

to compensate for the cyclic motion of the earth's magnetic poles. Although it has never been especially looked for, there is no reason to suppose that there has been any such movement in migratory birds over the many years that they have been observed. There have been occasional references to the occurrence of insect migrations in the tropics simultaneous with magnetic storms, but they are so few that they are best regarded as being coincidences.

PHEBUS IN ALABAMA.

	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
1920		✓	✓	✓				✓	✓			
1921		✓	✓	✓				✓	✓			
1922								✓	✓	✓	✓	✓
1923							✓	✓	✓	✓	✓	✓
1924				✓	✓		✓	✓	✓	✓		
1925			✓	✓			✓	✓	✓	✓		
1926	✓						✓	✓	✓	✓		✓
1927				✓			✓	✓	✓	✓		✓
1928						✓	✓	✓	✓	✓		✓
1929							✓	✓	✓	✓		
1930								✓	✓	✓		
1931								✓	✓	✓	✓	✓
1932				✓				✓	✓	✓		
1933							✓	✓	✓	✓	✓	✓
1934			✓				✓	✓	✓	✓		✓
1935							✓	✓	✓	✓		✓
1936			✓	✓			✓	✓	✓	✓		✓
1937	✓		✓	✓								

52

FIG. 52.—Evidence of return flight in *Phoebis eubule* in Alabama.

IX. THE PROBLEM OF THE RETURN FLIGHT.

By C. B. WILLIAMS.

The Evidence.

The problem of the existence of a return flight in some or all of the migrating butterflies still remains one of fundamental importance and it is proposed to review first the evidence that has accumulated on this point so that the discussion which follows need not be encumbered by enumeration of facts or data.

Phoebis (Catopsilia) eubule.

The most striking evidence of a return flight of this species has been observed, at Montgomery, Alabama, over a period of about seventeen years by Mr. P. H. Smyth (Williams 1938b). He recorded the direction of flight of the butterflies observed crossing a park at frequent intervals from the autumn of 1920 to the spring of 1937. During that period very large numbers passed towards the south-east every year from the end of July to the beginning of December, and much smaller numbers were occasionally seen in the spring during March and April passing in the opposite direction to the N.W.

Fig. 52 gives a summary of his observations and shows how regularly the flights occurred.

Catopsilia pyranthe (and possibly other *Catopsilia* spp.).

At Kōdaikanal in South India, Evershed has observed (1927, Williams, *Trans. ent. Soc. Lond.* 75 : 9) large flights of *Catopsilia pyranthe* and other species to the south in October and November in several years; and flights in the opposite direction, towards the north, in February and March. *C. pyranthe* was definitely identified in these return flights, but other species were probably also present.

Colias croceus.

In my previous summary of this species (Williams 1930 : 133) only seven directional flights were recorded of which two were towards the south in the autumn. One of these was in Dorset, England, in September 1928 and the other near Cannes in the South of France in September and October 1921.

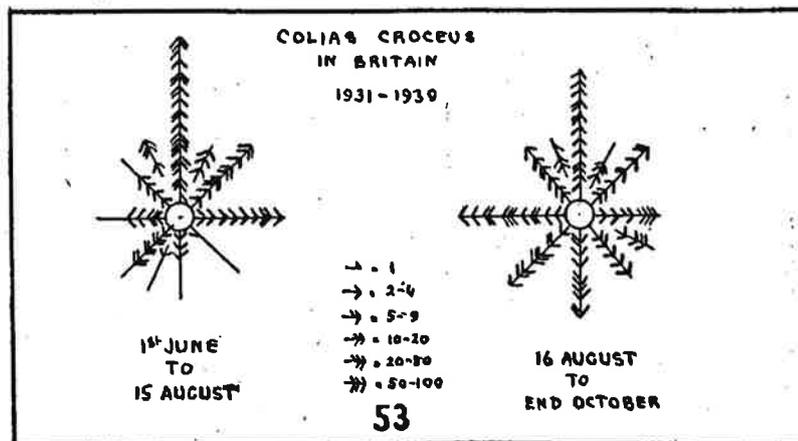


FIG. 53.—Evidence of return flight in *Colias croceus* in Britain.

Since then three other late summer or autumn flights have been recorded as follows :—

1900, Oct. 10. **Hautes Pyrénées, France. To S.**

Serried column seen by M. Rondu (Williams 1935d).

1928, Aug. 7-14. **Nr. Chamonix, Switzerland. To S.W.**

Incredibly abundant and moving steadily. Warren (1928).

1934, Sept. 27. **Royan, Charent Inf., France. To S.**

Suddenly abundant and moving to S. Bon (Williams 1935d).

On the other hand, an examination of a large number of records of the direction of flights of *C. croceus* in England, usually, however, fewer than a dozen individuals at a time, does not show any predominantly southerly flight (fig. 53), such as that shown in *V. atalanta* by the same method.

Since, however, in south England one is very near the northern limit of the normal distribution of *C. croceus* it might be expected that the southerly autumn flight would not be so obvious here as it would be farther south in France when larger numbers of individuals would be available to join in them.

Kricogonia lycide.

S. F. Aaron (1929) states that in the Rio Grande district of Texas countless numbers of this species fly southwards towards and into Mexico at the end of the dry season about September : then, in April and May, another flight takes place in the opposite direction towards the north in greatly reduced numbers.

Several other records exist of the spring flight to the north, but the large autumn flights to the south have not so far been recorded by other observers.

Ascia monuste.

Although this species undoubtedly flies both to the north and to the south in Florida, it is not certain that it comes under the category of a species with a true return flight at a later period.

The evidence available up to the end of 1937 has been summarised (Williams 1938) and seemed at the time to support Fernald's Theory that there was one

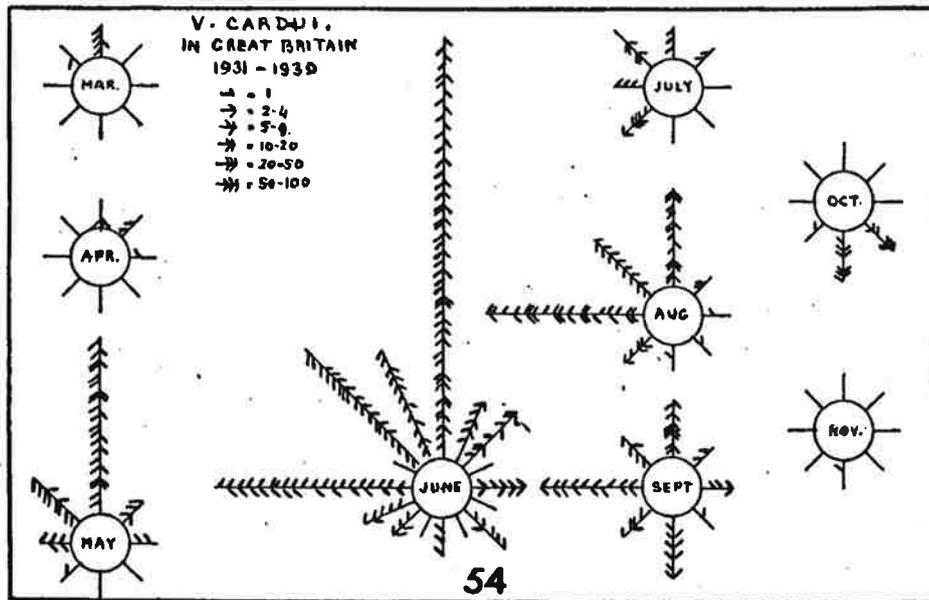


FIG. 54.—Evidence of return flight in *Vanessa cardui* in Britain.

centre of migration in North Central Florida from which butterflies flew away both to the north and to the south.

