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Williams, C. B. 1951. Seasonal changes in flight direction of migrant butterflies in the British Isles. *Journal of Animal Ecology.* 20 (2), pp. 180-190.

The publisher's version can be accessed at:

- https://dx.doi.org/10.2307/1537

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Seasonal Changes in Flight Direction of Migrant Butterflies in the British Isles
Author(s): C. B. Williams
Source: *Journal of Animal Ecology*, Vol. 20, No. 2 (Nov., 1951), pp. 180-190
Published by: British Ecological Society
Stable URL: https://www.jstor.org/stable/1537
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SEASONAL CHANGES IN FLIGHT DIRECTION OF MIGRANT BUTTERFLIES IN THE BRITISH ISLES

By C. B. WILLIAMS

Rothamsted Experimental Station, Harpenden

(With 9 Figures in the Text)

For many years naturalists were reluctant to admit that butterflies, moths and other frail insects were capable of undertaking unidirectional 'migration' flights of hundreds of miles or more.

When the evidence of this became overwhelming, it was held that the flights were 'over-flow' movements from over-populated districts, and could not be compared with the 'real' migration of birds. True migration must consist of a to-and-fro movement of the population in one direction at one time of the year and in an opposite direction at a later season. In fact, in the north temperate areas, what was considered necessary to establish the existence of migration was evidence of a movement to the north in the spring and to the south in the autumn.

Round about the year 1920 only one butterfly was generally admitted to be a migrant in this sense: the monarch (*Danaus plexippus* L.) of North America. In this insect there was considerable evidence of a southward movement in the autumn, and slight evidence of a return movement in the spring.

In 1930, I published a book on the *Migration of Butterflies* (Williams, 1930), bringing forward evidence, of various degrees of incompleteness, for migration in over 200 species of butterflies from many parts of the world. There was also small evidence of a return flight in about half a dozen species.

Even at that date, however, there were competent entomologists who would not accept the idea that such movements were anything but exceptional outflows, without any relation to regular migration of birds. Dr A. H. Clark, one of the best of the North American lepidopterists, did not even accept the reality of the migration of the monarch butterfly till about eight years later.

Heape, in his book on *Emigration, Migration and Nomadism*, which was published posthumously in 1931, but actually written before my own book appeared in 1930, expressed fully the then prevailing view that 'to-and-fro' migration was fundamentally different in origin from overflow movements in one direction only, and that true migration was only known in one single species of butterfly—the monarch.

In 1936, Grant brought forward evidence of a northward movement of the red admiral butterfly (*Vanessa atalanta* L.) in the British Isles which lasted during May, June and July, and of a southward movement in September and October. This will be referred to again later.

In 1942, I brought forward evidence for a return flight at a different time of the year in a dozen species of butterflies and two species of moths (see Williams, Cockbill, Gibbs & Downes, 1942, pp. 240–8). The butterflies included, in addition to those mentioned above, *Phoebis sennae* L. in America, *Catopsilia pyranthe* L. in India; *Colias croceus* Fourc. in western Europe; *Kricogonia lycide* Godt. and *Ascia monuste* L. in southern North America and in Central America; *Vanessa cardui* L. in Europe; *Dione vanillae* L. in Florida; *Libythea labdaca* Westw. in West Africa; and *Danaus berenice* Cr. in Florida.

In fact I had then come to the conclusion that evidence for a return flight is found in a species as soon as close observations are made and a sufficient number of observers are available. It appears that in many cases the flight in one direction is gregarious and in large numbers, while the flight in the opposite direction is in small numbers with the butterflies flying singly. So long as we remained dependent for information on the accidental reports of field naturalists, the evidence was biased in favour of the conspicuous flights in one direction; when more careful observations were made the second movement began to be noticed.

Shortly after the publication of my book in 1930, an organization was formed in south-eastern England, largely by the energy and enthusiasm of Captain T. Dannreuther, to watch for evidence of directional movements of butterflies and other insects in the British Isles; and also to collect records of the occurrence of known immigrants in Britain even if there was no immediate evidence of directional movements. This organization is known as the 'Insect Immigration Committee of the South-Eastern Union of Scientific Societies'. Hundreds of

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amateur naturalists have co-operated by sending in their observations, which are sorted and tabulated by Captain Dannreuther and later sent to this Experimental station for storage and further investigation. As a result of these activities we have now accumulated over 20,000 cards with records.

In 1938, the Leverhulme Foundation made a grant for two years to further the study of insect migration, and by this means Dr G. F. Cockbill made a very complete survey of the literature on the occurrence of migrant Lepidoptera in Britain, especially in the period 1850–1930 (Williams *et al.* 1942, pp. 105–28). In this investigation more than 20,000 records were filed.

A scale indicating numbers is added to each figure. In the preparation of the diagrams the records were arranged in chronological order starting from the centre so that records near the inside are for earlier years than those on the outside of the rosettes. A method was tried for putting a date to each arrow, but this was abandoned owing to the untidiness of the results, and the comparatively little gain. Only eight points of the compass were recognized and the very few records which were more exact, e.g. NNW. (usually from lightships) were placed on the nearest diagonal (NE., NW., SE. and SW.) as a small effort to counteract the preponderance of other records to the four main points N., E., S. and W.

