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THE MIGRATIONS OF THE PAINTED LADY BUTTERFLY, VANESSA CARDUI (NYMPHALIDAE), WITH SPECIAL REF-ERENCE TO NORTH AMERICA

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The nymphaline butterfly *Vanessa* [or *Pyrameis*] *cardui* Linn., known in Britain as the "Painted Lady" or "Thistle" butterfly, and in France as "La Belle Dame", is probably the most widely distributed of all butterflies. It is found, at some time of the year, in every continent except South America, where it is rare or absent (see Fig. 1).

In Australia, New Zealand and some of the Pacific Islands there is a form *kershawi* which has slight differences in structure and wing markings, and has sometimes been considered as a distinct species. Apart from this the Painted Lady is very free from local variation in form or colour. Specimens from Japan, India, South Africa, Europe and N. America are indistinguishable. Such widespread uniformity is an indication of the constant intermingling of populations, and is characteristic of many other insects which migrate with wide distributions.

In the great land mass of Europe, Asia and Africa, it ranges, according to the season, from the tropics northwards to within the Arctic Circle and southwards to the limit of the land. In South Africa this is about latitude 43° S. In southern India and Ceylon about 10° N and in the East Indies about 10° S. The Australian form reaches nearly 44° S in New Zealand and Tasmania.

Ecologically the Painted Lady prefers drier and more open country and in the tropics is more often found on higher and drier land. It is never common in the wet tropical forest, which may account for its absence in most of S. America.

Over the greater part of its range in temperate climates it is not a permanent resident, and, unlike most of the Nymphalidae, seems unable to survive cold winters in any stage. As a result, such areas depend for their

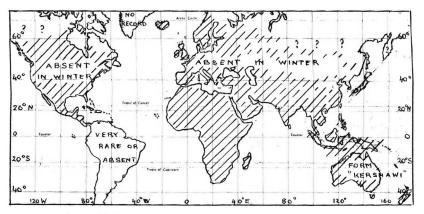


Fig. 1. The world distribution of the Painted Lady, which is found, at one season or another, in almost all parts of the world except South America.

Painted Lady population on migratory flights from the more permanent habitats in the warm-temperate and subtropical climates.

In Western Europe and North Africa, where its occurrence has been studied for many years, there appears to be very little winter survival north of the Mediterranean. Each spring there is a northward movement, sometimes very small, sometimes in immense numbers, spreading from North Africa, and even from across the desert area further to the south.

In the north the butterflies reach Iceland in some years, and have been recorded beyond the Arctic Circle in Scandinavia and Finland. The main immigration into the British Isles occurs about the end of May or June, but sometimes earlier. The immigrants lay eggs and local-bred butterflies appear about August. Further south in Europe, there may be two or more generations before the fall. There is no evidence of any winter survival, but there is increasing evidence of a return flight to the South in the fall on a much smaller scale than the northward flight in the spring. This southward movement is difficult to observe in Britain, but appears to augment in numbers as it goes south, and quite definite flights have been seen crossing the Pyrenees in September and October. Still further south I have seen (in late Sept. 1943) a very extensive southward flight over the Atlantic between southern Spain and the westward bulge of North Africa.

In eastern and southern Africa the Painted Lady is widespread and there are records of large numbers making sudden appearances and sometimes of definite directional flights. In Ghana and Nigeria records of abundance are chiefly in September and October.

In the East, as far as the Caspian Sea, there are many records of north-

erly spring migrations, and a very large flight has been observed crossing the Shandur Pass in Chitral at 16,000 feet.

Still further east and as far as Japan I have found no direct information of seasonal movement, but it may well occur without being noticed.

In Australia the form *kershawi* is uncertain in appearance and has at times been observed in mass flights similar to those in the northern hemisphere. There is also a possibility that the population in New Zealand may occasionally be reinforced by flights across the 1200 miles of sea which separates it from Australia.

There are, in addition to the cases mentioned above, many records of the butterflies far out to sea. In the North Atlantic there is a remarkable record of several being seen in 1865 on a steamer about half way between Iceland and Newfoundland, and another record in 1950 of several being seen on the tropic line more than half way across the Atlantic between the Mediterranean and the West Indies. I have also one captured about 500 miles from land in the Indian Ocean. These are probably individuals which have been blown out of their normal routes by strong wind currents.