Since then, however, considerably more evidence has come in from the regular observations of Mr. and Mrs. Hodges (see p. 143) and they have shown that at Melbourne, Florida, in both 1938 and 1939 there was a quite definite and sudden reversal in direction in the middle of the flight season. In 1938 the insects flew to the south from mid-March to the 16th May and to the north from the 18th May to the end of June. In 1939 they flew again to the south from early March to the 10th June and to the north from the 11th June to the end of July.

Vanessa cardui.

There is as yet no evidence of a southerly movement of this butterfly in the U.S.A. and there is little or no new evidence in favour of a return flight in Europe.

In my previous summary (Williams 1930b) the most important piece of evidence brought forward for the southerly movement was information received from an entomologist and ornithologist Dr. Walter Innes in Egypt. He stated that he had on many occasions been on the north coast of Egypt at the time of the autumn immigration of the quail. These arrive in great numbers in the early morning, flying low over the sea. Dr. Innes states that on several occasions he had seen small numbers of Painted Ladies, sometimes in groups

of two or three, come ashore from the north with the quail. There is no reason to doubt the truth of these observations, but so far no one has had the opportunity to repeat them.

In England the direction of flights of individuals and small numbers of butterflies recorded by numerous observers from 1931 to 1939 have been tabulated in fig. 54, but while they show a preponderance of northerly flights in May and June, there is in the autumn, except in October, no definite preponderance of flights to the south. It can be said, however, that there are more records of southerly flights in the autumn than earlier in the year.

The evidence for the return flight of this butterfly is disappointing in view of the regularity of the appearance of the insect in two continents. It appears likely that the return does take place in Europe and North Africa, but the evidence is not easy to obtain.

Vanessa virginiensis.

On p. 154 of this report evidence of a return flight in this species is brought forward from the observations of Mr. and Mrs. Hodges in Florida. They record a southerly movement in September 1938, and a northward movement during March 1939. The autumn movement to the south had also been previously recorded by Shannon (1917, *Amer. Mus. J.* 17 : 33).

Vanessa atalanta.

Evidence about the movements of the Red Admiral Butterfly in Great Britain has greatly increased in the past ten years and the results of two years' close observations have been summarised by Mrs. K. Grant (1936a).

She has shown first by a study of the numbers present in different parts of England that they begin to disappear in the north before the south, and further that the disappearance in the north (usually about the end of September) is accompanied by a sudden increase in the numbers in the south.

Secondly when the recorded flight directions of individuals or small numbers of butterflies sent in by numerous observers were tabulated for the years 1934 and 1935 Mrs. Grant found that (1) up to the end of July the flights were predominantly to the north and (2) during September and October the flights were predominantly to the south.

Since then the records for 1936-1939 have been studied, and fig. 55 shows the combined results of the observations in the 6 years 1934-39.

The previous conclusion is completely supported and the preponderance of northerly flights in May, June and July and of southerly flights in September and October is quite striking.

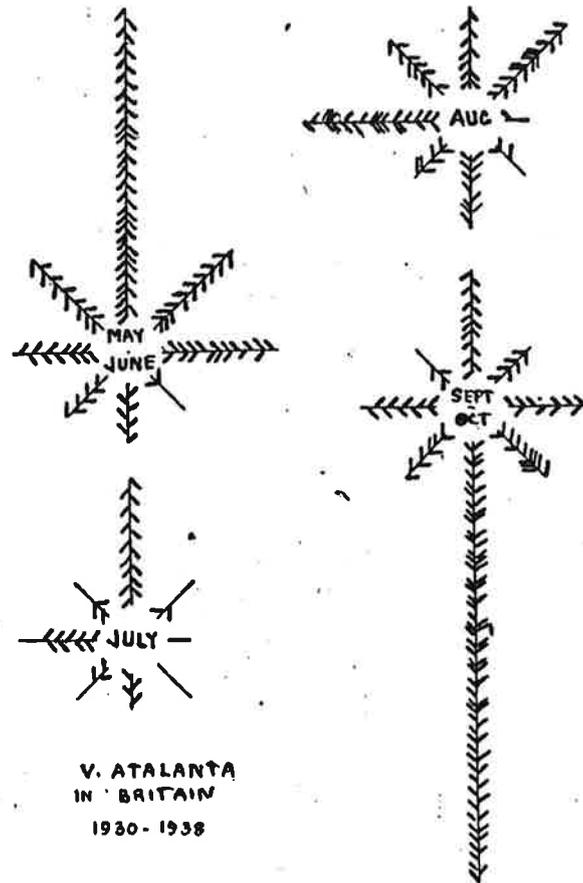
On two or three occasions, for example on the 23rd September 1934 at Start Point Lighthouse in Devon, and on the 26th-27th September 1935 at Round Island Lighthouse in the Scilly Islands, Red Admirals were seen to pass out to sea towards the south in numbers.

Still further evidence of autumn movement, although not of the direction of flight, is found in Fletcher's observations that butterflies marked in the autumn at Stroud, Gloucester, were very seldom seen again at the point of marking (see p. 224).

On the continent of Europe evidence of a return flight in the autumn has been brought forward by E. Fisher (1919), who saw a definite flight to the south near Zurich in September 1910, and by Foltin (1937a and b), who records definite southerly flights at Zell-am-Pettenfurst in Upper Austria at the beginning of October in each of the three years 1932, 1934 and 1936.

Dione vanillae.

Strong evidence of a return flight in *Dione vanillae* has been brought forward in this report (p. 149) by Mr. and Mrs. Hodges in Florida. They observed thin but definite movements towards the north in the spring, especially March and April, of 1938 and 1939, and very definite and quite conspicuously large flights towards the south in September and October of the same years.



55

FIG. 55.—Evidence of return flight in *Vanessa atalanta* in Britain.

Libythea labdaca.

Farquharson (1918 and 1922) recorded this butterfly in Nigeria as flying southward early in the rains about April; and returning northwards "towards the end of the rains." The month when this return occurred was not given nor were there any exact records of either flight.

In 1930 I had collected about a dozen records of flights for Nigeria, Gold Coast and Sierra Leone. Most of the flights, including all from Nigeria, were in March, April and May and in a southerly direction as stated by Farquharson. There were, however, two flights recorded later in the year (in August and September in the Gold Coast) but they were also to the south.

Since the above summary was made several new records have come in (Williams 1933b and 1939a), three of which are in the second season in October, but only one of these is towards the north. On the other hand, there is a record

of a flight to the north in January and February which is difficult to reconcile with Farquharson's statement. Miss Vinall (Poulton 1933d) has recorded migrations of *L. labdaca* at Bongandenga in Belgian Congo in April and in August 1932, but in neither case was the direction of flight reported.