1937 Year	13 AUG. Month and Dates	START LIGHTHOUSE S. DEVON Locality (Place and County)	TO S. Flight direction if definite
01.30 Time of day	N.E. 1 Wind direction and force	7 Numbers seen	2 AT ROTHAMSTED No. captured and in whose collection
BOTH Sex	GOOD Condition	FLYING DUE SOUTH Notes :—Extent of flight ; speed : pairing ; egg-laying etc.	
THUNDER STORM BETWEEN MIDNIGHT & 04,00 · OVERCAST · HEAVY SHOWERS · BAROMETER FALLING · MAX. TEMP. 67° Present & past weather conditions :—temperature, rain, sun, cloud, thunder, barometer, etc.			200 FT. Height above ~~Ground~~ SEA
A.W. GODFREY START LIGHTHOUSE Recorder's Name and Address	Observer (if not Recorder)	Source of Information	
V. ATALANTA Species (Specific name)	ABOUT 2 DOZEN P GAMMA Other insects in same flight	A.W.G. Identified by	

MIGRANT INSECT RECORD.

Fig. 1. Example of record of insect migration in Britain extracted on the standard card used in these investigations.

We have thus available for study a vast amount of information, mostly on standard cards of which an example is shown in Fig. 1. The cards usually give the date and locality of the observation, the number of insects concerned and the direction of flight if definite. All the cards collected in the course of our work on insect migration, including all those used for the present study, are stored in the Entomological Department at Rothamsted Experimental Station, Harpenden, and are available for inspection and study at any time by previous arrangement.

The diagrams have been prepared by the following method. Each arrow-head represents one recorded movement of butterflies and the length of the arrow represents on an approximately logarithmic scale the number of insects concerned in the flight.

The present investigations are based almost entirely on these records, and none of the conclusions would have been possible without the enthusiasm of Captain Dannreuther, Dr Cockbill, Mrs Grant (now Mrs Richardson) and the hundreds of naturalists who recorded their isolated observations.

Out of about sixty-eight species of butterflies known to have occurred in the British Isles (of which two or three are extinct or very rare) evidence for migration exists in about seventeen species. Many of these, however, are only occasionally immigrants and for them the total evidence of movement even over a long period of years is insufficient for discussion. It is in the commoner immigrants that evidence of change of direction of flight is most likely to be found. In the following pages the evidence is

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discussed for six species, three of which belong to the family Pieridae, namely *Pieris brassicae* L., *Colias croceus* Fourc. and *Colias hyale* L. and three to the Nymphalidae, namely *Vanessa atalanta* L., *Vanessa urticae* L. and *Pyrameis cardui* L.

THE RED ADMIRAL BUTTERFLY

(*Vanessa atalanta* L.)

Vanessa atalanta was long considered as a permanent resident in Britain, hibernating in the adult stage in the same way as its close relatives *V. io* the peacock and *V. urticae* the small tortoiseshell. In the absence of any convincing evidence of hibernation, however, opinion changed and it was then thought to be only an immigrant from the south. Now it is considered probable that a small number of adults survive the winter, but that the majority of our summer breeding stock come in as immigrants from the south.

In 1936, Mrs K. Grant tabulated the relatively few records then available in our files relating to movements of the red admiral in the years 1934 and 1935, and showed that they indicated a preponderance of records in a northerly direction up to the end of July and in a southerly direction during September and October. In 1942, I tabulated the records for the six years 1934–9 and these supported the same conclusions (see Williams *et al.* 1942, p. 244).

Fig. 2 shows all the records that we have on our files from 1920 to 1949, classified into periods of half-months from the beginning of March to the end of November. The records vary from many referring to a single individual, to a few recording hundreds or even some thousands.

It will be seen that there are very few records in March and April, and nearly all these refer to single individuals, but even as early in the year as this there is evidence of movement in a northerly direction. In both the first and second half of May there is an increase in the number of records, with a strong northerly component. The first half of June has an unexpected number of records to the east, but in the second half of June the northerly component is again dominant. This persists into the first half of July, but by the end of this month activity seems to have died away. This is the period between the first and second broods. At the beginning of August there is renewed activity, at first chiefly in a northerly or westerly direction but after the middle of the month a definite southerly component appears and this becomes dominant during September and October, although there are flights in other directions. The frequency of observations recording a large number of individuals is much greater after the middle of August.

Our records thus support completely the earlier analyses and indicate a definite northerly movement (immigration from the south) in the spring and early summer, and a southerly movement (return to the south) in the early autumn.

THE CLOUDED YELLOW

(*Colias croceus* Fourc.)

The clouded yellow is in the British Isles a summer-breeding immigrant from the south, and there is no evidence of hibernation in any stage in this country. It is very irregular in its appearance, being in some years almost completely absent from our islands, while in other years it is abundant right up into Scotland. The year 1877, when it appeared in countless thousands all over the country, was for decades known as the 'Clouded Yellow Year'; and no similar outbreak was recorded until 1947 when it again swarmed in equal or even greater numbers. The number of records available for this latter year are sufficiently great to justify their separation into a separate analysis, which has been done below.

In 1942, (see Williams *et al.* 1942, p. 244) I tabulated records from 1931 to 1939 into two groups, those before the 15 August and those after that date. The results indicate a definite northerly movement in the first period, but movements in all directions in the second.

Figs. 3 and 4 show all our available records, with the exception of those for 1947, up to and including the year 1949, divided as before into half-month periods. Before May there are only a few records of single insects; by the second half of May, records are definitely increasing and reach a peak in June with a distinct northerly component. There is a reduction in the first half of July but with still a northerly trend, chiefly of single individuals.

Towards the end of July there is increasing activity which culminates in a great outburst of movement in the first half of August; in which, however, the northerly or westerly components are still strong: this continues also in the second half of August. By the first half of September, however, a southerly component begins to assert itself and becomes very definitely dominant in the first half of October.