Food Plants and Life Cycle

The caterpillars of the Painted Lady have been recorded on over a hundred different food-plants, in many different orders, but chiefly the Malvaceae, the Compositae and the Leguminosae. A number of plants of economic importance are included. In subtropical regions of Eurasia they frequently destroy the leaves of *Malva parviflora* (Khoubeiza in Egypt), which is an important vegetable food, and in Eastern Europe (Yugoslavia) they can be quite serious pests of maize, lucerne, beans, sunflowers, and soya-beans. On the other hand, their great preference for thistles in temperate countries, such as the northern U. S. A. has made them welcome visitors there in grazing country.

Little is known of their seasonal life-cycle in the tropical countries, but in Europe and North America there appear to be one or two broods during the period of summer residence. The Painted Lady shows no ability to enter into a definite resting stage (diapause) or to be able to survive a cold winter in any stage.

The Seasonal Distribution of the Painted Lady in North America

Summer Distribution: In the summer months Vanessa cardui may be found breeding in any part of the United States from the Pacific to the Atlantic. It is more irregular in appearance in the northeastern States; and is not often recorded in the southeast, though if this is due a real rarity or

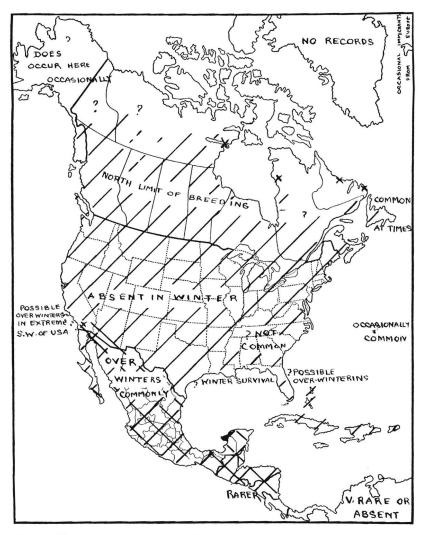


Fig. 2. The approximate summer and winter distribution of $V.\ cardui$ in North and Central America.

to lack of interest is not certain. It may here be confused with *V. virginiensis* Drury which is generally more common.

In Canada it is known to breed in the southern portions of all the provinces from British Columbia to Newfoundland. In the latter it is sporadically quite common. In the extreme north, adults have been seen on the Labrador coast, and in the Northwest Territories at Chesterfield Inlet on Hudson Bay, in north latitude 64° . This is nearly as far north as Iceland to which the migrant Painted Ladies from the European fauna occasionally stray. Adults have also been captured on Great Slave River in the Mackenzie District at about $60^{\circ}30'$ N.

I have no records from northern British Columbia or from the Yukon, although I would have expected it to go at least as far north in the west as in the east, particularly as the summer isotherms run farther north in the west. The only evidence for its occurrence in Alaska is that W. H. Edwards in 1887 mentions it, without any details, in a list of butterflies known to occur there.

The Painted Lady also appears sporadically in numbers in the Bermuda Islands, about 600 miles east of South Carolina. The origin of these may be in the Antilles, to the south, but this is not certain.

Winter Distribution: In the winter months, by contrast, there is no evidence of survival in any stage in any part of Canada or the United States, except possibly in Florida, along the Gulf Coast, and more definitely in the extreme southwest of California, where breeding has been recorded in mid-winter.

In Mexico V. *cardui* appears to breed throughout the year, sometimes in abundance, but more records, including the months of activity are still needed. Still further south in the Central American States it becomes less common as the climate changes to the wet-tropical type. In Panama it is rare and in S. America almost unknown.

It occurs at times, and may breed, in most or all of the Caribbean Islands, but not on any scale of abundance that could account for the masses of the northerly spring migrations. In the most southerly island of the Antilles, Trinidad, it is a rarity. I know this from my own experience, as I lived in Trinidad for six years, and did not see one.

In the Hawaiian Islands in 20° N latitude, the same as that of Southern Mexico, one of the earliest records was reported by Blackburn in 1879. He stated that it was abundant in that year, though he knew of no previous record and had seen none before in his three years residence. Today it appears to be accepted as a regular breeding resident.