Fig. 56 shows a summary of the present known records. In spite of Farquharson's definite statement, the question of return flight in this species is still somewhat doubtful.

LIBYTHEA LABDACA	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	MONTH NOT STATED
SIERRA LEONE.					↑								
GOLD COAST.			↓ ← +	+				↓	↓	↑ +			
NIGERIA.	↑ ↓ ↑	↑	↻ ↻ ↻	↻ ↻ ↻	↻ ↻ ↻					↻			

56

FIG. 56.—Evidence of a return flight in *Libythea labdaca* in West Africa.

Danaus plexippus.

There is now no doubt whatever as to the existence of a return flight in the movements of this butterfly. No other explanation will fit the numerous records that have already been given (Williams 1930b and 1938b and on p. 165 of the present report).

The evidence in this species is even more definite as it seems certain that the northerly flight in the spring in North America is performed by the same individuals which moved south in the autumn, and not merely by other individuals of a later generation. In no other species does the evidence suggest this conclusion.

Danaus berenice.

Mr. and Mrs. Hodges have observed in Florida thin but definite northward flights of this species in spring and early summer, and quite definite southward flights in the autumn, particularly in September and October (see p. 148).

Andronymus neander.

The recorded flights of this butterfly in East Africa are discussed on p. 220.

The majority of flights are in March and April towards the south and south-east. The only records at this period of the year not in this general direction consist of a few individuals in flights of other species of butterfly. On the other hand, the only record at another period of the year, in October, is towards the north.

The evidence is suggestive but does not yet prove a return flight.

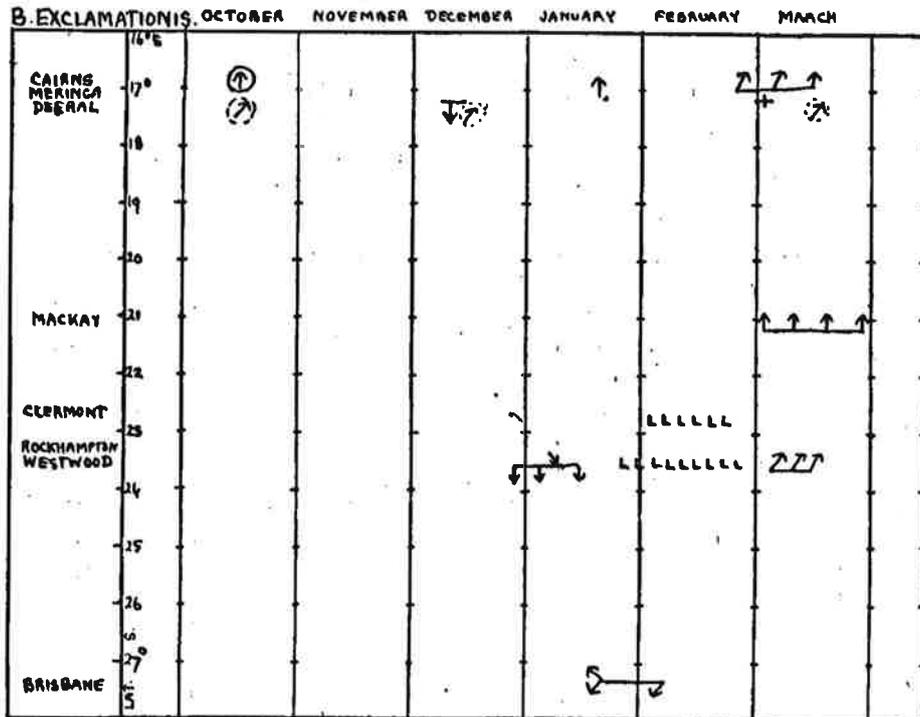
Badamia exclamationis.

Burns (1933) has stated that in the coastal district of Queensland he has observed flights of this butterfly more or less towards the south at Cairns, near Rockhampton, and at Brisbane in December and January; the flight being later in the south than in the north. Then after an interval of about six weeks (during which a generation develops at Rockhampton) flights in the reverse directions, towards the north, have been seen at Rockhampton, Mackay and Cairns. The observations are shown diagrammatically in fig. 57.

Plusia gamma.

The evidence for the return flight of this species in Great Britain has been recently summarised by K. Fisher (Mrs. Grant) (1938) and the summary diagram of her results has been reproduced in fig. 58.

It will be seen that from May to July the majority of the insects are observed moving to the north; in the first half of August there are movements to north, west and south, but not to east; while from the middle of August to the end of October most of the flights are towards the south. Throughout the whole year there is little or no evidence of any easterly movement.



57

FIG. 57.—Evidence of a return flight in *Badamia exclamationis* in Australia.

The southward movements included two very large flights observed at the Start Point Lighthouse in South Devon by Mr. W. A. Godfrey: one on the 12th September 1934 and one on the 4th August 1935; in both cases the insects were flying in thousands out to sea to the south.

Urania fulgens.

Many years ago Friedrich (van Bemmelen 1857) stated that this day-flying moth migrated every year in the state of Vera Cruz, Mexico, beginning in April for two or three weeks towards the north and returning in the opposite direction about six weeks later.

It is now known that this insect migrates regularly in most of the Central American States and the evidence on reversal of flight has recently been summarised (Williams 1937c).

There is evidence of two flight periods: one from about March to May and the other in July and August. In the former the flights are predominantly to the north and in the second to the east and south, but there are exceptions in both seasons.