Thus *C. croceus* has a northward immigration in May and June similar to *Vanessa atalanta*, but the southward autumn movement begins to show about a month later than in the red admiral. The hatching of the second brood about the beginning of August is a signal for great activity—but not for the start of the return autumn flight.

Fig. 5 shows the records of the same species in 1947, and they support the above conclusions in every possible way. There is evidence of a northerly immigration in the second half of May and the first half of June. The sudden outburst of activity at the beginning of August is again obvious: and also the

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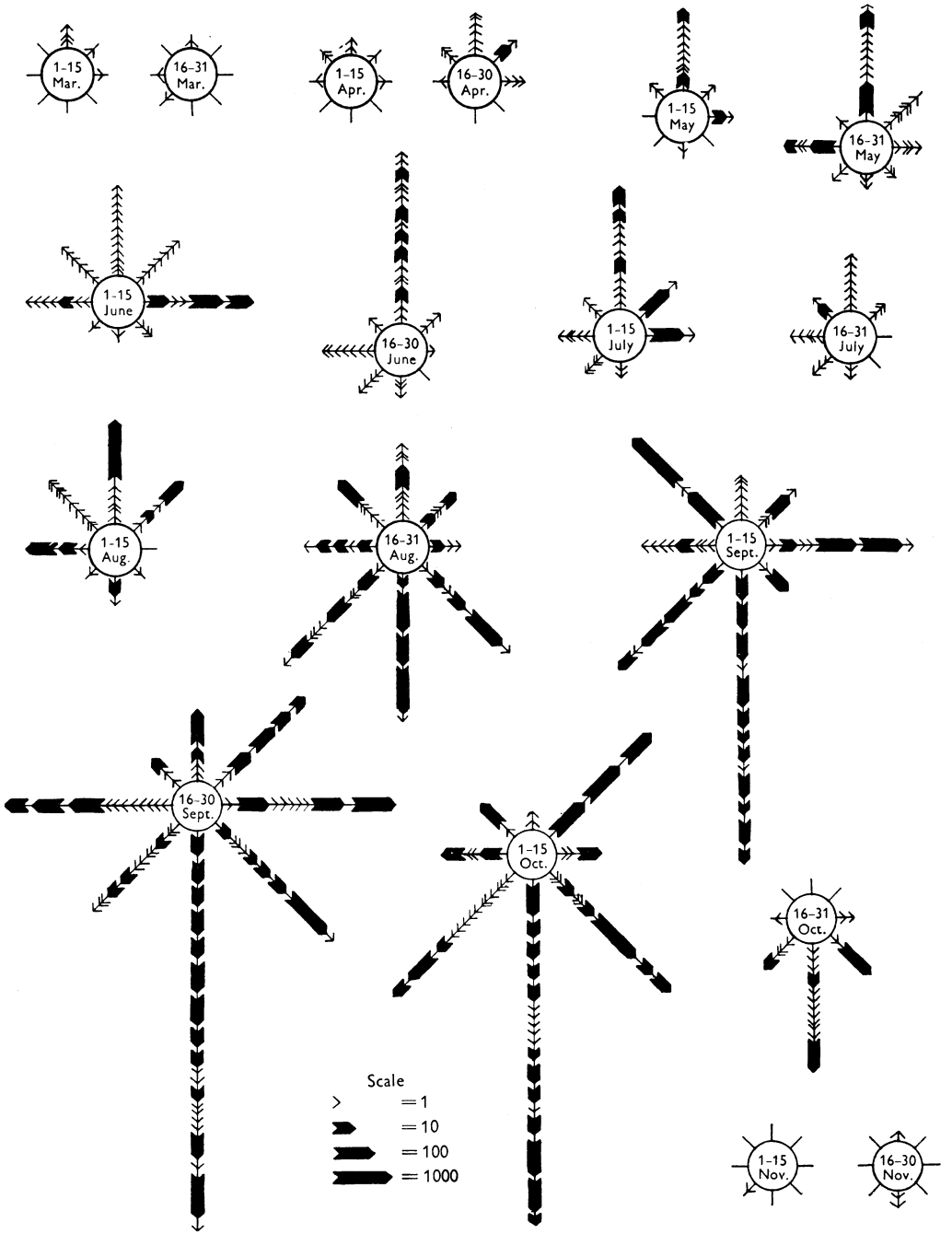

Fig. 2. Directional flights of the red admiral butterfly (*Vanessa atalanta* L.) recorded in the British Isles up to the end of 1949. Each arrow-head shows a single observed flight, the length of the arrow-head indicating approximately the numbers concerned as shown by the scale on the diagrams.

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southerly autumn movement first appearing about the middle of September and becoming dominant in October. There were practically no observations in this year after mid-October.

years of comparative abundance seldom reaches as far north as Scotland.