Pattern of Migration

The only solution that appears to fit our present knowledge is that the main, and perhaps the only, source of the parent swarms which invade N. America in the spring is to be found in those parts of Mexico, particularly in the northwest, which have a relatively dry climate. This area cor-

responds both in latitude and climate with the semi-desert parts of N. Africa which provide the main source of our European immigrants.

This would imply that the immigrants that appear fairly regularly in Newfoundland, or their parents, have their origin in western Mexico, nearly three thousand miles away.

Such mass movements could be carried out either by large numbers being blown by strong winds far out of sight at high altitudes, or by directional movements near the ground, possibly independent of the wind. For the former type of distribution we have at present no evidence, but this is not proof that it does not occur. For extensive movements at ground level evidence is steadily accumulating and a summary is given below.

Direct Evidence of Northward Spring Migration at Ground Level

Over the course of many years I have collected nearly 100 records of flights seen by naturalists in North America when the butterflies were all moving definitely in one direction. These vary from observations of a few dozen butterflies only, to one (quoted below) which was estimated to include 3000 million individuals. The characteristic, as in other migrant species and in other parts of the world, is a continued "purposeful" flight in a steady compass direction, apparently independent of the angle of the sun or the direction of the wind (see later). Such flights may last an hour or two, or go on for days and, though usually observed at a single locality, may cover a front of a hundred miles or more.

It might be interesting to quote here from E. A. McGregor's account (1924) of a gigantic movement of Painted Ladies to the north in California, to give an idea of a migration in its extreme form. He writes: "Continuing from 11th to 13th inclusive, there was a remarkable migration of this butterfly. All through the day there was an average of about 300 butterflies per acre at a given moment. The flight direction appeared to be from south-east to north-west.

"In travelling, the flight was not characteristic of butterflies in general, but was of a more steady and purposeful nature. During calm intervals the flight took place on an average of perhaps 10–20 feet altitude, but during the periods of windiness the butterflies flew very close to the ground. There appeared to be no attempt at pairing and the individuals flew well separated—possibly 10 feet apart on the average. It was very noticeable that they all pursued their flight in the same direction. It was rarely that individuals were seen to alight on vegetation but this they did at times.

"The above flight occurred at the warmest period yet experienced this

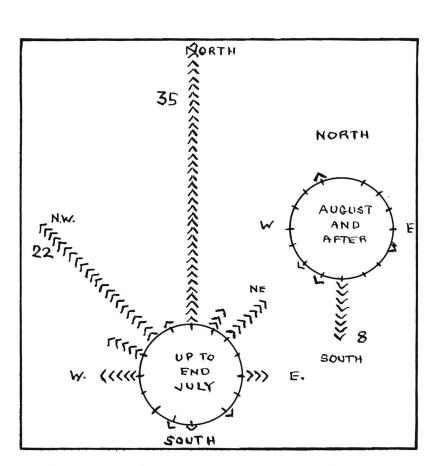


Fig. 3. Analysis of the direction of flight in nearly 100 recorded flights of migrating Painted Lady butterflies in North America, divided into those which occurred in the spring and early summer up to the end of July; and those which occurred in August and the fall. The records provide strong evidence for a large northerly flight in the spring, and a smaller return to the south in the fall.

season, temperature maximums ranging from $80-88^{\circ}$ F. The temperature suddenly dropped late on the afternoon of the 13th, accompanied by a chilly wind, and the flight as suddenly terminated. On the 15th the temperature rose again, but a gusty wind occurred, so that only a few individuals could be seen migrating.

"An attempt to estimate the number of individuals comprising this three-day migration is here presented. The flight was estimated to

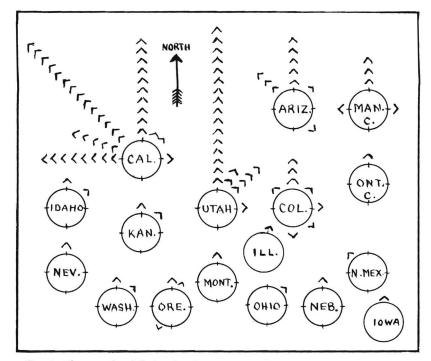


Fig. 4. The records of flights for the spring months, as detailed in Fig. 3, sorted according to the state or province in which they were seen.

have been at least forty miles in width (it no doubt was much wider). The daily duration of the migration was at least twelve hours, or a total for three days of thirty-six hours flight on any given point.

