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A POSSIBLE METHOD OF EVOLUTION OF THE MIGRATORY HABIT IN BUTTERFLIES

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CONTENTS

A new theory of migration in butterflies is outlined and present concepts are examined. During the course of evolution many butterflies have become adapted in the larval stage to foodplants that occur in small and scattered localities, the distribution of which changes constantly. It is argued that whenever this happens selection might be expected to produce a butterfly which flies from one foodplant site to another. Further it is argued that while they were crossing areas devoid of foodplants selection would have favoured those individuals that flew at a constant angle to the sun. At first all angles to the sun would be represented equally in the population but each individual would pass on to its offspring a bias towards its own particular angle. It is suggested that the temperature gradient experienced by a butterfly dispersing in this way would constitute a marked selective pressure. This selective pressure would cause an increase in the number of individuals flying at certain angles and a decrease in the number flying at others.

The effects of temperature on rate of development and fecundity were demonstrated for *Pieris rapae* and *P. brassicae* in the laboratory. The effects of seasonal and geographical temperature variations on these two species in the field were also demonstrated. Based on these results the relative selective advantage of each flight direction was calculated for different times of the year. As a result of these calculations it was predicted that *P. rapae* should fly at 159° to the sun until 27 August, when it should fly at 0°. For *P. brassicae* it was predicted that the first brood should fly at 159° and the second brood at 339°. Observations of flight direction of these two species from August of one year to October of the following year agreed well with these predictions.

The observations of flight direction also showed that *P. rapae*, and probably also *P. brassicae* and *Vanessa atalanta*, were using the sun as the environmental clue by which they were orientating themselves. There was no compensation for the sun's movement during the day or season.

Experiments showed that *P. rapae* is sensitive to photoperiod during the adult stage. It is by this

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means that the same individuals can change their flight direction from 159° to 0° at the most selectively advantageous time.

A calculation based on the results of this investigation suggested that a return flight would be a selective disadvantage to both *P. rapae* and *P. brassicae*. Observation of these two species suggested that in neither does the southward movement function as a return flight, i.e. is equal in distance to the northward movement.

Introduction

Through the pioneer work of C. B. Williams and his followers the past fifty years have seen the initiation and acceptance of various concepts of the migration of butterflies.

It is generally considered that a population of any recognized migratory species consists partly of residents and partly of migrants (Williams 1958). As a result of this concept, counts of directional movement, such as those made by Williams (Williams, Cockbill, Gibbs & Downes 1942) on *Pieris brassicae*, are interpreted in the following way: if the main direction of movement is, say, towards the south, those individuals flying south are migrants and those flying in other directions are residents engaged on trivial flights.

For many years Williams has said that the lack of evidence of a return flight in migratory butterflies was an expression of our ignorance rather than of our knowledge. The reasoning which led him to this conclusion is also based on the resident-migrant concept. Briefly, his argument (Williams 1958) is that if the migrant part of the population flies away from the breeding grounds every year and is lost as far as continuing the species is concerned, then it has to be admitted that a habit which is fatal to every individual possessing it can persist for, presumably, millions of years. This does not preclude the possibility that it is to the benefit of the species as a whole if large numbers are sacrificed at times such as during overcrowding and food shortage. However, Williams (1958) points out that this still does not overcome the difficulty of the continued production of migrants by parents in whose direct ancestry the habit of migration has never showed itself.

Williams (1958) says that every migration consists of three parts: (1) an emigration from the original home; (2) a 'trans-migration' through an area where the migrants are only in passage; and (3) an immigration into the new area where the animals settle down. Migrations are also considered to have a point of origin. For instance, Williams (1958) says that the midsummer movement of *P. brassicae* appears to originate chiefly in southern Scandinavia. Offshoots of this are supposed to break away to the west or south-west and reach our east and south-east coasts. It is also considered that individuals which would not normally migrate can be caught up in swarms of their own or other species (Williams 1958, p. 56 for *P. rapae* and p. 33 for *P. napi*).

Several suggestions have been put forward as to the advantage of migration. Williams (1958) considers that the reason may be either overflows from over-populated areas, escape from over-development of parasites and predators, or escape from a seasonally recurring food shortage or other unbearable condition. Roer (1959) thinks that the migratory habit arose in *P. brassicae* as a means of escaping the very high summer temperatures at the southern edge of its range and that genetically the habit became so fixed that it persisted as the species spread north. Finally, Southwood (1962) has pointed out that those insects that live in temporary habitats have a higher percentage of migratory species than those that live in permanent habitats.