There is also a second factor that makes the records of the species of less value than *C. croceus*, and that is

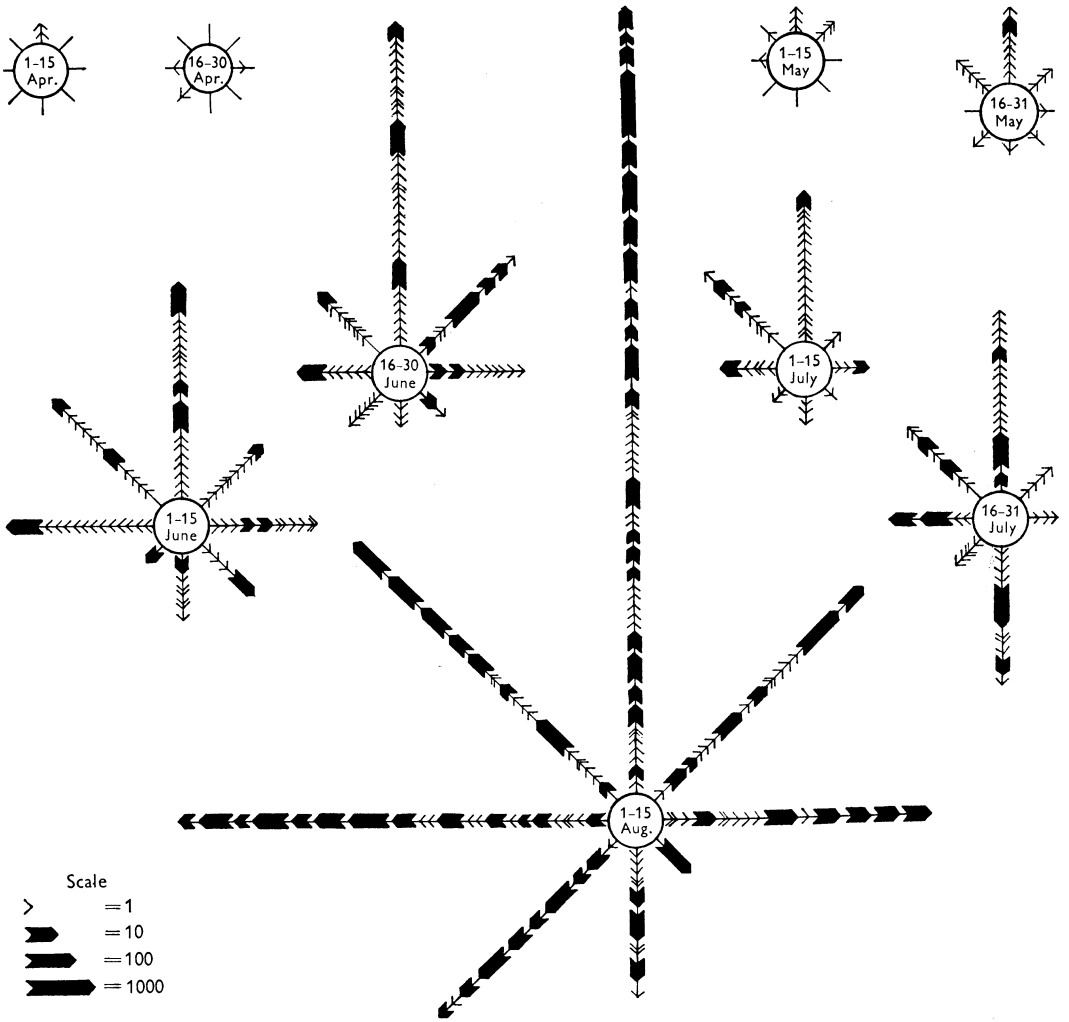

Fig. 3. Directional flights of the clouded yellow butterfly (*Colias croceus* Fourc.) recorded in the British Isles up to 1949, but excluding the year 1947 (for which see Fig. 5), for the period up to the middle of August.

THE PALE CLOUDED YELLOW

(*Colias hyale* L.)

This species is a spring immigrant which comes in from the south, breeds here in the summer, but never survives the winter. Thus it resembles its close relative *C. edusa*, but is much rarer and even in its

that the latter has a pale form of the female (variety *helice*), which is in the field very difficult to distinguish from *C. hyale*, so that all records of '*hyale*' not supported by specimens are suspect.

Fig. 6 shows the small number of records attributed to this species and it will be seen that they resemble closely those of *C. edusa*. There is evidence of a small