"Now the rate of travel was estimated at 12 miles per hour, which would give a total dispersion length of 432 miles for the three days. Within such a zone (40 miles by 432 long) is contained about 17,280 square miles or 11,059,200 acres. With the established occurrence of about 300 butterflies per acre, it is readily computed that at least 3,000,000,000 had passed on the 40-mile wide zone between Sunland and Lemon Cove."

To return to the evidence available for the northerly spring flight, Figure 3 shows a summary of the direction of movement in 96 recorded flights that I have been able to trace, arranged according to the time of the year. Of these, 84 occurred before the end of July (mostly from April to June) and these have an overwhelming trend to the NW, N, and NE quarter. Fig. 4 shows the same flights sorted according to the state or province, and it will be seen that the NE component is almost completely accounted for by records west of the Rockies from California and Arizona. Records of spring flights in the middle and NE states are very few, and are completely lacking from the SE.

This northerly flight, at or near ground level in North America, has its exact counterpart in Europe, where we have hundreds of observations of such movements from the Mediterranean northwards; and also smaller numbers from northern Africa, and others at sea crossing the one to four hundred mile barrier of the Mediterranean Sea, or coming in to southern England across the Channel.

Evidence for a Southward Migration in the Fall

If North America is repopulated each year from the south, do all the offspring of the earlier immigrants die out before the fall, or is there a partial or general return to the south, to repopulate or replenish their winter headquarters?

Fig. 3B shows the very little evidence from North America that we have available on this point. There are only a dozen observations of flights after the beginning of August, and all but one of these have a southerly component, and eight of the twelve were said to be flying "to the south". The states and provinces, in which these flights were seen, are California (2), Colorado, Minnesota (several years, but no definite dates), New Jersey, New York, Florida, Ontario and Manitoba.

One of the most definite of these flights was seen by W. B. Henson at Sault Ste. Marie in Southern Ontario on the 30th Sept. 1949, and several days following. He estimated that 100 to 150 butterflies were crossing a ten-yard front every ten minutes over a front of at least a mile. This is equivalent to approximately 100,000 butterflies per hour on the observed mile. All the butterflies were flying to the south *across* a westerly wind.

It will be noted that many of these fall records are from the more easterly states, where mass flights in the spring are not so regularly recorded. This may perhaps be a psychological effect in that observers in the west are so satiated with Painted Ladies by the time the fall comes, that they cease to be interested.

The flight in Florida, referred to above, was that two V. *cardui* were captured by Mr. and Mrs. Hodges, along with several V. *virginiensis* in a long continued movement to the south of many species of butterflies in the fall of 1952. Further observations in this area are much needed.

As with the spring flight, the probability of a fall movement to the south in North America is supported by many records of a similar movement in Europe. My own observations of thousands of Painted Ladies flying to the south far out at sea between Spain and the bulge of Africa in September 1943 has already been mentioned. The butterflies were very far apart, but the flight covered the whole fifteen hundred miles from off the mouth of the Mediterranean to the latitude of Sierra Leone, and was observed at all times of the day for eight successive days, and mostly fifty to a hundred miles from land.

Year to Year Variation in Abundance and Range

In some years the immigrant Painted Ladies and their larvae are abundant over most of the United States and southern Canada; in other years they may be so rare as to escape notice except in a few places. Such variations in numbers almost certainly reflect different weather conditions either in their winter breeding areas, or in the districts they pass through on their way north.

In the course of years I have collected between one and two thousand records of their presence (rare, common or abundant) in N. America in different years and in different areas. Table 1 shows a very condensed summary for the years 1900–1959, indicating when the immigration has been above average. It must always be remembered that "absence of evidence" is not the same as "evidence of absence"; and the further one goes back, the more frequently one is frustrated by the former state of affairs. In general there are more records of mass flights and unusual abundance west of the Rockies. There are however only a few records of either abundance or migration in Texas, which suggests that the immigration from Mexico is more concentrated in the western half of the country.