However, Williams (1958) and Nielsen (1961) both confess to being uninterested in speculations as to the selective advantage of the migratory habit. Williams (1958) has said that even if an advantage were to be demonstrated for some particular species this would not explain why or how the species began to develop the habit; nor would it explain the mechanism of orientation without which the movement would lead anywhere, which is nowhere.

Wittstadt (1959) goes even further and believes that the seasonal fluctuations in flight direction of *P. brassicae* are of no selective advantage. Instead he regards them as psychological recollections of the glaciations and interglaciations. He rejects the possibility that the southerly autumn movement is a means of escaping the central European winter, because the pupae can withstand quite low temperatures.

Johnson (1966) points out a correlation between migration and sexual immaturity in female insects and suggests that the two are physiologically related. Williams *et al.* (1942) remark that during the passage of a southerly migration of *P. brassicae* through Harpenden in July and August 1940 considerably fewer eggs were laid than might otherwise have been expected.

Finally, the mechanism by which butterflies orientate during migration is completely unknown. Williams (1958) discusses and dismisses in turn every facet of the environment known to man that could possibly serve as the clue to the discovery of the mechanism.

The present picture of butterfly migration can now be summarized. Under certain conditions, as yet unknown, migrant individuals appear in what would be otherwise a resident community. These butterflies then emigrate and for a while fly in a constant geographical direction. During this period of 'trans-migration' they are rarely distracted by food or oviposition sites, but they may be joined by individuals of their own or other species which take up the same orientation and fly with them. Eventually, perhaps at the onset of sexual maturity, the migration ceases and the butterflies settle down in an area which is some distance, even thousands of miles, from their place of origin. Finally, if the migratory habit is to persist, some at least of the offspring of these migrants must later make the return flight.

Although the mechanisms by which the pattern is achieved are not known, most of the observed facets of migration fit into the above picture. There is one facet, however, which does not. In the northern hemisphere the usual pattern of flight direction is for there to be a northerly flight in the spring and a southerly flight in the autumn (Williams *et al.* 1942; Williams 1958). The reason(s) for this can only be expressed in terms of the evolution of the migratory habit and the relative selective advantage of each flight direction. The above picture in itself does not explain why, for instance, the pattern should not be south in the spring and north in the autumn, or even east and then west.

In the following pages a theory is outlined which attempts to trace the most likely course of evolution of butterfly migration. On the basis of this theory and the results of certain experiments that have been done on *P. rapae* and *P. brassicae*, an attempt was made to predict the patterns of migration in these two species. These predictions were then tested in the field.

An explanation of the north–south pattern of flight direction could have been an addition to the concept of migration described above. However, in deriving the theory on which this explanation is based, it was found necessary to reject the greater part of this concept. As a result, the theory outlined in this paper is suggested as an alternative to the present interpretation of the phenomenon of butterfly migration.

A THEORY OF THE EVOLUTION OF THE MIGRATORY HABIT IN BUTTERFLIES

Southwood (1962) has pointed out that those insects that live in temporary habitats have a higher percentage of migratory species than those that live in permanent habitats, and the first part of the theory outlined in this paper is essentially a consideration of this point. As Southwood (1962) also discusses in some detail which habitats he considers to be temporary, it is only necessary here to consider a few of the facets of these habitats.

It is possible to discuss the plants in any area in terms of whether or not they form a climax vegetation (Odum 1959). Even within such a vegetation, however, a number of factors, such as uprooted trees, the digging of animals, and landslides, are continually producing patches of bare ground and during the course of evolution many plants have become adapted to exploit these patches before they are recolonized by plants of the climax vegetation. These temporary species, as a result of their ecology, have a characteristic pattern of distribution. They tend to be found in small and scattered localities, except perhaps where man has cleared large areas of ground, and because they are only temporary in any one place their distribution changes continuously.

During the course of evolution the larvae of many species of butterflies have become adapted to live on plants that happen to have a distribution of this type, and while larval adaptation was taking place in any particular species, the distribution of these plants seems likely to have constituted a selective pressure on the behaviour of the adult. For instance, at intervals, depending on just how temporary the foodplant, emerging females must find an absence of oviposition sites in the locality in which they themselves developed and as a result be forced to search further afield in order to lay their eggs. Given this enforced exodus of the females, the males must then either mate with the females before they leave or leave also and if, as could easily happen in a small area, females are often absent anyway, selection would probably favour the latter.