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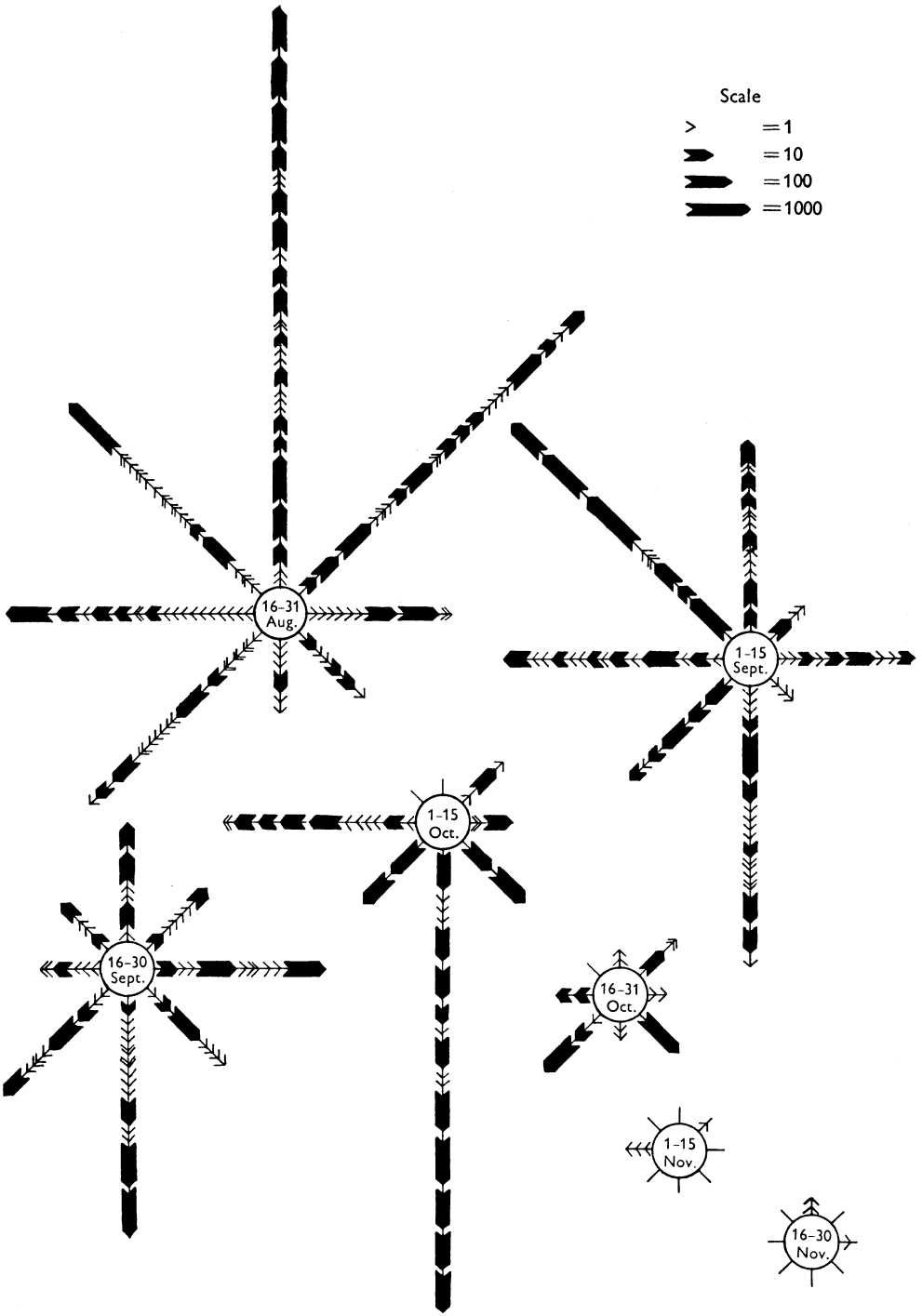

Fig. 4. Directional flights of the clouded yellow butterfly (*Colias croceus* Fourc.) recorded in the British Isles up to 1949 (but excluding the year 1947) from the middle of August onwards.

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immigration in the spring in a northerly direction; a period of quiescence followed by an increase of activity in August; and finally a southerly movement at the end of September and in October.

no evidence of survival in any stage in Britain during the winter.

Fig. 7 shows all the records available in our files on the same system as before. After a few wanderers in

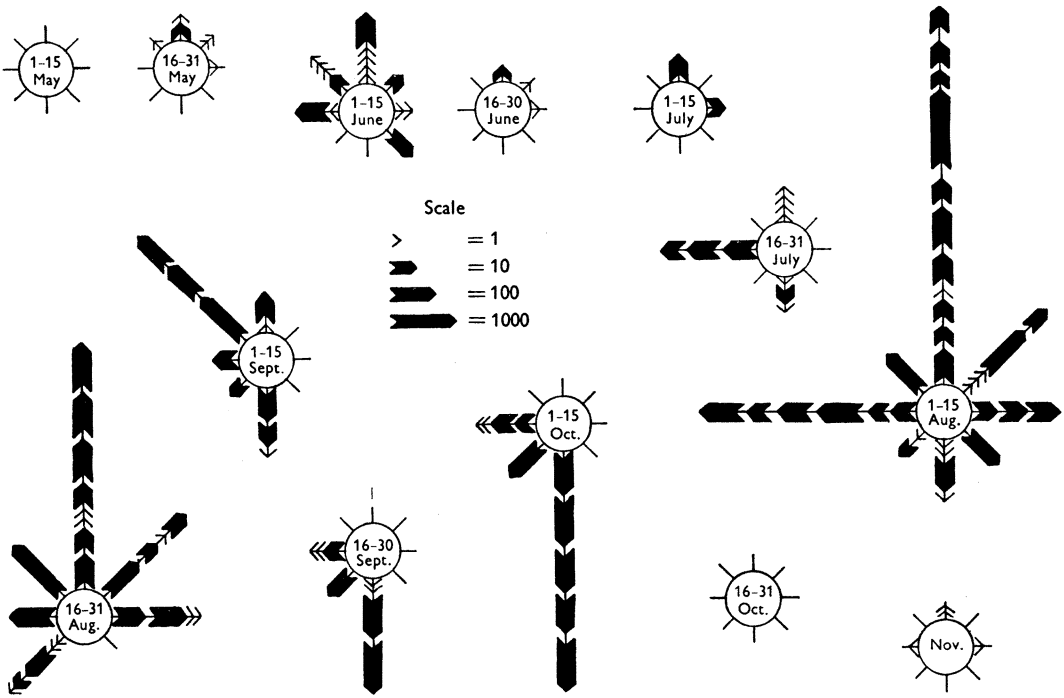

Fig. 5. Directional flight of the clouded yellow butterfly (*Colias croceus* Fourc.) recorded in the British Isles in the year 1947 during the greatest immigration since 1877.

