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number
hich the

1	+0.12 105								
2	+0.07 75	-0.08 10							
3	+0.02 16	-0.03 5	-						
4	+0.05 30	-0.05 10	-0.16 2	+0.36 1					
5	0 12	-0.08 3	-0.21 1	-0.03 2	-				
6	0 15	-0.03 5	-0.10 1	0 2	-0.08 1	-			
7	-0.05 75	-0.07 25	+0.01 5	-0.22 10	-0.11 5	-0.06 5	+0.14 10		
8	-0.10 45	-0.15 15	+0.03 3	-0.17 6	-0.12 3	-0.08 3	-0.20 15	+0.22 3	
9	-0.16 30	-0.13 10	+0.03 2	-0.15 4	-0.15 2	-0.05 2	-0.07 10	-0.13 6	+0.14 1
	1	2	3	4	5	6	7	8	9

B

con.																			
-0.12	extr.																		
-0.20	+0.36	pelt.																	
-0.21	0	-0.05	sacr.																
-0.10	-0.01	+0.01	-0.08	ner.															
+0.11	-0.26	-0.30	-0.18	-0.04	ant.														
-0.15	-0.28	-0.23	+0.05	-0.15	+0.16	lath.													
-0.06	-0.25	-0.27	-0.23	0	+0.07	+0.07	euph.												
+0.06	-0.08	-0.01	-0.08	0	+0.12	+0.06	+0.18	gal.											
+0.07	-0.20	-0.30	-0.13	-0.11	+0.37	+0.26	+0.12	+0.01	frac.										
+0.05	-0.29	-0.19	-0.09	-0.26	-0.08	-0.23	+0.01	-0.24	-0.29	brass.									
+0.03	-0.18	-0.24	-0.11	+0.04	-0.01	0	-0.17	-0.28	-0.28	+0.10	napi								
+0.01	+0.04	-0.13	-0.17	-0.02	-0.27	-0.29	-0.26	-0.39	-0.21	+0.17	+0.40	rap.							
+0.04	-0.16	-0.03	-0.06	+0.13	-0.17	-0.17	-0.07	-0.12	-0.08	+0.16	-0.16	-0.22	plex.						
+0.01	-0.20	-0.20	-0.24	-0.22	+0.08	+0.12	-0.15	-0.20	+0.12	-0.01	-0.35	-0.21	+0.14	pul.					

It seemed likely that some species would fall into groups and that others would be isolated cases, on the axiom that things like another must be themselves alike, but things unlike another need have no relation to one another.

By arranging the species in order of their average correlation with all other species, an indication was given of the arrangement of the groups.

The disposition of the signs can be seen from Table 33, B, where the average intercorrelations of the species taken in fives are shown. Those species in Section A show an average positive correlation, but wherever else they occur, *i.e.* in Sections B, D, G, K, P and V the average correlation is negative.

From Table 33, C, a clear-cut group is seen in Sections O, T, Z, U, AA, and BB, consisting of the species from *P. gamma* to *C. hyale* inclusive, within which there are high positive correlations but which show negative correlations with other species.

An attempt was then made to form the remaining species into groups according to their relationship with themselves and with the first group.

Table 34, A, shows the species provisionally arranged in seven groups. Group 1, already defined, consists of fifteen species which are positively inter-correlated but negatively correlated with species outside the group.

Group 2 is a somewhat unsatisfactory group of five species, the members of which show positive correlations with Group 1 but show little or no relation between themselves, except in the cases of *H. celerio* and *C. livornica*, where a significant correlation is shown. *V. atalanta* is highly negatively correlated with all but *A. atropos* in the group.

Groups 3, 4, 5 and 6 consist of species which show negative relationship with other groups. In Group 4, *L. unipuncta* and *N. peltigera* are taken together since they are highly positively correlated with themselves and with *N. noctuella*, and show somewhat similar relationships with other species.

In Group 7 are five species which form a group much less evident than Group 1 but which show more interrelationships than do other species outside Group 1.

Group 8 is another clear-cut group consisting of the three "Whites." These species are markedly negatively correlated with other species, but show their highest positive correlation between themselves.

Group 9 consists of two species negatively correlated with other species but showing a slight positive correlation between themselves.

Groups 8 and 9, although both negatively correlated with other species, show no interrelation between themselves.

Table 34, B, shows the average correlations of the species within the groups. In cases where there is only one species within the group, there is no average correlation within that group, and the appropriate space is left blank.