Frequently, therefore, both sexes must leave their place of emergence and spend some time searching for larval foodplants. During these periods there will not only be selective pressure on visual and olfactory acuity and speed of flight but also on the form of the flight path. The magnitude of this pressure on any species will depend on how frequently the above situation arises and this in turn will depend on the temporariness of the larval foodplant. Therefore, in considering the evolution of the migratory habit, or indeed its absence in any particular species, it is first necessary to know approximately how long the larval foodplant remains in any one locality before it gives way to the next species in the sere.

Although the magnitude of the selective pressures on the form of the flight path depends on how temporary the larval foodplant is in any one place, the nature of this pressure depends on the pattern of distribution of the foodplant. For instance, the larval foodplant of one species could occur in small localities, half a mile apart, which are distributed randomly throughout the entire range of the butterfly. The larval foodplant of another species could also occur in small localities, half a mile apart, but these could be restricted to two areas of ten square miles which are two hundred miles apart. The nature of the selective pressures acting on these two species might be expected to be very different. The pattern of distribution of foodplant, therefore, must also be taken into account in considering the evolution of the migratory habit or its absence in any particular species. In the following paragraphs the selective pressures are discussed which might be expected to act on those butterflies with larval foodplants having the former of the two types of distribution described above.

While searching for these foodplants, selection will favour those individuals that spend least time in unsuitable areas, and, as the plants for which the butterfly is searching are immobile, the most efficient flight path will be that which does not lead the butterfly over the same area more than once. This immediately renders disadvantageous anything approaching random movement. Some of the suitable alternatives are shown in figure 1.

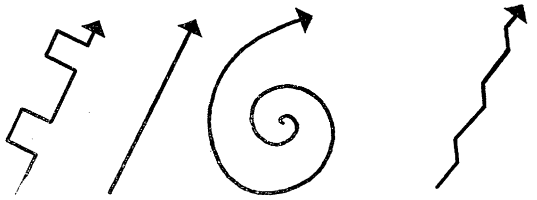

Figure 1. Equally efficient flight paths for searching for randomly dispersed, immobile objects. All flight paths that do not cover the same piece of ground more than once will probably be equally efficient.

With the exception of the spiral flight path, which might be expected to be the most difficult to execute anyway, the alternatives have two features in common. One is that the butterfly must be capable of flying in a more or less straight line for a greater or lesser part of its time and the other is that unless occasional doubling back one day over ground that had been searched a previous day is to occur, some appreciation of direction is necessary.

There is no need to postulate a very complicated means of judging a straight line just to enable a butterfly not to double back on itself. Nevertheless, some adaptations would seem to be more efficient than others.

A butterfly could fly in a straight line over some distance by visually fixing some distant object and flying towards that. However, a butterfly engaged on the type of flight being considered will be distracted continually by solitary flowers and other butterflies. Such distractions would cause it to lose sight of its original objective for shorter or longer periods so that without postulating a quite sophisticated memory this method would not serve to prevent it from often doubling back on its tracks.

A second possibility would be to fly at a constant angle to the wind (Vleugel 1962). However, a few feet above the ground, which is where most flight occurs, topographical features, such as hills, trees, and hedges, set up so many local currents and eddies that a butterfly flying at a constant angle to the wind could often find itself flying in a circle. In addition to this the wind frequently reverses its direction overnight so that a butterfly could often find itself doubling back one day over areas that it had searched the previous day.

However, as butterflies rarely fly in temperate latitudes when the sky is overcast, and as the sun is the one facet of the environment known to be detectable by insects that would enable both flight in a straight line and some appreciation of direction, it seems likely that this would be the environmental clue by means of which adaptation to the selective pressures being discussed would occur. Even though the sun changes position during the day, its rate of movement across the sky is so slow relative to the speed of the butterfly that an individual always flying at a constant angle to the sun would never double back over ground that it had covered previously. It is suggested, therefore, that in those butterflies in which the larval foodplant has a distribution of the type described, the habit would have evolved of flying at a constant angle to the sun during those periods that they were searching for this foodplant.