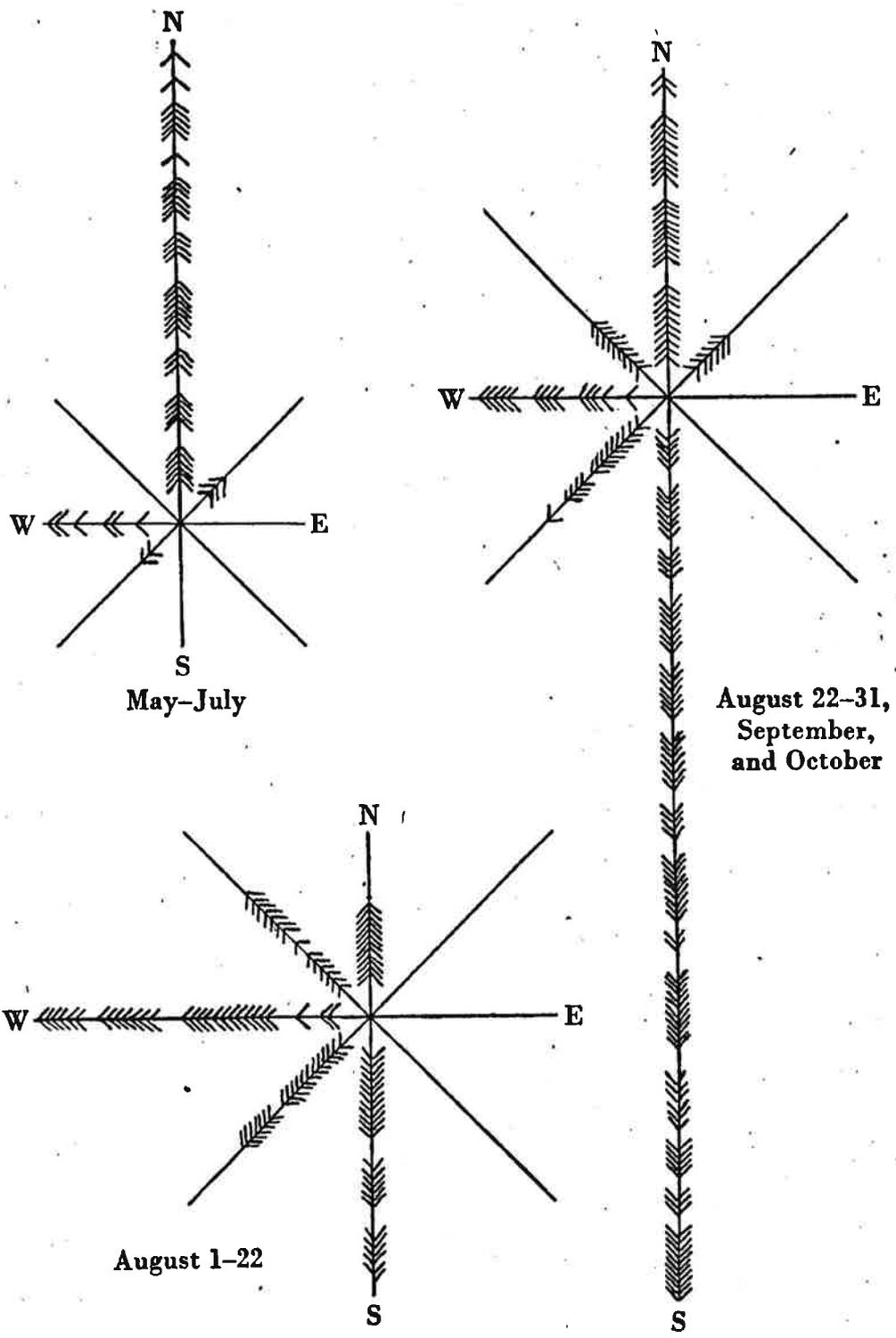


FIG. 58.—Evidence of a return flight in *Plusia gamma* (from *J. anim. Ecol.* 1937).

Since the above summary was made, Mr. A. F. Skutch has reported that in Costa Rica in 1938 he observed flights to the north in April and May, and then about the beginning of June the insects began to fly to the south and continued till the end of August. Even during this period, however, a minority continued to fly to the north. The flight ceased at the beginning of September.

Mr. P. A. Vedoua also reports a flight to the north at the end of March and beginning of April, 1939, at San José, Costa Rica.

Mr. W. Schaus also writes that he had on several occasions observed the north-westerly flight of *U. fulgens* in Mexico on the eastern slopes; and that on one occasion he thought that there had been a flight in the opposite direction, but no date was recorded.

On the whole the new evidence lends support to the theory that this moth has a definite return flight at a later season of the year.

The evidence for a return flight is summarised above for the following fifteen species.

PIERIDAE.

Phoebis eubule (U.S.A.).

Catopsilia pyranthe (India).

Colias croceus (W. Europe).

Kricogonia lycide (U.S.A.)?.

Ascia monuste (Florida)?.

NYPHALIDAE.

Vanessa cardui (Europe).

Vanessa atalanta (Europe).

Dione vanillae (U.S.A.).

LIBYTHEINAE.

Libythea labdaca (W. Africa)?.

DANAIDAE.

Danaus plexippus (U.S.A.).

Danaus berenice (U.S.A.).

HESPERIIDAE.

Andronymus neander (E. Africa)?.

Badamia exclamationis (Australia).

NOCTUIDAE.

Plusia gamma (Europe).

URANIIDAE.

Urania fulgens (C. America).

Of these the evidence is not very definite in five but in the ten remaining insects there is good evidence of the existence of a return flight. This is not a high proportion of the known migrants, but is quite a high proportion of those in which there is sufficient evidence to justify any conclusions.

Reference should also be made to the fact that the flights of moths and butterflies recorded at the British lightships showed a change in direction from predominantly west and north-west up to mid-August to south and south-east after this date (see p. 140 of this report).

Discussion.

In 1931 there appeared posthumously a book *Emigration, Migration and Nomadism* by Dr. Walter Heape, F.R.S. The author had died in 1929 and the book was edited and supplied with a preface by Dr. F. H. A. Marshall. Thus the essential portions of it were written before my own book on the migration of butterflies appeared, but it was published afterwards.

The author, from previous experience as a physiologist, starts with the basic assumption that there are two fundamentally different types of mass movement in the animal kingdom. The one, in which there is a return movement at a later season, he designates "migration"; and the other, in which there is no return, he calls "emigration." He also considers that the two types of movement are due to two fundamentally different physiological causes which he defines as "gametic" and "alimentary"; or, in other words, one due to an urge for reproduction, and the other to the need for food.

In the former class he puts the migration of most birds, turtles, most fishes

including the eel, some crabs, and among insects the APHIDAE, some locusts and the single butterfly *D. plexippus*.

Among the "emigrants" are the lemming, the spring-buck of S. Africa, the moose, certain rats, a few birds, including Pallas' Sand-Grouse, most locusts, dragonflies, and all "migrant" butterflies and moths with the single exception given above.

He objects very strongly to the use of the word "migration" for any movement in which a return has not been demonstrated, and wished to confine the use of the word "emigration" to movements which are believed to be in one direction only.

His classification appears at first to have the merits of simplification, but on the whole I am not in agreement with his theories, particularly as they concern the *Lepidoptera*.

Terminology.

If it is correct that there are two essentially different processes of migration with fundamentally different causes and so presumably separate origins, it is most certainly desirable to have different words to express them. I have, however, already pointed out (1920, *Trans. ent. Soc. Lond.* 1920 : 215) that a "migration," in whatever sense the word is used, consists in sequence of three processes according to the locality from which it is viewed; there is an "emigration" from the point of origin; a "transmigration" at any point on route; and an "immigration" at the point where the migrants come to rest. It seems therefore very unsatisfactory to take a word that means an essential part of any migration and to restrict its use to a phenomenon which one believes to be fundamentally distinct. If the word "migration" is used in any restricted sense, then "emigration" should not be used in any other meaning than a portion of this process. I suggest that if "migration" is limited to movement in which a return journey is established, then the word "exodus" might be used for those without a return.

The reality of the difference between "migration" and "exodus" in Lepidoptera.

Twenty years ago a return flight at a different time of the year had not been established in any species of *Lepidoptera* with the doubtful exception of the Monarch (*D. plexippus*).

In my book in 1930 it was definitely established for this butterfly and suggested to occur also in *V. cardui* in Europe, in certain *Catopsilias* in India, in *L. labdaca* in West Africa, in *Catopsilia sennae* (*P. eubule*) in U.S.A. and in the moths *Urania fulgens* in Central America and *Agrotis ipsilon* in India.

Up to that time it can be said that practically no regular observations on the migrations of butterflies had ever been made. The evidence available was only a large number of scattered records of any flights that had been conspicuous enough to force themselves on the notice of some observer who, up to that moment, had not been in any way interested in the problem.