Figs. 5 and 6 show the constrasting conditions in the two consecutive years 1951 and 1952. In the former year there was scarcely a record of abundance anywhere, and an unusual number of cases commenting on its rarity or absence. By contrast, in 1952, the species was abundant in most of the Pacific States, with records of mass flights through the north-central and northeastern U. S. and the whole of southern Canada as far east as Nova Scotia, and as far north as Chesterfield Inlet (64° N) on Hudson Bay. There are however no records of abundance from Texas or from any of the Gulf States except Mississippi, where it was said to have been "abundant".

Possible Relation Between the Abundance of Immigrant Populations in Western Europe and North America

The history of the varying abundance of *V. cardui* from year to year in North America, given briefly in Table 1, makes it possible to compare the

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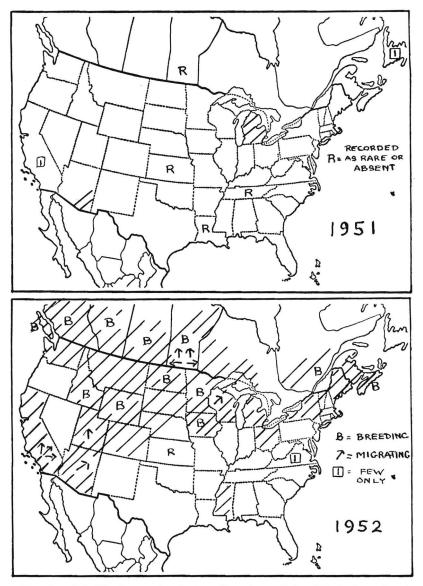
	Brit.	N. Am.		Brit.	N. Am.		Brit.	N. Am.
1900	с	с	1920	с	с	1940	с	с
01		с	21	с	-	41	с	с
02	е	с	22	с	-	42	-	-
03	с		23	с	_	43	с	-
04	с	с	24	-	с	44	-	-
05	-	-	25	с	-	45	с	С
06	с		26	с	с	46	с	с
07	-	с	27	с	_	47	с	с
08	с		28	с	-	48	с	-
09	_	-	29	-	-	49	с	с
1910		-	1930	-	-	1950	с	
11	-	_	31	с	с	51	-	-
12	с	-	32	_	-	52	с	с
13	с	с	33		-	53	-	-
14	с	с	34	_		54	_	-
15	-		35	-	с	55	с	-
16	-		36	-	с	56		-
17	С	-	37	с	_	57	-	с
18	с	_	38	с		58	с	с
19	с	с	39	с	с	59		с

TABLE 1. THE YEARS BETWEEN 1900 AND 1959, IN WHICH, ACCORDING TO THE AVAILABLE EVIDENCE, THE PAINTED LADY BUTTERFLY WAS MORE THAN USUALLY COMMON (C) IN NORTH AMERICA AND IN BRITAIN

changes here with those observed in western Europe over the same period.

In this part of the Old World, interest in the immigration of butterflies from the south has been high for many years. In Britain we have annual reports on migrant insects, including the Painted Lady, for over thirty years; in Holland, since 1940, in Ireland since 1950, and in Austria since 1956. Also a study of earlier records, from 1850 to 1930, from old natural history books and journals in Britain, was published by Cockbill in 1942 (Williams et al., 1942). The information available for the years 1900– 1959 for years of unusual abundance in Britain has been added to the North American records in Table 1. From this double set of data Table 2 has been made, showing in how many years, out of the total of sixty, the Painted Lady has been common in both continents (A); in how many years rare in both continents (D), and how often common in one and rare in the other (B and C).

It is possible to calculate from the total number of "rare" and "common" years in each continent, how many of the sixty years should be in each of the four classes, on the assumption of no relation whatever between the two. These numbers are shown in brackets in Table 2.



Figs. 5 and 6. The known distribution of immigrant Painted Lady butterflies in North America in the years 1951 and 1952. The former, a year of almost complete rarity or absence, the latter, a year of widespread immigration.