It would be expected with almost 600 correlations that, by chance, there would be 30 values significant at 1 in 20 level, and 6 at the 1 in 100 level. Actually as seen from Table 32, C, there are 118 values at the 1 in 20 level, and of these 52 are significant at 1 in 100 level.

This result is in itself evidence of the real biological nature of the values.

Fluctuations in abundance of correlated groups.

The material was available for a study of the question of periodicity in migrant Lepidoptera. Since the species tended to form groups, the group was taken as a unit. It was considered that the "good" and "bad" years within a single group would be accentuated by this means.

Table 35 shows the average abundance indices of the principal Groups 1, 2, 7 and of all species from 1857 to 1931 (allowance being made for species of shorter duration).

TABLE 35.

Mean annual abundance of certain groups of associated immigrants, and of all immigrants, 1857-1931.

	0	1	2	3	4	5	6	7	8	9
Group 1 (15 species)										
1850								2.8	3.6	3.1
1860	1.5	1.5	1.5	1.2	1.3	2.8	1.4	2.5	3.2	2.0
1870	1.9	1.6	2.0	1.0	1.0	1.5	1.5	2.4	2.2	2.3
1880	1.5	1.3	1.4	2.2	2.4	1.8	1.6	1.1	1.9	2.1
1890	1.7	1.5	3.5	3.1	2.7	2.2	1.5	2.5	2.8	4.0
1900	4.4	3.3	2.6	2.5	2.3	1.1	3.2	1.6	2.3	1.2
1910	1.1	2.3	2.5	2.3	1.5	1.5	1.0	1.9	1.5	1.7
1920	2.3	2.3	2.1	1.9	1.6	1.1	2.2	1.6	3.3	2.0
1930	1.7	2.3								
Group 2 (5 species)										
1850								3.3	3.3	2.8
1860	2.8	1.3	2.5	1.3	2.0	3.5	2.0	3.3	4.0	3.0
1870	3.5	3.0	3.0	2.3	1.8	2.0	3.0	3.8	3.8	2.5
1880	2.0	2.0	2.2	2.6	3.0	3.2	2.4	2.2	2.8	2.0
1890	1.6	2.0	3.4	3.0	3.4	3.6	3.0	2.6	3.2	3.8
1900	4.2	3.0	3.4	2.8	2.6	3.0	3.2	1.4	2.8	2.8
1910	1.6	2.8	3.2	2.8	2.6	2.0	1.4	2.2	1.8	1.6
1920	3.2	2.2	2.4	2.0	2.8	2.0	1.8	2.2	2.4	1.8
1930	2.6	2.8								
Group 7 (5 species)										
1850								3.0	3.4	3.2
1860	2.4	1.2	1.0	1.2	1.6	2.2	1.8	1.6	3.8	1.6
1870	3.0	2.4	4.2	1.8	2.2	2.4	2.2	1.4	2.2	1.2
1880	3.2	1.6	1.8	1.8	1.4	1.6	1.4	2.0	2.8	3.0
1890	1.4	1.0	1.8	1.8	1.4	2.4	2.4	1.4	1.6	1.8
1900	2.4	2.6	1.8	1.4	1.4	2.0	1.4	1.2	1.2	1.4
1910	1.6	1.8	1.2	1.2	1.4	1.6	1.2	1.8	1.6	1.6
1920	1.0	2.0	1.6	1.6	1.8	1.4	1.4	1.0	1.6	1.8
1930	1.4	1.4								
All species (35 species)										
1850								2.8	3.2	2.8
1860	1.7	1.6	1.7	1.4	1.6	2.4	1.4	2.2	2.9	2.0
1870	2.0	2.0	2.3	1.4	1.6	1.9	1.9	2.3	2.0	1.8
1880	1.8	1.7	1.6	1.8	2.0	2.1	1.7	1.7	2.1	1.9
1890	1.6	1.8	3.0	2.5	2.2	2.2	2.1	2.3	2.5	3.0
1900	3.5	2.7	2.2	2.2	2.1	1.4	2.8	1.6	2.0	1.6
1910	1.4	2.3	2.2	2.0	1.7	1.6	1.4	2.1	1.6	1.8
1920	2.2	2.0	2.0	2.0	1.8	1.4	2.1	1.5	2.6	1.7
1930	1.9	2.0								

A 10-year running mean was calculated from these averages and shown in Table 36.