Now for about ten years there has been a greatly increased interest in the subject and a few scattered observers actually watching for movements and ready to observe both thick and thin flights. The need for a classification (see p. 260) which includes densities down to one butterfly per 100 yards per minute shows how thin a flight can now come under observation.

As a result, the number of species with suspected returns (pp. 240 to 248) has more than doubled. The southward autumn flight has been demonstrated beyond doubt in such species as the Red Admiral (*V. atalanta*), which twenty years

ago was hardly considered as a migrant; and in the Silver-Y moth (*P. gamma*), known as a migrant for fifty years, but never previously considered to return S.

In fact, evidence of a return begins to appear in nearly every species when sufficient records are available, and particularly when efforts have been made to get continuous observations at all times of the year, instead of only during the period of conspicuous flight.

The more that information is available about the species in which a return flight occurs, the more frequently it appears that the flight in one direction is conspicuous and the flight in the other direction difficult to observe. Thus the Monarch migrates southward in autumn gregariously in large bands which attract popular attention, but the butterflies go northward in the spring individually, and it requires a careful watch to demonstrate the movement.

Phoebis eubule, as observed by Smyth in Alabama (fig. 52), has a conspicuous autumn flight in large numbers, and a spring flight in the opposite direction in very much smaller numbers.

The southward flight of *V. atalanta*, already referred to, has been demonstrated almost entirely from the flights of individual butterflies, recorded by a number of observers none of whom was probably conscious of any extensive directional movement taking place. Thus it is likely that many, if not most, "return flights" have been still overlooked.

Even today the available evidence on Lepidoptera is still strongly biased in favour of conspicuous mass flights, and it is dangerous to theorise too much on the meaning of the apparent absence of a return. Absence of evidence is not evidence of absence.

There is still another difficulty in connection with movements without a return flight, which I have already pointed out and which has been discussed by Elton (1930). This difficulty is not a practical one of obtaining unbiased evidence, but a theoretical one of evolutionary development. If in any species there is a permanent home from which an "exodus" of part of the population occurs at intervals (regular or irregular); and if this portion goes away to die elsewhere without leaving any progeny, while the species is kept going only by the progeny of the individuals which stay behind: under such conditions how is the instinct to "migrate" perpetuated?

If for fifty thousand years (or so) *Vanessa cardui* has persisted in parts of North Africa, and every year a large portion of the population develops an urge to fly away to Europe—there to die—why does the urge to move continue to appear in the North African butterflies all of whose ancestors in a direct line for many thousands of generations must have been the individuals who did *not* develop the urge to migrate?

Modern theories of evolution, from Darwin to the statistical geneticists, demand a survival value for any characteristic which is to persist. How then can an instinct be so widespread, if, instead of a survival value, it carries a certainty of extinction and sterility to the individual possessing it?

This difficulty is so serious that in 1930 I wrote of migration without a return flight "the majority of butterflies seem to come under this heading, but whether this expresses a biological truth or is only the result of our lack of knowledge it is impossible to say at this time."

After a further ten years of examination of evidence I still cannot overcome the evolutionary difficulty and I can still point to no butterfly in which the absence of a return flight has been established beyond reasonable doubt. It is of course always difficult to prove a negative case, but in Lepidoptera, at least, the search for evidence has not been carried out sufficiently far to justify a theory

requiring two fundamentally different processes of migration, using the word in its widest sense.

I should also suggest that, even in the case of so well known a creature as the lemming, no one has made any serious effort to watch for movements on a very small scale in between the periods of great overflow nor has anyone tabulated the direction of movement of large numbers of single individuals of any of Heape's "emigrant" mammals at all seasons of the year or for a series of years. The difficulties are great, but Mr. Smyth's seventeen-year diagram (p. 240) might be set up as an example worth following.

Heape's classification of the causes of the two apparent types of migration also brings many difficulties in its train. He himself finds that it breaks down almost immediately, and he has to recognise several other causes including "climatic" and "over-population." In fact he finally states that the causes of "emigration" can be: (1) alimantal; to get food; (2) climatic; to get to a better climate; or (3) the result of over-population.

In "migration" the movement towards the breeding area is gametic (the urge for reproduction), while the movement away from the breeding area is either climatic, or alimantal, or the result of over-population, in fact the causes are the same as his "emigration." So in his fundamentally distinct "migration" the gametic urge has to alternate with a non-gametic urge to produce the regular backward and forward movement of the population. He cannot have a gametic "migration" without an alternating "emigration."

Nearly all butterflies and moths he would classify under the "alimantal" stimulus, yet they do not migrate until the adult stage when all the main feeding of that individual has been done. So far from having received any early indication of approaching food shortage, the migrating butterflies, moths (and locusts) have usually large stores of reserve energy stored up in the form of fat-bodies, which can later be used for locomotion or for egg production.

Most of the evidence that Heape produces is from the birds, fishes and mammals. At one point he discusses the effect on the regularity of migration of the exceptionally long life and slow reproduction of the elephant, but he does not seem to have taken into consideration sufficiently the opposite effect of the short life of insects and other invertebrates. Is it only a coincidence that most of his examples of "migration" are from long-lived vertebrates, and most of his examples of "emigration" from the invertebrates?, or that the only species among butterflies that he will allow to "migrate" is the Monarch which has an exceptionally long adult life of nearly one year?

The phenomenon of the return flight cannot occur with quite the same regularity in *Lepidoptera* with their short lives, high birth and death rate and violent fluctuations in population numbers as in, for example, the birds with relatively long lives, and low death and birth rate, or at the other extreme the elephant with very long life, low birth rate and (until the evolution of *Homo sapiens*) a low death rate.

It is perhaps at this point worth drawing attention again to the curious fact that among the butterflies in which the return flight has been established, in Europe the spring flight to the north appears to be the more conspicuous and undertaken by larger numbers than the return flight in the autumn; while in the case of the American butterflies (except *V. cardui*) the southward flight in the autumn is much more conspicuous than the northward flight in the spring. The American migrants seem to increase their numbers in the north during the summer and reduce them in the south during the winter; while the European migrants appear to reduce their numbers in the north during the summer and increase them during the winter in the south.

If the evidence has been correctly interpreted, it is difficult to find a reason. Two suggestions can, however, be made. In the first place most of the evidence of migrations of butterflies in Europe has been collected in England and Germany in latitudes approximately 48–55° N.; whereas in America most of the records come from areas in latitudes 30–40° N.; at least 15° or a thousand miles nearer the Equator and at a level equivalent to North Africa and the Mediterranean basin on the other side of the Atlantic. It is possible that if more intensive studies could be carried out in the south of Europe the autumn flights would be found to be more conspicuous, as indeed has already been found with *Colias croceus* in the south of France.

The other possibility is that the different configurations of the two continental areas may have an effect. In Europe there is the Mediterranean in latitude 30–45°, apparently frequently crossed by large numbers of migrants, and south of which the sub-tropical area still continues in North Africa, where many of our European immigrants breed during the winter.