Table 2. An analysis of the records in Table 1 to show the number of years, out of 60, in which the Painted Lady was: (A) unusually common in North America and in Britain; (B) common in North America but not in Britain; (C) common in Britain but not in N. America; and (D) rare in both areas. The numbers in brackets are the number of years expected in each class if there were no association between the two areas

		common	rare	total
IN NORTH AMERICA	L	А.	В.	
	common	18	6	24
	CO	(15.4)	(9.6)	
AME		C.	D.	
RTH	rare	18	18	36
N N		(21.6)	(15.4)	
_	total	36	24	60 years

IN BRITAIN

It will be seen that in the classes of "simultaneous abundance" the observed number of years are both greater than that calculated on the assumption of no relation, but in the two classes of "common in one continent and not in the other", the observed numbers are below the calculated.

A statistical calculation (using Yate's correction for small numbers) gives the parameter χ^2 as 2.78, which, from 60 observations and one degree of freedom, indicates a probability of 0.10 that the result obtained could be due to chance. Otherwise the chances are 9–1 the result has some significant cause. This is not *proof* of a relation, but suggests a possibility worth further investigation. It is however interesting to note that Grant (1937) has already shown a similar relation between high levels of

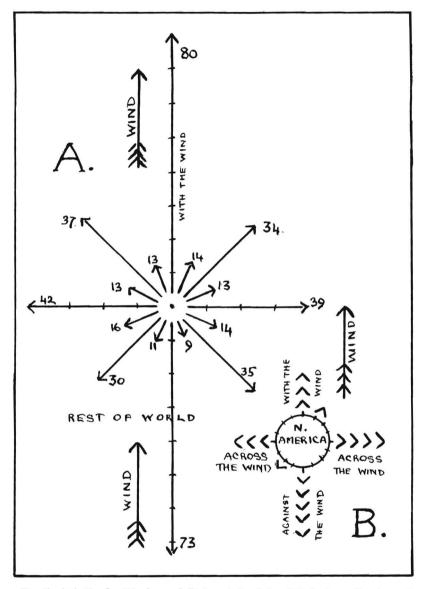


Fig. 7. (A) Nearly 400 observed flights of the Painted Lady butterfly, from all parts of the world, in which both flight direction and wind direction were recorded, arranged according to the angle between the flight direction and the wind. (B) Seventeen records from North America arranged on the same plan.

immigration of the hawk-moth *Celerio lineata* Fabr. in North America and its subspecies *C*. *l. livornica* Esp. in Europe.

Since the idea of common origin for the two continents can be ruled out, it seems likely that there is some common factor, presumably meteorological, which bring about the unusual abundances, either in Europe or in North America, or more probably in the sources of the immigrants in North Africa or in Mexico. If this is so, such specially favourable conditions cannot be local events, but must include causes which are linked together from North Africa (10° W to 30° E) to Mexico (100° - 120° W longitude), a distance of nearly one third of the earth's circumference.

The Problems of Orientation and Wind

There is no doubt that in North America, as also in Europe and North Africa, there are very regular movements of insects which are different in direction at different seasons of the year. They normally have a northerly component in the spring and early summer and a southerly component in the fall.

The mechanism of this orientation is still uncertain. It has been attributed to the direction of the sun's rays (polarised or unpolarised), or to the earth's magnetic field; but most often to the direction of the wind. The main wind-orientation theories are first that the insects are helplessly blown by the winds and take no part themselves in determining the general direction of movement of the population. The second suggestion is that the insects are able to appreciate the direction of the wind while they are flying, and can either fly at a constant angle to it or can straighten out their flight in the direction in which they "want" to go, by allowing for the drift.

It is of course obvious that when an insect is flying in an air current of greater velocity than its own maximum speed, the insect *must* drift downwind. The smaller it is, the more likely it is to drift. The main aerial movements of insects like Aphidae and small Diptera must be generally downwind. But the more powerful fliers such as the larger butterflies and moths can fly steadily against moderate winds, and the butterflies usually shelter during periods of strong wind. The locusts are an exception as, although they have an air speed of about ten miles per hour, the swarms often rise to several thousand feet, where the wind speed is greater than this. As a result these high-flying swarms tend to move down-wind.

I have seen Painted Lady butterflies in Egypt flying, against a light wind, at a ground speed of about 12 miles per hour; and other observers have given ground speeds of 15 to 18 miles per hour (the latter also against a light wind). In California McGregor has also estimated a speed of about 12 miles per hour, so that provided that they fly near the ground, they can make headway, except in high winds, when they tend to settle.