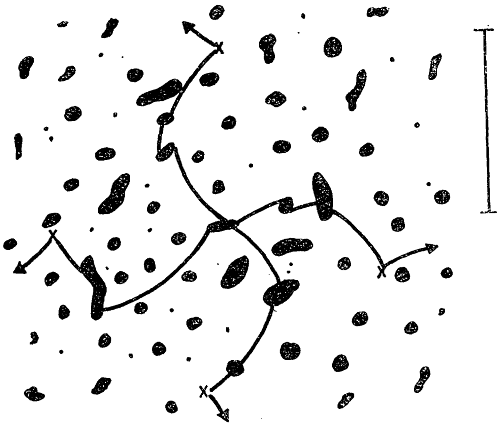

FIGURE 2. Flight paths of a group of butterflies that use the sun to fly in a straight line over each piece of ground devoid of foodplants. Solid black indicates areas in which foodplants are present and in which flight is more or less random; ×, overnight resting sites. Deviation from a straight line is caused mainly by the movement of the sun. In effect the group radiates from its place of origin. The time period is just over a day. The scale (approx. 5 miles) applies to *Pieris*.

There seem to be two ways in which this angle could be fixed for any particular individual. The first is for there to be some form of imprinting whereby the angle subtended on the eye when the freshly emerged adult first comes in direct sight of the sun is the one adopted for the rest of that individual's life, and the second is for there to be an inherited bias towards a particular angle. In the long run, because of its independence of environmental complications such as periods of cloud at emergence, the second alternative would probably prove to be the more advantageous.

So far we have been concerned with the selective pressures acting during the enforced exodus of males and females from their place of emergence. However, even when larval foodplants are still present, it could be an advantage for a butterfly to leave its place of emergence. There are two factors that support this possibility. First, it has been well documented for some time (Allee, Emerson, Park, Park & Schmidt 1949) that the percentage mortality of any species due to parasites and predators is greater at higher host population densities than at lower. Those females will be at an advantage, therefore, that lay most eggs in sites that have a low larval population density and in the species being considered these sites will be those that have only just formed. Consequently, given a reasonably efficient flight path for searching for foodplants, it might be expected that selection would favour those females that did not stay in any one place but instead flew from one foodplant site to another. Secondly, the distribution of adult foodplants seems likely to be important. Butterflies feed mainly on the nectar of flowering plants and are invariably adapted to more species than are the larvae. As a result the adult foodplants are usually more widely distributed, and it could frequently happen that while nectar is available elsewhere, there is insufficient in those sites containing larval foodplants. It seems likely that this selective pressure would also favour those individuals that did not stay continuously in any one place.

It is therefore suggested that in many species of butterflies there would have been an independent evolution of a way of life in which both sexes stay for a certain length of time in each area that they find to contain foodplants, and then after this time fly at a constant angle to the sun until another area is found. This pattern is repeated continually from emergence to death and is only interrupted by periods of cloud and darkness.

Although selection would favour that the angle flown relative to the sun should be constant for any particular individual, there is no selective pressure at this stage that would favour the use of any one angle over any other, except perhaps at the extreme edge of the range. It would be expected, therefore, that all angles would be represented equally in the population, but that each individual would pass on to its offspring a bias towards its own particular angle. In figure 1 several more or less equally efficient flight paths are illustrated. However, once having adopted this method of flying in a straight line between foodplant sites, an inevitable consequence is that the total flight path becomes a more or less straight line. Deviation from a completely straight line will be caused mainly by the movement of the sun. The resultant movement for just over a day of a group of individuals that emerge in a particular area is probably as shown in figure 2. In effect they radiate from their place of emergence.

Now, given the situation illustrated in figure 2, it is only necessary for there to be some selective pressure that favours one flight angle relative to the sun more than any other and the result would be an increase in the number of individuals flying at that angle and a decrease in the number flying at others. Furthermore, if the most advantageous angle was different at different times of the year, and if it was within the capabilities of a butterfly to judge time of year, selection would favour that butterfly flying in one direction at one time of year and in another direction at another time of year.

In order to select in favour of a particular flight angle, a feature of the environment must exist, initially at least, in the form of a geographical gradient at that angle. There are four possibilities: (1) a gradient of abundance of a parasite or predator; (2) a gradient of abundance of a foodplant; (3) a gradient of day length; and (4) a climatic gradient. Of these possible selective pressures, (3) and (4) will always be present and (1) and (2) may or may not be present, depending on the species.