In America, on the other hand, there is the much wider Caribbean Sea in latitude 10–30° N., cutting out a very large sub-tropical breeding area. North of this there is only a very narrow belt of sub-tropical land (Florida and parts of Mexico) and south of it there is the essentially different damp tropical climate. Considering the frequent sea traffic and the number of small islands, there are very few records of migrant insects crossing from the north of South America to the Gulf States of the U.S.A.

It is interesting to note in this connection that *Vanessa cardui*, the one butterfly that migrates into the U.S.A. from the south in very large numbers in the spring in the same way as in Europe, comes apparently from western Mexico, the only portion of the southern boundary of the U.S.A. where there is a large land area with a dry sub-tropical climate such as is found in North Africa.

X. CORRELATION BETWEEN OCCURRENCE OF MIGRANTS IN U.S.A. AND EUROPE.

By C. B. WILLIAMS.

In 1937 Mrs. K. Grant made a study of the years of occurrence in numbers of the Striped Hawk-Moth (*Celerio lineata livornica*) in Europe and of the American race of the same species (*C. lineata lineata*) in the United States. Fairly good information was obtained from both continents over a period of sixty years, 1876–1935.

The insect occurred in unusual numbers in Europe in 23 of these years and in America in the same number. When the years were divided into the four possible groups of (1) occurring in both Europe and America, (2) occurring neither in Europe nor America, (3) occurring in Europe but not in America, and (4) vice versa, the frequency distribution was as shown in Table 29, A.

If the sixty years, including 23 occurrences in Europe and 23 in America, were completely randomised in the four categories the number expected in each would be as shown in Table 29, B.

From these it will be seen that the observed numbers are in excess in the categories "occurring both in Europe and America," and "occurring in neither," but are below the expected in the other two. The evidence therefore shows that there is a tendency for large migrations to occur simultaneously in both continents.

For those who are statistically minded, the test of the significance of the departures of the observed results from those calculated from an assumption of no correlation, gives $\chi^2 = 4.0$, which is a significant result with a probability

just below 1 in 20. In other words, such a result could be got by accident only about once in about twenty-two trials.

This conclusion was of great interest and an opportunity has been taken

TABLE 29.

Distribution of occurrence of *C. lineata* in Europe and N. America. A. Observed frequency; B. Frequency calculated on no correlation.

	A.—Observed frequency.			B.—Frequency calculated on no correlation.		
	In Europe	Not in Europe	Total	In Europe	Not in Europe	Total
In America . . .	13	10	23	9	14	23
Not in America . . .	10	27	37	14	23	37
Total . . .	23	37	60	23	37	60

to get a similar series of data for the Painted Lady Butterfly (*Vanessa cardui*), which also migrates in both continents and is not even racially distinct in each.

It has not been easy to obtain good information for all the years as the insect is not a serious pest and thus is not so frequently recorded in the literature of Applied Entomology. On the other hand, it is not sufficient of a rarity to be recorded regularly by collectors. However, it is unlikely that many really large outbreaks have passed unrecorded.

After examination of a large number of records the information in Table 30 has been collected to show whether or not the insect has been above the average in numbers in either Continent in each of the 74 years from 1865 to 1938.

From these data Table 31 has been prepared on the same lines as Table 29

TABLE 30.

Years of above the average abundance of *V. cardui* in Europe and America, 1865-1938.

Eur.	Am.	Eur.	Am.	Eur.	Am.	Eur.	Am.				
		1880		1900	o	o	1920	o	o		
		1881		1901	o	o	1921	o	o		
		1882		1902	o	o	1922				
		1883	o	1903	o		1923				
		1884	o	o	1904		1924	o			
1865	o	o	1885	o	1905		1925				
1866	o	o	1886	o	1906	o	1926	o	o		
1867			1887		1907	o	o	1927			
1868	o		1888	o	o	1908	o	1928	o		
1869	o	o	1889	o	o	1909		1929			
1870			1890			1910		1930			
1871			1891			1911		1931	o	o	
1872			1892	o		1912	o	1932			
1873			1893			1913	o	o	1933		
1874			1894	o		1914	o	o	1934		
1875			1895	o		1915		1935	o		
1876			1896			1916		1936			
1877	o		1897			1917	o	1937	o		
1878		o	1898			1918		1938			
1879	o	o ¹	1899	o	o	1919					

¹ Abundant in the Hawaiian Islands after not having been seen for several years.

and gives the same indications as the data for *C. lineata*, namely that there is a tendency for migrations to occur simultaneously in both continents.

The test of significance gives $\chi^2 = 8.0$, which is significant at a level of about 1 in 200. The significance is, however, made considerably larger by the number of years with no records for either Continent. If one omits ten of these as possibly due to lack of evidence and only considers 30 years with outbreaks in neither Continent one still gets $\chi^2 = 4.9$, which is significant at the 1 in 35 level.

TABLE 31.

Distribution of occurrence of *V. cardui* in Europe and N. America. A. Observed frequency; B. Frequency calculated on no correlation.

	A.—Observed frequency.			B.—Frequency calculated on no correlation.		
	In Europe	Not in Europe	Total	In Europe	Not in Europe	Total
In America	13	7	20	7.6	12.4	20
Not in America	14	40	54	19.4	34.6	54
Total	27	47	74	27	47	74

If a record of the occurrence of large numbers of Painted Ladies in Hawaii in 1879 (a year of great abundance in Europe) may be taken as evidence of migration in North America, the results become even more significant with $\chi^2 = 6.269$, which is significant at just above 1 in 100, even when ten of the years with no records are omitted.

The observations analysed for the two species therefore both show a tendency for large migrations to occur, or not to occur, simultaneously on both sides of the Atlantic.

This implies that, whatever the causes of extensive migration may be, they cannot be localised as independent happenings, but must be due to some widespread event, tending to vary in the same direction over areas covering nearly half the circumference of the earth.

XI. CORRELATIONS OF OCCURRENCE OF BRITISH IMMIGRANTS.

By G. F. COCKBILL.

About ten years ago, Williams commented on the appearance in entomological journals of such notes as "This year has been a good one for migrants," or alternatively, "Very few migrants have been reported this year," and asked if this represented a biological truth or a series of selected coincidences (Williams 1930b : 406).

There have been, in the literature, frequent allusions to the fact that when *V. cardui* is very abundant, *P. gamma* and *N. noctuella* also tended to be abundant, but beyond such remarks there is very little information of the activities of migrants in relation to one another.

Sufficient information has now been collected concerning the yearly abundances of thirty-five migrant species discussed in Section III of this report (p. 105) to allow correlations to be made and so to discover whether any species tend to occur or not to occur together.

The indices of abundance already described (p. 106) were used as a basis for the correlations.

Table 32, A, shows all the correlations of each of 35 species with all others. The species are arranged in four groups, Rhopalocera, Sphingae, Noctuae and an assortment of PYRALIDAE, GEOMETRIDAE and others labelled "Miscellaneous."

The correlations were taken over a period of 75 years from 1857 to 1931 in all but 5 cases. This period was decided upon because before 1857 records were scanty and after 1931 the records were of quite a different order due to the greatly increased numbers of records obtained through the Insect Immigration Committee of the S.E.U.S.S.

