposium on Long-Range Displacement and Migration of Flying. Insects on August 18th 1960 at the Congress in Vienna, the following was said during the discussion of my paper. For flying insects the velocity of the wind seems to be too great to make it possible for them to use the method of assessing the direction of the wind by means of its changing strength. The insects would be transported passively by gusts of the wind. However, in my opinion this method would be possible, but it would be unwise to make decisions before we have more observations under what weather conditions migrating insects prefer to make their flights by night. In this respect I hope that students of insect behaviour and other entomologists who have made observations on this subject will send them to me or publish them. References to literature on this subject would also be very welcome.

In the discussion mentioned before, one or two entomologists—I thought they were Americans—said that there are observations (publications?) that some insects are able to discern very well landmarks on the ground above which they are flying by night. In this case the method of wind orientation I advocated in this paper would be possible at night too. Again I would be very grateful, when observations of this kind, whether published or not, would be made known to me.

Acknowledgement

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Summary

1. A description is given of a method of wind orientation which could be used by migrating butterflies to maintain a straight line of flight. This method was published for the first time by the present writer in 1959, when it was applied to migrating Chaffinches. It was applied to migrating butterflies in a paper read at the Int. Entomol. Congress in Vienna in 1960.

2. It is thought by the present writer that the primary orientation of migrating butterflies takes place at the beginning of the daily flights with the help of the direction of the sun.

3. To maintain a straight line of flight, butterflies would have to maintain a constant "angle of deviation' during the hours of their migration, provided the velocity and direction of the wind do not alter.

4. By "angle of deviation" is meant the angle between the butterflies' course (heading, body-axis) and their track which is the resultant of (a) their course and air-speed and (b) the velocity of the wind.

5. When the butterflies fly their angle of deviation they must see to it that the wind strikes them constantly on the same side of the head. Further they have to take care that their velocity alters little if at all, because they have to maintain their flight against or with the wind as they did in the beginning of their daily migration. The reason is that with every wind direction there are four possible angles of deviation equal in size (see Fig. 2).

6. It is not thought by the present writer that migrating butterflies orientate themselves often with the help of the moving sun and an "internal clock", although this method is possible theoretically and has been proved experimentally for Starlings in migrational restlessness and for honey-bees in more or less experimental situations. The reason is that both for migrating birds and butterflies this method is far more complicated than was the case in the experiments.

7. It is thought by the present writer that wind orientation is also possible for butterflies which migrate by night. Which type(s) of wind orientation could be used by night is so far uncertain. First we have to know to what extent butterflies which migrate in the dark can see the configurations on the ground over which they are passing.

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