Climatic gradients can be of temperature, sunshine, humidity, barometric pressure, or rainfall. Not all of these, however, will influence butterflies to the same extent. Barometric pressure is only likely to exert an influence through its effect on rainfall and this in turn will mainly exert its influence through its effect on the foodplants. Similarly, sunshine is only likely to exert its influence through its effect on temperature. Temperature and humidity, however, are likely to be important throughout the whole of a butterfly's life history. Of the two perhaps a gradient of temperature is most likely to be effective: so far as many species of butterflies are concerned, geographical gradients of humidity are likely to be obliterated by the relative constancy of microclimatic conditions, especially during the larval stage. For instance, fourth and fifth instar larvae of *P. rapae* live in the hearts of cabbages where the relative humidity is probably 100% in all geographical areas.

Although day length is only likely to act as a selective pressure on the egg, larval, and pupal stages through its effect on temperature, it could influence the adult stage directly through the amount of time available for ovipositing, feeding, flying and courting. Even here, however, it is most likely to act through its effect on temperature.

It is therefore possible to compile a list of environmental factors and to arrange them initially in order of their probable magnitude as selective pressures on a butterfly that has the way of life illustrated in figure 2, viz.: (1) temperature; (2) day length; (3) humidity; (4) foodplants; (5) predators and parasites.

As a result it is suggested that perhaps the most profitable approach to a consideration of the presence or absence of the migratory habit in any particular species of butterfly is to, first, investigate the consequences of selection due to the temperature gradients experienced by that species. Then, if this facet of the environment does not fully explain the pattern of migration observed in that species, selection due to the other possible causes should be considered. It is this method that is the basis of the investigation into the migratory habit of *P. rapae* and *P. brassicae* that is described in the following pages.

THE EVOLUTION OF THE MIGRATORY HABIT IN *PIERIS RAPAE* AND *P. BRASSICAE*

Larvae of both *P. rapae* and *P. brassicae* feed on crucifers. Since these plants have a distribution and ecology that corresponds almost exactly to that of the plants discussed in the above theory, it seems likely that these butterflies will have evolved the way of life illustrated in figure 2. On the basis of the method suggested above, therefore, it is now necessary to determine whether the temperature gradient to which these two species are subjected constitutes such a selective pressure that the resultant adaptation is the one now observed.

Figure 3 is an isotherm map of Europe for July. Of two points 100 to 150 miles apart on a north–south line, the northernmost point experiences an average monthly temperature that is about 1 °C lower than the southernmost point. The isotherms drawn in figure 3 are of temperature corrected to sea level. The reason for this is that uncorrected isotherm maps so resemble contour maps that they do not give a clear indication of temperature variation with latitude. This does not mean that on average the situation illustrated in figure 3 does not exist but that it is more difficult to see. Even though it is greatly simplified, therefore, figure 3 does represent a factor that is relevant to *Pieris*.

1. *Selective pressures acting along a temperature gradient*

(*a*) *The effect of temperature on rate of development, weight and fecundity*

The effect of temperature on the rate of development of *P. rapae* and *P. brassicae* is shown in figure 4 and the effect of temperature during larval development on the weight of the resulting pupae is shown in figure 5. Throughout these experiments the larvae were maintained in glass aquaria. Relative humidity was not controlled but varied from about 50% during the first instar to nearly 100% during the remaining instars. This approximates to normal conditions for *P. rapae*, which spends the last two larval instars in the cabbage heart. However, the relative humidity was probably higher than normal for

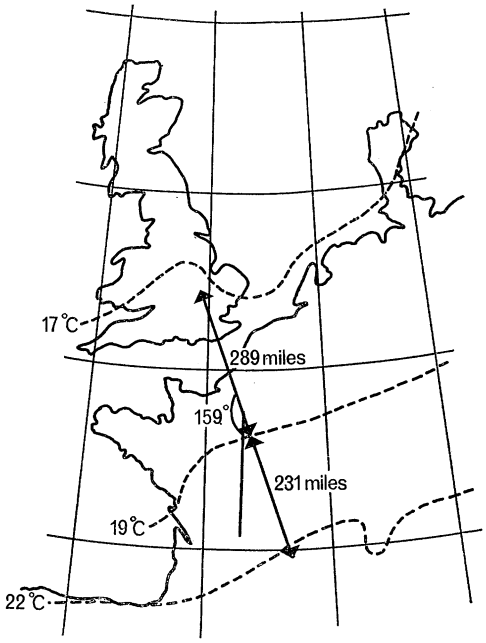

FIGURE 3. Map of western Europe to show July isotherms (corrected to sea level). The isotherms do not extend from east to west but subtend an angle of about 159°, measured clockwise from the east. Isotherms from Thran & Broekhuizen (1965).