Fig. 60 shows a histogram of the average abundance indices of Groups 1, 2, 7 and of all species, together with their respective 10-year running means in broken lines. The 10-year running mean of Group 1 shows a peak around the year 1900, but otherwise the average is fairly uniform.

Group 2 10-year mean also shows a peak about the year 1908, with a minor peak at about the year 1868.

Group 7 has a slight peak around the year 1872, with a general falling off in abundances to 1931.

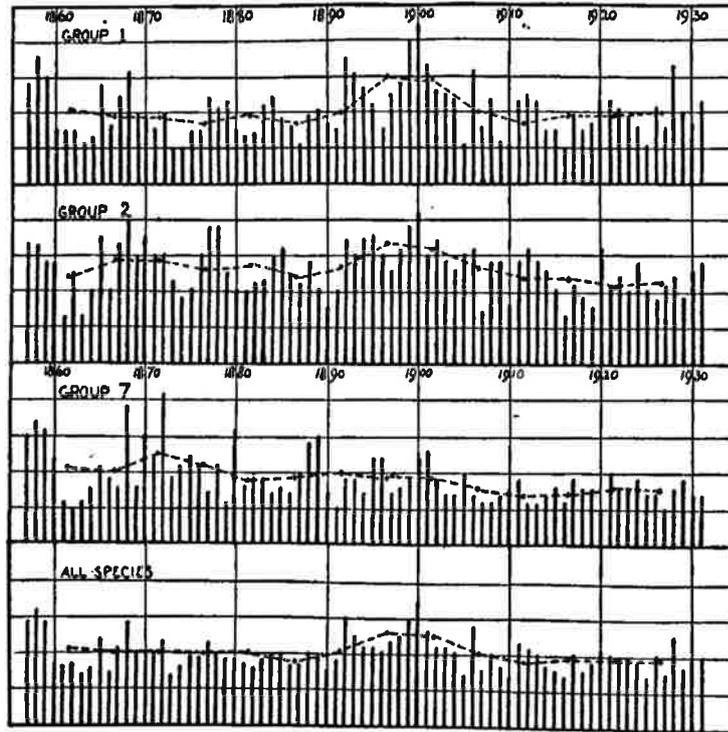
TABLE 36.

Ten-year running mean of average annual abundance of certain groups of associated immigrants, and of all immigrants, 1857-1931.

Group	1857-1866	1862-1871	1867-1876	1872-1881	1877-1886	1882-1891	1887-1896	1892-1901	1897-1906	1902-1911	1907-1916	1912-1921	1917-1926	1922-1931
1.	2.1	1.9	1.8	1.7	1.9	1.7	2.0	3.0	2.9	2.0	1.7	1.9	1.9	2.0
2.	2.6	2.8	2.9	2.6	2.8	2.4	2.7	3.3	3.2	2.0	2.3	2.3	2.2	2.8
7.	2.1	2.0	2.5	2.2	1.8	1.8	2.0	2.0	1.8	1.5	1.4	1.5	1.6	1.5
All species	2.1	2.0	2.0	2.0	2.0	1.8	2.1	2.6	2.5	2.0	1.8	1.9	1.9	1.9

The 10-year running mean of all species shows a steady curve with a slight peak at about 1900.

It appears evident from the diagrams that there is no indication of an 11-year cycle, that could fit in with the Sun Spot Cycle, and also that the



60

FIG. 60.—Average annual frequency, and 10 years' running mean of the same, for certain groups of associated immigrants, and for all the 35 immigrants studied.

records show no appreciable falling off or increase during the years 1857-1931. Even during the years 1914-1918, when one might have expected a decided lack of interest in the activities of insects, the average recorded abundances show no evidence of it.

Relationship between the groups and the geographical range of the species.

It is a feature of migrant Lepidoptera that they are widespread in their distribution. In most cases, the British immigrants range from N. Europe to N. Africa. However, there are a few species to be mentioned which are more restricted in their range. It can be shown that where a species has a less ubiquitous range, its position in the groups can often be accounted for, and that where species have a common source, they are related in the same group.

Thus *D. plexippus*, the only immigrant from America and from the west, shows a decided negative relationship with other species (Table 19). It is doubtfully placed with *D. pulchella* in a group only since this latter species has a similar relationship with other species, and there is a slight positive correlation between the two. The probability is that the factors which determine the arrival of *D. plexippus* in Britain are of quite a different nature from those determining the arrival of migrants from the east and south.