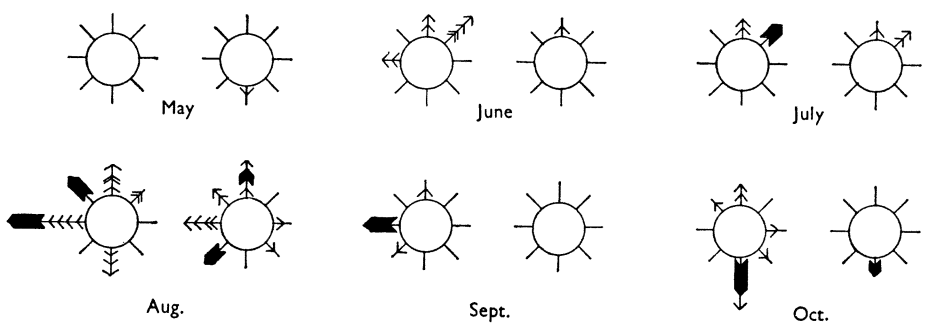

Fig. 6. Directional flights of the pale clouded yellow butterfly (*Colias hyale* L.) recorded in the British Isles up to 1949.

THE PAINTED LADY

(*Vanessa cardui* L.)

This is one of the greatest migrants in the world, and comes north to Britain from the North African area each spring in varying numbers. There is practically

early spring, the real northerly movement starts in May and reaches its peak in the first half of June. In the second half of June and in early July there is still evidence of a northerly or north-westerly movement but in reduced numbers. In the second half of July there is evidence of a westerly movement which

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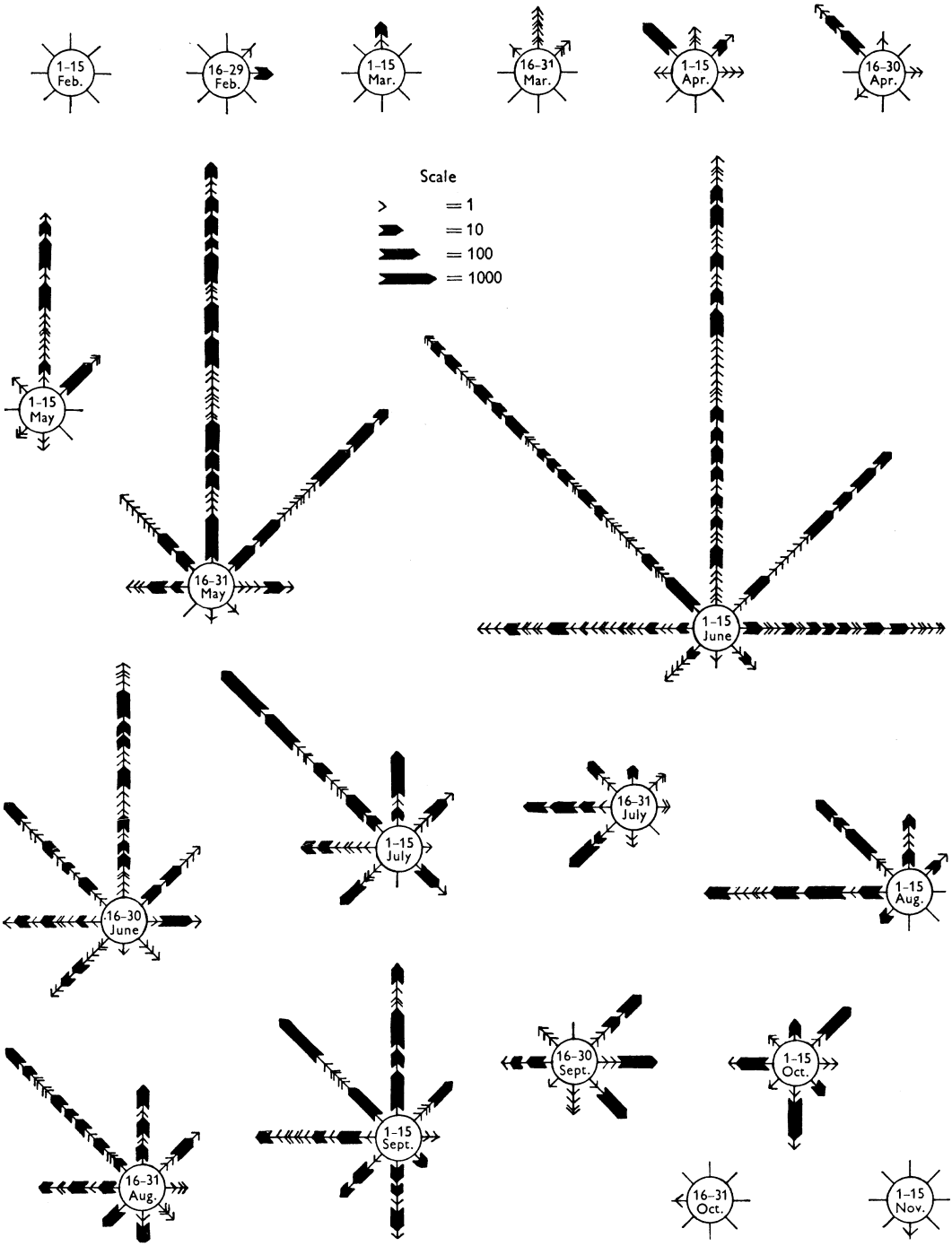

Fig. 7. Directional flights of the painted lady butterfly (*Pyrameis cardui* L.) recorded in the British Isles up to the end of 1949.

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increases in August, but tends to become more north-westerly at the end of August and in the first half of September. At no period in the autumn is there evidence, from these records, of a dominant movement in a southerly direction.

This is curious and unexpected—and may be associated with the fact that there are several records of immigration into south and south-east England in the autumn from the Continent, indicating an instability of population.

THE SMALL TORTOISESHELL

(*Vanessa urticae* L.)

The small tortoiseshell butterfly has not, up to the present, been usually considered as one of our immigrant species. It is a regular hibernator and undoubtedly our population is in no way dependent on immigration for survival. On the other hand, there are a few records of directional movements on the Continent, and on twenty or thirty occasions individuals have been seen at lightships up to thirty miles or more from our south, south-east and east coasts (see Williams *et al.* 1942, p. 133).