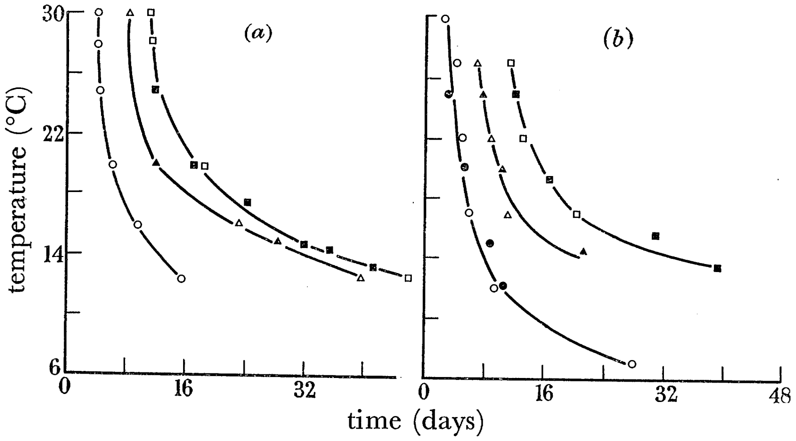

FIGURE 4. Effect of temperature on rate of development of eggs, larvae, and pupae of *P. brassicae* and *P. rapae*.

(*a*) *P. brassicae*: □, larvae (after David & Gardiner 1962*b*); ■, larvae (author's results); △, pupae (after David & Gardiner 1962*b*); ▲, pupae (author's results); ○, eggs (after David & Gardiner 1962*a*);

(*b*) *P. rapae*: □, larvae (after Richards 1940); ■, larvae (author's results); △, pupae (after Richards 1940); ▲, pupae (author's results); ○, eggs (after Richards 1940); ●, eggs (author's results).

P. brassicae during the last two instars. To counteract this as much as possible the cages were cleaned and dried once or twice a day.

Pieris develops its eggs continuously throughout its 3 weeks of adult life and lays eggs nearly every day. There is thus no completely satisfactory method of estimating the fecundity of any particular individual. The only measurement that is completely independent of environmental conditions during adult life is to count the number of developing

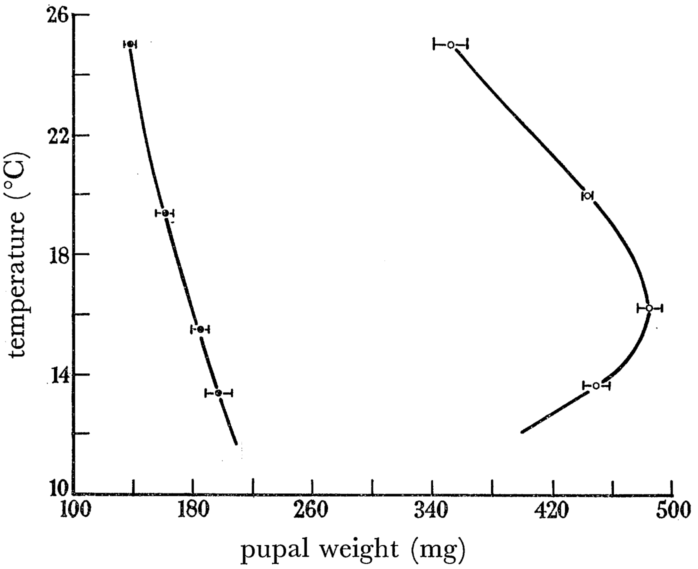

Figure 5. Effect of temperature during larval stage on weight of resulting pupae (weighed 24 h after larval–pupal ecdysis). ●, *P. rapae*; ○, *P. brassicae*.