In Group 8, the Pierids show a positive relationship between themselves. This could be accounted for by the fact that the species are indigenous in Britain, and that their migrations originate from a common source. Accumulated evidence lends weight to the view that they originate in northern Europe.

In Group 7, the only species with a limited distribution appear to be *V. antiopa* and *C. fraxini*. These species show a significant positive intercorrelation. It is noteworthy that migrations of *V. antiopa* originate in Scandinavia and that *C. fraxini* is distributed over northern Europe and does not appear south of N. Italy. This point is reflected in the number of negative correlations shown by these species with members of Group 1, which contains species from the Mediterranean region and N. Africa.

In Group 1 appear the butterflies from the Mediterranean region, namely *C. hyale*, *C. croceus*, *V. cardui* and *P. daphidice*. In addition, *M. stellatarum*, a day-flying hawk-moth, is included. *V. atalanta* is also a Mediterranean species and shows positive correlations with Group 1. However, the average correlation of this species with all others (-0.03) is below the lowest average of Group 1, and excludes it from this Group.

The distribution of the other species is too general to permit a more detailed classification at this stage.

XII. SUGGESTED CLASSIFICATION OF DENSITY OF MIGRATION.

By C. B. WILLIAMS.

In describing migrations observers have used various terms to indicate the density of the flight "thin," "sparse," "copious," "obvious," "thick," "snow storm" etc. etc. Others have stated the number of butterflies present at any one time on a given area, or, more frequently, the numbers passing across a front of a given width in a given time. The last is the easiest figure to obtain with any accuracy.

It seems desirable to have some simple scale of grading by which the whole range from very thin to very thick flights could be classified. For this one must first have some idea of the extreme limits of density which such a scale must cover.

I have myself produced evidence of migration of white butterflies in Harpenden from observing about 20 butterflies passing in 20 minutes over a front of about 100 yards. Such a movement would only be noticed by very careful watch by an expert observer and even then the evidence only becomes convincing

when several periods of 20 minutes' watching have given similar results. It is undoubtedly near the lower limit of demonstration.

At the other end of the scale are snowstorm migrations in which the butterflies are too numerous to count even on a short front. In one flight of *Andronymus neander* in East Africa which was just above the limit of accurate counting I estimated at the peak flight that 500 per minute were crossing a 22 yards front, or about 2300 per minute on a 100 yards front. Denser flights than these are known. It seems therefore that the numbers passing per 100 yards per minute are likely to range from 1 to perhaps 10,000 insects. It was decided that a convenient classification of this range would be a geometric one with seven groups with the following mean numbers:—1 : 4.6 : 21.5 : 100 : 464 : 2154 : 10,000 (Table 37).

TABLE 37.

Proposed classification of density of migrations with numbers that would be observed on fronts of different lengths in different periods of time.

Density	Width of front in yards ¹	Duration of observation in minutes				
		1	5	10	15	20
I	100	1-2	2-11	5-21	7-32	9-43
	50	1	1-5	2-10	8-16	5-21
	25	—	1-2	1-5	2-8	8-10
	10	—	1	1-2	1-3	1-4
	5	—	—	1	1	1-2
II	100	3-10	12-50	22-100	33-150	44-200
	50	1-5	0-25	11-50	17-75	22-100
	25	1-2	3-12	6-25	9-37	11-50
	10	1	2-5	3-10	4-15	5-20
	5	—	1-2	1-5	2-7	3-10
III	100	11-46	51-232	101-464	151-696	201-928
	50	6-23	26-116	51-232	78-348	101-464
	25	3-11	13-58	26-116	38-174	51-232
	10	1-4	6-23	11-46	16-69	21-92
	5	1-2	3-11	6-23	8-34	11-46
IV	100	47-215	233-1,077	465-2,154	697-3,231	929-4,308
	50	24-107	117-538	233-1,077	349-1,615	465-2,154
	25	12-53	59-269	117-538	175-807	233-1,077
	10	5-21	24-107	47-215	70-323	93-430
	5	3-10	12-53	24-107	35-161	47-215
V	100	216-1,000	1,078-5,000	2,156-10,000	3,232-15,000	4,308-20,000
	50	108-500	539-2,500	1,078-5,000	1,616-7,500	2,156-10,000
	25	54-250	270-1,250	539-2,500	808-3,750	1,078-5,000
	10	22-100	108-500	216-1,000	324-1,500	431-2,000
	5	11-50	54-250	108-500	162-750	216-1,000
VI	100	1,001-4,640	5,001-23,200	10,001-46,400	15,001-69,600	20,001-92,800
	50	500-2,320	2,501-11,600	5,001-23,200	7,501-34,800	10,001-46,400
	25	251-1,160	1,251-5,800	2,501-11,600	3,751-17,400	5,001-23,200
	10	101-464	501-2,320	1,001-4,640	1,501-6,960	2,001-9,280
	5	51-232	251-1,160	501-2,320	751-3,480	1,001-4,640
VII		Numbers above group VI.				