The little evidence we have for North America about the relation of flight to wind direction is shown in Fig. 7B, in which all the available records are shown; the wind is assumed to be blowing from the bottom of the diagram. The number of records is small, but they show almost equal numbers of flights with the wind, against it and across to left or to right. This evidence is very strongly upheld by a large number of records of flight direction and wind in *V. cardui* in other parts of the world, which are summarised in Fig. 7A. There are 473 observations by many different observers in many different countries and they give no support to the idea that there is within sight of the ground, any constant relation between wind direction and flight. The slight excess of flight records with or against the wind is probably a biassed observational error, as observers are more likely to take notice of cases where the wind is with the flight ("obviously the cause"), or against it ("how curious"), than merely across.

Association of Species in a Migratory Flight

A remarkable feature of the northward spring migration of the Painted Lady into Europe is its frequent association with two other species of Lepidoptera, a noctuid moth *Plusia gamma* Linn., known popularly as the "Silver-Y", and a pyralid *Nomophila noctuella* Schiff. Many records exist over the last hundred years of the simultaneous appearance in numbers of all these species. It has been noted at sea in the middle of the Mediterranean, on the south coast of France, in the British Isles and elsewhere. In Yugoslavia, where the caterpillars of the Painted Lady destroy soya-beans and other crops, the association is regular that it has been suggested that the use of light traps to attract *P. gamma* might give an early warning of possible immigrations of the butterfly.

The pyralid known as *N. noctuella* is widespread in N. America, and for many years it was thought that *Plusia gamma* also occurred, but the North American species has been separated off under the name of *pseudo-gamma*. Little appears to be known of its migratory habits.

In all the available history of outbreaks of V. *cardui* in America I have found only one reference to a similar association, when damage by caterpillars of V. *cardui* and *Plusia ni* Hubn. occurred simultaneously in Utah in 1965. This species (related to *P. gamma*) is known as a rare immigrant into Britain.

Close observations are needed to see if any association of species occurs in North America similar to those in Europe.

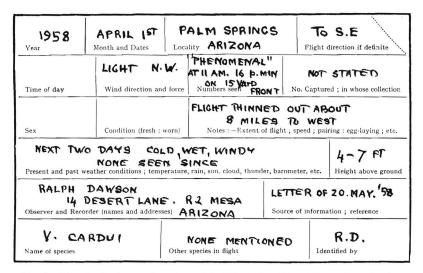


Fig. 8. The standard record card used in Britain for filing information of migrant insects, filled in from a letter describing a migration of Painted Ladies in Arizona in 1958.

Discussion

My object in writing this brief account of the status of *Vanessa cardui* in North America is three-fold: firstly, to summarise our knowledge and ignorance of the facts, and to emphasise what seems to be their basic pattern; secondly, to get more information on the history and past outbreaks to check our conclusion; and thirdly, to get fuller information about immigrations in the future.

The first of these requires little comment.

For the second, there must be lying about in note books, files, collections, museums, in obscure journals and in memories, much information about the occurrence of the Painted Lady in past years, and in different parts of the continent. Every record which includes at a minimum the year and the locality, with some idea of the numbers, is a new piece to fit into the jig-saw picture.

For observations in the future, we can only hope that if entomologists are prepared in advance they may be able to observe new details, when they are fortunate enough to witness an actual migration, or even merely the presence or absence of the butterfly. For many years in Britain we have been using a standard record card for summarising information. Fig. 8 shows one of these on which is extracted information of a migration of V. cardui in Arizona. The different sections on the card give some idea of the points that should be noted and recorded. It is unlikely that all can be filled in, but as many as possible should be attempted, and particularly the direction of flight and of the wind (with any variations during the observations). If specimens can be captured, dissections of the female to see if fat body or developed ovaries are dormant, can give important information on probable previous or later activity.

The field study of insect migration is a science in which little can be planned in advance: also observations can seldom be repeated. The observer must be ready to take advantage of the opportunity of the moment, and all students must depend on the experience of others as well as their own.

"By mutual confidence and mutual aid

Great deeds are done, and great discoveries made."

Please make sure that your observations as well as your conclusions are made available for others.

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