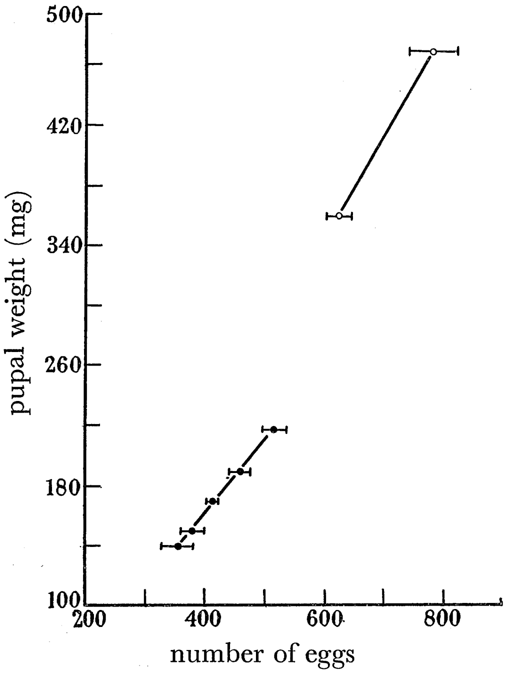

Figure 6. Relationship between pupal weight 24 h after larval–pupal ecdysis and number of developing eggs contained by female at emergence. ●, *P. rapae*; ○, *P. brassicae*.

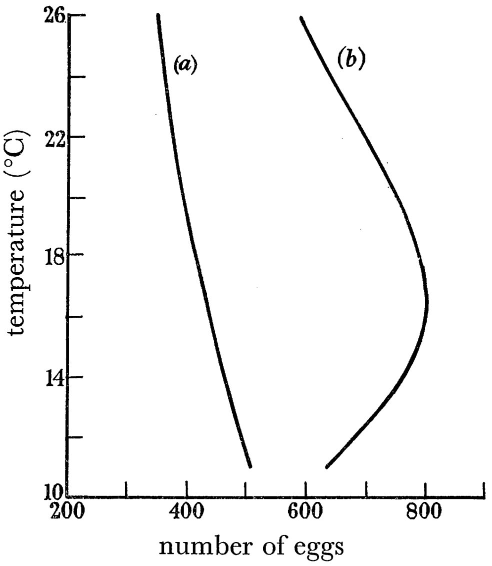

Figure 7. Effect of temperature during larval stage on number of developing eggs contained by female (*a*) *P. rapae* and (*b*) *P. brassicae* at emergence.

eggs contained by the female at emergence. This assumes that the number of eggs laid by a female is directly proportional to the number of eggs that she contains at this stage. In figure 6 the relationship is shown between weight of pupa 24 h after larval–pupal ecdysis, and the number of developing eggs contained 6 h after adult emergence. It can be seen that the heavier the female the more developing eggs she contains at this stage and presumably therefore the greater her fecundity. From figures 5 and 6 the relationship between temperature during larval development and fecundity can be calculated (figure 7).

(*b*) *Geographical weight distribution*

Having shown the effect of temperature on weight in the laboratory, it was necessary to extend the experiment to determine whether this effect of temperature was detectable in the field.

Climatically there are two main sources of temperature variation, one of which is with season and one with latitude. From the curves shown in figure 5, it would be expected that in an animal such as *Pieris* that breeds throughout the summer, some variation in size should occur with season. Complications could arise, however, when considering variation with latitude. If there is stringent selection for a certain size and if this selected size is the same over the whole of the animal's range, it would be expected that collections over the whole of the range would yield animals of the same size. Nevertheless, collections made within the range of movement of a single individual should still show variations in size equivalent to the variations of temperature within that range.

In 1966 an attempt was made to determine whether these size variations occurred in the field. In order to reduce the effects of microclimatic variation as much as possible, collections were made only from cabbages that were in direct sunlight for the greater part of the day. Further, because of the habit of half-grown *P. rapae* larvae of moving into the heart of the cabbage for the rest of their development, collections of this species were confined to cabbages with hearts. Collections were made up to about 200 miles from Bristol. It was considered that there was sufficient temperature variation within this area for its effects to be measurable, whereas the movement of individuals over the area would reduce to a minimum any effects of constant-size selection.

Larvae were collected from various places all over this area throughout the summer. Once collected, they were brought back to Bristol and kept outside in the shade in glass aquaria until larval–pupal ecdysis. Each individual was weighed within 24 h of larval–pupal ecdysis to reduce the error due to loss of weight during the pupal and pharate adult stages. This method of collecting and then bringing back to Bristol meant that all collections spent 2 to 3 days at 'Bristol temperature' as opposed to the temperature of the place of collection. To reduce this effect to a minimum, only fully grown larvae were collected. This severely reduced the number collected in any one place but any other course would have affected the accuracy of the results.