¹ For fronts measured in metres reduce observed numbers by 10% before finding place in the above table.

It will be seen that each grade mean is 4.6 times the previous grade and the ratio of the 4th to the 1st and the 7th to the 4th is 100. The limits between these have been calculated and the general characteristics of each are as follows:—

Density I. Extremely thin. (1)—2.2 insects per 100 yards per minute. Up to about 2275 insects per mile front per hour. Only noticeable by careful watch by an expert.

- Density II. Very thin. 2.3—(4.6)—10 insects per 100 yards per minute. About 2275—10,000 insects per mile front per hour. Should be seen by an expert and any careful naturalist on the look-out.
- Density III. Thin. 10—(21.5)—46 insects per 100 yards per minute. Ten to fifty thousand per mile front per hour. Should be obvious to any observant field naturalist.
- Density IV. Definite. 47—(100)—215 insects per 100 yards per minute. 50,000 to 227,000 per mile front per hour. Should be obvious to any normally observant individual.
- Density V. Thick. 216—(464)—1000 insects per 100 yards per minute. 227,000 up to a million per mile front per hour. Obvious to the general public.
- Density VI. Very thick. 1000—(2154)—4640 insects per 100 yards per minute. One to five million per mile front per hour. Gets into newspapers.
- Density VII. Snowstorm. 4650—(10,000) or more insects per 100 yards per minute. Over five million per mile front per hour. "Stops motor cars." "Interferes with pedestrians." "Like a snowstorm." Newspaper headlines.

As observations are frequently taken over fronts of varying width and for varying periods of time I have drawn up in Table 37 the numbers for each grade to be observed crossing fronts of several different lengths in times from 1 minute to 20 minutes. From this any data given could rapidly be classified into the corresponding grade. If observations are taken on a front measured in metres the observed numbers must be reduced by 10% before comparing them with the table, as one yard is approximately 10% less than one metre.

It is recognised, of course, that none of the observations made in the field is really accurate. The front is seldom measured exactly, the time is often guessed, sometimes measured with an ordinary watch, and very seldom with a stop-watch, and finally the numbers counted get more and more inaccurate as the density increases. It is doubtful if more than 100 insects per minute can be counted with accuracy, so that in dense flights the front over which the count is made should be reduced to five or ten yards.

The other inaccuracies remain, but in view of the fact that in each group the maximum possible is over four times the minimum, a large error will have to be made before the wrong group is estimated. If a case is near the borderline it is probably of little practical importance to which group it is assigned.

The adoption of this system would give a greater definition to terminology and might enable more simple comparisons of intensity to be made, as has already been done with a similar classification of the British migrants by Cockbill (see p. 108).

XIII. SUMMARY.

I. The report gives a general account of recent progress along various lines in the study of the migration of Lepidoptera particularly in the last ten years since the publication of Williams' *Migration of Butterflies* in 1930.

II. Among interesting early records of Butterfly Migration is an account of one seen in the year 1508 near Calais in France.

III. A detailed history of the abundance each year for over 100 years is given for about forty of the principal British Immigrant Butterflies and Moths.

A geometric scale is adopted and all species are graded each year in one of six levels of abundance, the scale for each species being in proportion to its maximum occurrence. As much as possible of the early literature has been examined and the records are believed to be sufficiently complete to justify discussion. A summary of the results will be found in Table 4 and figs. 1-4. The monthly distribution of most species has been worked out (Table 3) and in one or two it has been possible to show a relation between early appearance and abundance during the summer.