The cards recording movement in any definite direction were comparatively few and are shown in Fig. 8 divided into three seasons. Surprisingly, they show evidence of a northerly movement in the spring and up to the end of July; and a southerly movement in the autumn, from September on. A closer watch must be kept on this species, which appears now to be an immigrant.

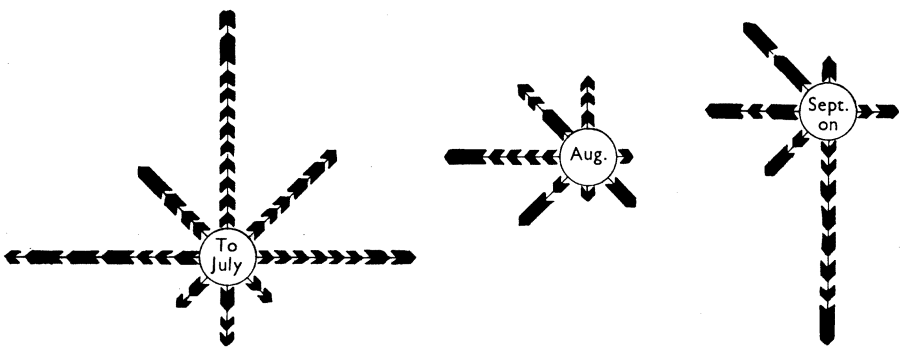

Fig. 8. Directional flights of the small tortoiseshell butterfly (*Vanessa urticae* L.) recorded in the British Isles up to the end of 1949.

THE LARGE CABBAGE WHITE BUTTERFLY

(*Pieris brassicae* L.)

The known movements of this butterfly (see, particularly, Williams, 1939; Williams *et al.* 1942, pp. 189–204) are very different from those of the species so far discussed. There is in central Europe a definite southerly migration about the end of July, which sometimes reaches 'snow storm' densities. Off-shoots from this stream seem to break away to the west, cross the North Sea, Holland, Belgium and northern France, and invade our south-eastern shores. There is also some evidence of an earlier migration season at the end of May. There are, quite a number of records of this in the British Isles, but comparatively few on the continent: but whether this difference is due to the relative numbers of skilled observers or to the behaviour of the butterflies cannot yet be decided.

A high proportion of our records in England relate to flights coming in from the sea along our southern and eastern coasts. As these are nearly always stated to be coming in more or less at right-angles to the coast, it was decided to divide the records into four categories: (1) flights observed well inland; (2) flights near the coast but not definitely stated to be coming in from the sea; (3) flights stated to be coming in from the sea; and (4) flights at sea recorded at lightships or from steamers in the Channel. It should be noted that estimates of actual numbers seen are less exact in this common butterfly, and flights of only a few individuals are seldom recorded. The representation of the flights on the diagram is therefore rather rougher than in the previous cases, and consists usually of 'a very few', 'dozens', 'hundreds' or 'thousands'.

Fig. 9 shows the records sorted into the four groups, as described above, and into half-monthly periods. In group 1—records inland away from the coast—there is some evidence of a northerly movement in the second half of May and first half of June; with a recrudescence of activity about the middle of July, rapidly reaching a peak and dying away soon after the middle of August. Although there are distinct southerly and south-easterly components in this second period they are by no means dominant and flights are recorded all round the compass.

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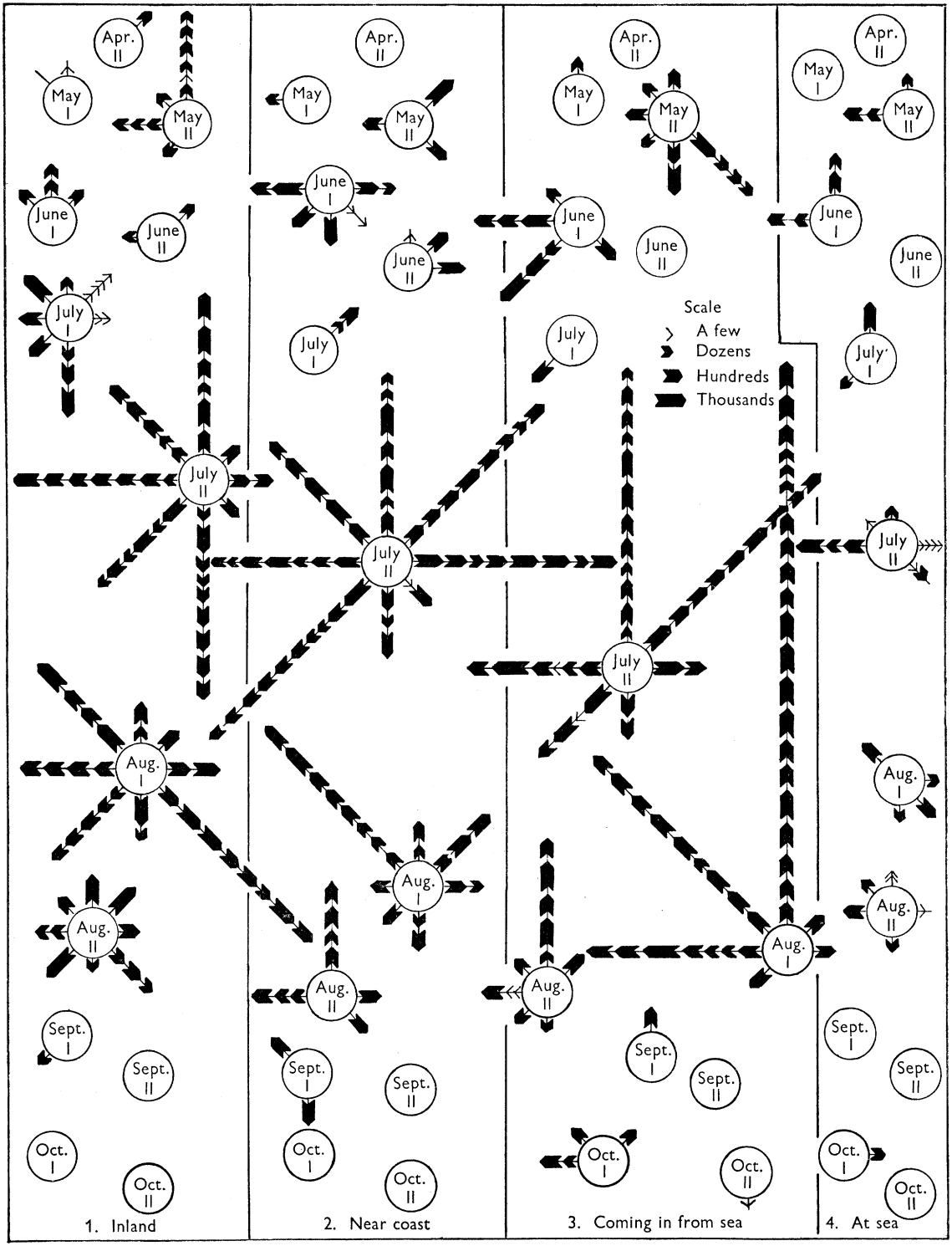