The five exceptions were of two kinds: (1) those species which were first recorded in Britain subsequent to 1857 were included for the period of their occurrence in Britain only. For this reason *D. plexippus* was considered over a period of 56 years and *L. albipuncta* over 64 years; (2) those species in which the early records were very scanty and vague were considered from the year when the records became fairly consistent. Thus *C. ambigua*, *P. napi* and *N. noctuella* were dealt with for 52 years.

The figures in the first column show the average correlations of each species with all others. Where 75 years are taken, the value of the correlation must be 0.23 or over to have a probability of 19 out of 20 that the result has not arisen by chance and a value of 0.30 or over to have a probability of 99 out of 100. Where 52 years are taken these values are increased to 0.27 and 0.35 respectively.

For convenience of reference in Tables 17, 18 and 19 a lettered key is provided in each case.

Table 32, C, shows all the significant values indicated by + or - signs. The large signs show values at or above 1 in 100 level, and the small signs show values below these but significant at or above the 1 in 20 level. In this table, it can be seen that in section A, some species are highly positively correlated, e.g. *V. cardui*, *V. atalanta*, *C. croceus* and *C. hyale*, and others, namely the "Whites," are negatively correlated with other species.

In Section B (key), the correlations "Butterflies against Hawk-Moths," it can be seen that *M. stellatarum* shows a high positive correlation with *V. cardui*, *V. atalanta*, *C. croceus* and *C. hyale*, and that here again the Pierids show negative correlations.

In Section C, "Hawk-Moths against Hawk-Moths," there is very little relationship shown.

In Section D, "Butterflies against Noctuids," the Pierids again show negative correlations, and *P. gamma* shows a positive relationship with *V. cardui*, *V. atalanta*, *C. croceus* and *C. hyale*. The relationships of the other species are not very clear.

In Section E little is shown with "Noctuids against Hawk-Moths," but in Section F the "Noctuids against Noctuids," a general high positive correlation appears.

In Section G, the "Miscellaneous group against Butterflies," *N. noctuella* shows positive relationship with the *V. cardui* and *V. atalanta* group, and *U. pulchella* shows a negative relation with the butterflies. Section H, "Miscellaneous against Hawk-Moths," shows little except that in the case of *U. pulchella* the only significant values are negative.

In Section I, the Noctuids show a high positive correlation with *L. salicis* and *N. noctuella*, while in Section J, "Miscellaneous against Miscellaneous," *N. obstipata* and *S. saccharia* show a positive relationship and *U. pulchella* shows negative values.

These observations are summarised in tab. 32, B, where the average correlations for each section are shown. The highest average correlations occur between "Noctuids and Noctuids" and between "Miscellaneous and Noctuids" (Sections F and I respectively).

The total number of correlations is 595, of which 161 are negative values and 434 are positive. This preponderance of positive values is better shown in a frequency distribution of all correlations, fig. 59. The mean of all 595 correlations is $+0.12$.

There are two possible explanations for this preponderance of positive values. It could be a biological fact resulting from a tendency for migrants to occur and to be absent together, *i.e.*, for there to be "good" and "bad" years for several migrant species simultaneously.

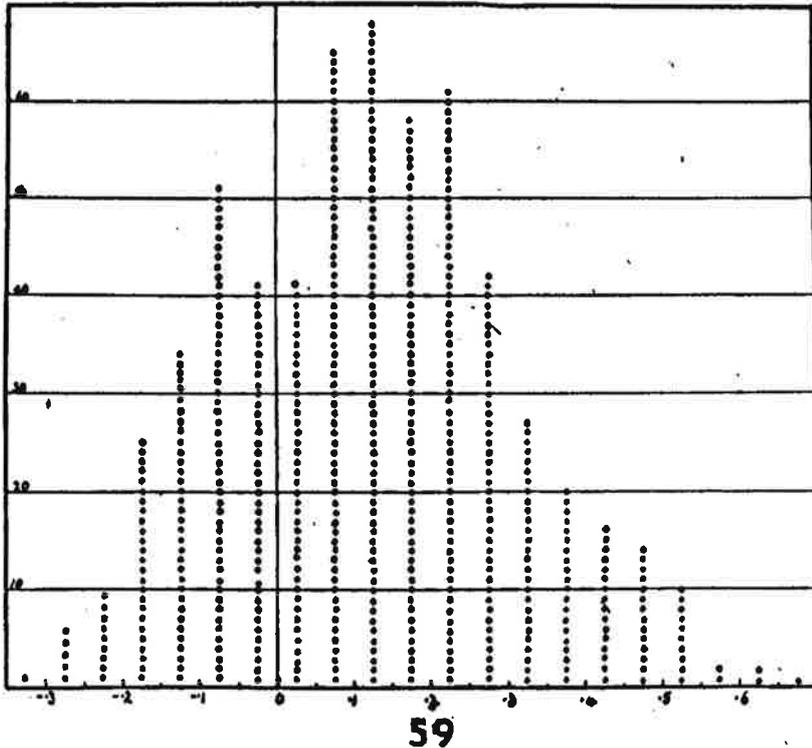


FIG. 59.—Frequency distribution of the 595 intercorrelations of 35 British immigrant butterflies and moths.

It could also be due to irregularities in the evidence resulting from waves of interest in observers of migrant species. If for a few years migrants tended to be recorded and then for a few more to be overlooked altogether, they would show a positive correlation.

It is possible that both explanations are contributory. In order to reduce the effect of the second possibility, the correlation values were expressed as departures from the mean $+0.12$ so that the positive bias was counteracted. The numbers of positive and negative values now become 291 and 304 respectively, which indicates an equal distribution about the mean.

Table 33, A, shows all correlations expressed as departure from the general mean ($+0.12$), the species now being arranged in order of their average correlation with all other species.