IV. An analysis of nearly 400 records of insects from ten lightships off the E. and S.E. coasts of Britain gave a list of 140 species of *Lepidoptera* of which 35 occurred on several occasions or in numbers which make it unlikely that their presence was accidental. Thirteen of these were known or suspected migrants. Others high up in the list were *P. meticulosa*, *A. monoglypha*, *E. similis* and *A. c-nigrum*. The flights were predominantly to the north and north-west from May to mid-August and to the east or south-south-east after mid-August.

V. Mr. and Mrs. Hodges of Florida made an almost continuous daily watch on the movement of butterflies for nearly two years. Their results are analysed. They show:—(1) a regular migration of *A. monuste* each year, at first to the south and then a sudden reversal of direction during May or June; (2) an almost continuous southerly movement of *P. eubule* and *T. lisa* at all times of the year; (3) regular movements to the north in spring, and/or autumn movements to the south in several other species, including *Danaus plexippus* and *D. berenice*, *Dione vanillae*, *Papilio cresphontes* and *Eudamus proteus*.

VI (1). The migrations of *D. plexippus* are discussed from several points of view. A study of geographical variations in America indicates a northerly migratory race in N. America; a southerly migratory race in S. America, south of the Amazon; and a non-migratory race between these two in the northern portion of S. America and many of the West Indian islands (fig. 18).

Downes observed the overwintering of *D. plexippus* in California and considers that most hibernating areas are very close to the sea and nearly all suitable spots are occupied to some extent. The males are sexually mature on emerging from the chrysalis in the autumn, pairing taking place throughout autumn, winter and spring; but the females do not normally mature eggs till the spring.

A large number of new records of migration for North and South America are discussed and figs. 20 and 21 summarise what is now known of the movements of this butterfly in N. America. A full list of the British and European records of appearance of *D. plexippus* is given, and a number have been examined, all except one of which are of the N. American race.

VI (2-11). Summaries are given of the present information on the migration of several other butterflies from America, Europe, Africa and Australia. Fig. 25 shows the known flights of *P. eubule* in the U.S.A. and West Indies. A regular to and fro movement is indicated. Plate 3 shows a migration of *Eunica monima* in progress in Mexico. A full account is given of recent extensive migrations of *Pieris brassicae* in England, including a flight at Harpenden that continued to the south for over three weeks. New records of *V. cardui* in West Africa indicate a definite migrating season south of the desert belt in September and October. New records are summarised for *Glycestha aurota*, *G. creona*, *G. java*, *C. florella* and several others.

VII. An account is given of some recent experiments in marking butterflies. Practically no recoveries have been made at a distance but much can be learnt from the rate of disappearance of the marked individuals from the locality of

marking. A satisfactory technique is described. It is important to be able to distinguish individuals of the same species marked on the same date.

VIII. Orientation might possibly be by wind, sight, or perception of the earth's magnetic field. These three are discussed. It is shown that an individual insect might determine the direction of the wind without the use of sight, but that there is no evidence that the direction of the wind determines the direction of migration. Recent work on orientation by sight is discussed in relation to migration. Experiments on young locusts showed no evidence of appreciation of a powerful magnetic field.

IX. Evidence for the occurrence of a return flight in migrant Lepidoptera is shown to be increasing. The question of the fundamental difference between migrations with and without a return flight is reviewed, and the evolutionary difficulty of the persistence of migration without a return flight is emphasised.

X. A significant positive correlation between the occurrence in unusual numbers of *V. cardui* in Europe and *N. America* is shown to exist. This supports the similar results previously obtained from *C. lineata*.

XI. Intercorrelations between 35 British Immigrant Lepidoptera have been calculated and discussed. The average correlation is slightly positive (+ 0.12). By sorting the species it has been possible to find several groups the members of which are positively correlated within their own groups, but usually negatively correlated with other groups (Table 34). The first of them is quite definite and contains fifteen closely associated species. The second is less definite. Group 7 contains five species and Group 8 the three *Pieris* species. To a certain extent the grouping follows the geographical range of the species.

The average frequency of the principal groups each year for 78 years is given in fig. 60 and shows no evidence of periodicity.

XII. A classification is suggested of the density of any flight as measured by the number of insects crossing a definite front in a definite time. This is a series of seven grades the numbers in which are in geometric proportion.

XIV. The Bibliography includes all references to the migration of butterflies that have been traced in the past ten years and which are not included in the previous Bibliography given in Williams 1930b.

XIV. BIBLIOGRAPHY.

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