Fig. 9. Directional flights of the large cabbage white butterfly (*Pieris brassicae* L.) in the British Isles up to the end of 1949, separated according to whether the flights were observed: (1) well inland, (2) near the coast, (3) coming in from the sea, or (4) at sea.

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In group 2—near the coast but not stated to be coming from the sea—there are the same two seasons, (i) end of May and June and (ii) second half of July and beginning of August, but there is no definite northerly trend in the first season and the second has scarcely any southerly component.

In group 3—coming in from the sea—there are the same two seasons, with strong northerly and westerly components in the second.

In group 4—insects observed at sea—there are very few records but some indication of a northerly trend in the first season.

The two seasons undoubtedly correspond to the first and second brood of adult butterflies.

There appears to be little doubt that the records in groups 2 and 3 are affected by the distribution of observers on our coastline. If the migrating butterflies on approaching a coast tend to fly straight in, or if observers on the coast tend to record the flights as coming directly in when the flight is really at an angle, the observations are likely to be misleading. The larger number of observers along our southern coasts, also tends to increase the number of records to the north.

Groups 1 and 4, records inland and out at sea, appear to be free from these errors, and it is curious that both of these show a northerly trend in the May-June season. There is no supporting evidence for this direction in this earlier season in the few records available from Central Europe, although they are most certainly more westerly and less southerly than the records for the later season (see Williams *et al.* 1942, p. 204).

SUMMARY AND DISCUSSION

An examination of over a thousand records of directional flights in the British Isles, relating to six species of butterflies, shows distinct evidence of a northerly movement in the spring and a southerly movement in the autumn in four species: *Vanessa atalanta*, *V. urticae*, *Colias croceus* and *C. hyale*. In *Pyrameis cardui* there is strong evidence of the northerly spring flight but the numerous autumn flights do not show any dominant southerly component. In *Pieris brassicae* there are two migratory seasons, one at the end of May and early June, and the second at the end of July and beginning of August: in the first there is evidence of a northerly movement when away from the apparently confusing effects of coast lines, but the second flight has no obvious southerly trend in Britain.

It thus appears that the analysis of numerous records of the type here available, sent in by hundreds of amateur observers, is capable of being used to demonstrate these movements, particularly when they do not occur in spectacular densities ('like snowstorm' etc.), and further that the reality of the double flight, towards the poles in the spring and towards the equator in the autumn, cannot now be questioned for a high proportion of our regular immigrants.

This brings the migratory movements of butterflies into line with the migration of birds, and partly at least disposes of Heape's physiological separation of the two types of movement which he called 'Migration' (in two directions) said to be due to reproductive influences, and 'Emigration' (in one only), due to alimentary or food impulses.

I have already (Williams *et al.* 1942, p. 250) pointed out the difficulty of accounting for the persistence of a habit of movement in one direction only on any theory of evolution. If we accept that directional movement in butterflies is simply an overflow from an over-populated area, and that none of the emigrants ever return; then the species must be perpetuated by the offspring of those individuals which do not emigrate. Thus a habit must persist for countless generations, in spite of the fact that all individuals which develop it die without contributing to the continuity of the species.

It is therefore of interest to see that the more closely the subject of directional flights in butterflies is studied, the more frequently it is found that flights in both directions exist, even if they need close observation to discover. In 1930, I wrote that the majority of butterflies seemed only to have flights in one direction, but 'whether this expresses a biological truth or is only the result of our present lack of knowledge it is impossible to say at this time' (Williams, 1930, p. 324). In 1942, I stated that the search for evidence of movement in Lepidoptera had not been carried out sufficiently thoroughly to justify a theory that required two fundamentally different origins for migration.

There is still much to be learned, but the continual accumulation of records is supporting my belief that the migration of butterflies will be found to come into line with the migration of birds, and will not contradict the fundamental theories of evolution.

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