TABLE 33.
 A. Intercorrelation of thirty-five British Immigrant Lepidoptera arranged in order of mean correlation with all others.
 B. Mean intercorrelation in groups of five. C. Significant correlations as in table 35.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25.	26.	27.	28.	29.	30.	31.	32.	33.	34.	35.			
1. <i>D. pulex</i>	-0.12																																					
2. <i>P. nupte</i>	-0.12	-0.21																																				
3. <i>D. plexippus</i>	-0.11	+0.14	-0.22																																			
4. <i>P. brassicae</i>	-0.10	-0.01	+0.17	+0.10																																		
5. <i>P. napi</i>	-0.10	-0.35	+0.40	-0.10	+0.10																																	
6. <i>C. euphoniae</i>	-0.07	-0.15	-0.26	-0.07	+0.01	-0.17																																
7. <i>C. frazini</i>	-0.06	+0.12	-0.21	-0.08	-0.29	-0.28	+0.12																															
8. <i>H. ateraria</i>	-0.06	-0.24	-0.17	-0.06	-0.09	-0.11	-0.23	-0.13																														
9. <i>A. bathonia</i>	-0.04	+0.12	-0.29	-0.17	-0.23	0	+0.07	+0.20	+0.05																													
10. <i>V. antiopea</i>	-0.04	+0.08	-0.27	-0.17	-0.08	-0.01	+0.07	+0.37	-0.18	+0.16																												
11. <i>L. extranea</i>	-0.04	-0.20	+0.04	-0.16	-0.20	-0.18	-0.26	-0.20	0	-0.28	-0.26																											
12. <i>C. goli</i>	-0.04	-0.20	-0.30	-0.12	-0.24	-0.28	+0.18	+0.01	-0.08	+0.08	+0.12	-0.08																										
13. <i>H. pellitica</i>	-0.03	-0.20	-0.13	-0.03	-0.10	-0.24	-0.27	-0.30	-0.05	-0.23	-0.30	-0.30	-0.01																									
14. <i>D. nerii</i>	-0.03	-0.22	-0.02	+0.13	-0.20	+0.04	0	-0.11	-0.08	-0.15	-0.04	-0.14	-0.04	-0.01	0	+0.01																						
15. <i>V. ululans</i>	-0.03	-0.30	+0.08	-0.23	-0.02	-0.01	-0.28	-0.18	-0.31	-0.34	-0.10	-0.08	+0.08	+0.00	+0.30	-0.00	-0.22																					
16. <i>C. leucanica</i>	-0.01	-0.02	-0.20	-0.20	-0.31	-0.23	-0.14	-0.03	-0.05	-0.03	-0.10	-0.08	+0.00	+0.30	-0.00	-0.22																						
17. <i>H. ceteris</i>	-0.01	-0.06	-0.35	+0.22	-0.03	-0.30	-0.04	+0.10	+0.12	+0.20	0	-0.22	-0.07	+0.08	+0.02	-0.41	+0.20																					
18. <i>L. albipuncta</i>	-0.01	+0.13	-0.35	-0.24	-0.38	+0.05	+0.00	+0.04	-0.02	-0.03	+0.14	-0.11	+0.00	-0.20	-0.17	-0.35	0	-0.01																				
19. <i>A. atrypa</i>	-0.01	-0.35	-0.04	-0.18	+0.03	-0.00	-0.15	-0.04	-0.13	-0.12	-0.14	-0.08	-0.12	-0.27	0	+0.14	-0.10	-0.04	-0.00																			
20. <i>H. concolor</i>	-0.01	+0.01	+0.01	+0.04	+0.05	+0.03	-0.00	+0.07	-0.21	-0.15	+0.11	-0.12	+0.00	-0.20	-0.10	+0.08	-0.17	-0.05	-0.11	+0.12																		
21. <i>P. gamma</i>	0	-0.22	0	-0.07	-0.15	-0.31	-0.08	-0.20	-0.21	-0.20	-0.21	-0.05	-0.08	+0.22	-0.02	+0.34	+0.03	+0.00	-0.19	+0.19	+0.00																	
22. <i>L. vitellina</i>	+0.02	-0.25	+0.07	-0.21	-0.18	-0.01	+0.13	+0.08	-0.18	-0.27	-0.16	+0.12	-0.10	-0.13	+0.11	+0.14	-0.20	-0.22	+0.16	+0.15	-0.04																	
23. <i>N. morsella</i>	+0.04	-0.15	-0.13	-0.20	+0.01	-0.25	-0.24	-0.39	+0.09	0	-0.23	+0.34	+0.11	+0.31	-0.01	+0.28	+0.20	-0.10	-0.01	-0.18	-0.03																	
24. <i>P. fuscata</i>	+0.05	-0.33	-0.08	-0.25	-0.03	-0.22	-0.00	-0.06	+0.36	+0.14	-0.08	+0.08	-0.03	+0.04	-0.15	-0.08	+0.08	+0.18	+0.10	+0.02	-0.00																	
25. <i>P. deplolice</i>	+0.05	+0.00	-0.32	-0.07	-0.11	-0.07	+0.08	+0.23	+0.01	+0.27	+0.14	-0.11	+0.10	+0.03	-0.01	-0.16	+0.16	+0.13	+0.23	-0.04	+0.00																	
26. <i>H. armigera</i>	+0.00	-0.30	-0.25	-0.13	-0.17	0	+0.08	-0.01	+0.20	+0.04	+0.04	-0.03	+0.04	-0.08	-0.04	-0.20	-0.01	+0.01	+0.33	+0.11	+0.01																	
27. <i>V. cardui</i>	+0.00	-0.30	-0.21	-0.14	-0.15	-0.34	-0.27	-0.20	+0.00	-0.15	-0.13	+0.13	-0.20	+0.38	+0.01	+0.35	+0.21	+0.12	-0.20	+0.06	-0.00																	
28. <i>L. celyna</i>	+0.00	-0.18	+0.02	-0.02	-0.13	-0.07	-0.17	-0.21	-0.00	-0.12	-0.11	-0.21	0	+0.41	+0.03	+0.25	+0.07	-0.08	-0.00	+0.09	-0.00																	
29. <i>P. saucia</i>	+0.07	±0	-0.02	-0.26	-0.15	-0.04	+0.07	-0.08	+0.03	-0.02	-0.15	-0.15	-0.02	-0.10	-0.01	+0.05	+0.10	+0.18	+0.17	+0.11	-0.01																	
30. <i>L. salicis</i>	+0.07	-0.07	-0.16	-0.18	+0.02	+0.07	0	-0.13	-0.00	+0.08	0	-0.05	+0.22	-0.12	-0.05	-0.00	+0.16	-0.04	+0.20	+0.16	-0.00																	
31. <i>C. croceus</i>	+0.07	-0.00	-0.26	-0.07	-0.03	-0.47	-0.20	-0.27	+0.02	-0.09	-0.21	-0.12	-0.03	+0.17	+0.08	+0.37	+0.04	-0.03	-0.03	+0.10	+0.01																	
32. <i>C. ambigua</i>	+0.08	-0.20	+0.05	-0.20	-0.20	+0.10	+0.13	-0.02	-0.28	-0.12	+0.11	-0.10	+0.01	-0.04	-0.12	+0.10	-0.12	-0.07	+0.54	+0.00	+0.01																	
33. <i>M. stellatarum</i>	+0.09	-0.24	+0.03	-0.16	-0.10	-0.01	-0.28	-0.21	+0.05	+0.08	-0.07	+0.05	-0.13	+0.04	-0.01	+0.28	+0.00	-0.04	-0.02	+0.21	+0.00																	
34. <i>A. iglora</i>	+0.09	0	-0.02	-0.38	-0.15	+0.02	-0.09	-0.02	-0.05	-0.16	+0.00	-0.05	+0.03	-0.07	+0.10	+0.10	0	+0.03	+0.09	+0.10	+0.00																	
35. <i>O. agala</i>	+0.11	+0.03	-0.12	-0.18	-0.08	+0.18	-0.01	+0.16	-0.02	+0.18	+0.02	+0.04	+0.08	-0.18	+0.06	+0.12	0	-0.03	+0.14	+0.11	+0.03																	

psl.	ps.	r.
psl.		
rap.		
plex.		
brass.		
napi.		
euph.		
fraz.		
ater.		
bath.		
ant.		
extr.		
gal.		
pell.		
ner.		
atal.		
lev.		
cel.		
albi.		
atr.		
con.		
gam.		
vitel.		
mors.		
fusca.		
depl.		
arm.		
card.		
cely.		
sauc.		
salic.		
croc.		
amb.		
stell.		
igl.		
agala.		