The results were first analysed by calculating the average temperature at which each batch of larvae had developed. This was done from the average weight of each collection and figure 5. The period over which they had developed could then be determined from figure 4. From the Meteorological Office publication 'Averages of temperature for Great Britain and Northern Ireland 1931–60' (HMSO M.O. 735), graphs were plotted of average monthly temperature throughout the summer for each collecting place. Then, knowing the average date of larval–pupal ecdysis for each batch and knowing the period over which each batch had developed, it was possible to read off the average temperature for that period as measured by the nearest meteorological station. This method has certain inaccuracies. For instance, in any particular place the average temperature for any month in 1966 may have varied from the 30-year average for that month. The aspect and microclimate of the gardens in which the collections were made would also be likely to differ from the aspect and microclimate of the meteorological station. Nevertheless, these variables were not considered to be absolutely prohibitive for the purposes of this investigation.

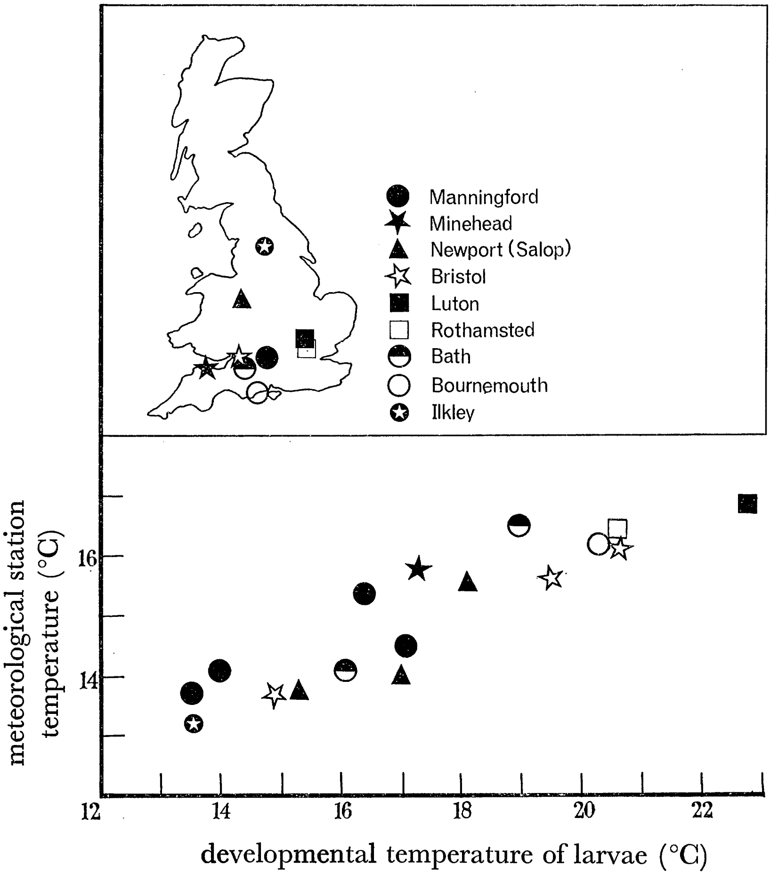

FIGURE 8. Relationship between average developmental temperature of *P. rapae* larvae as calculated from pupal weight and average temperature during development as recorded by the nearest metereorological station. Seasonal variations in size due to temperature are apparent from the several collections made at Manningford, Newport, Bristol, and Bath.

For each collection of *P. rapae* the temperature during development as calculated from the pupal weight can be plotted against the temperature as recorded by the nearest meteorological station (figure 8). It can be seen from the several collections made from each of Manningford, Bath, Bristol, and Newport that size does vary with season. However, because of this seasonal effect, the variation with locality is not so apparent. In figure 9, therefore, a correction has been made so that the temperatures for each locality are relevant to an average development date of 15 July. This figure shows that size also varies according to the temperature of the locality.

Finally, it is necessary to determine the relationship between the temperature experienced by a larva living on a cabbage in the sun and the temperature as recorded in a Stevenson screen. This is done for *P. rapae* by averaging the results shown in figure 8 (figure 10).

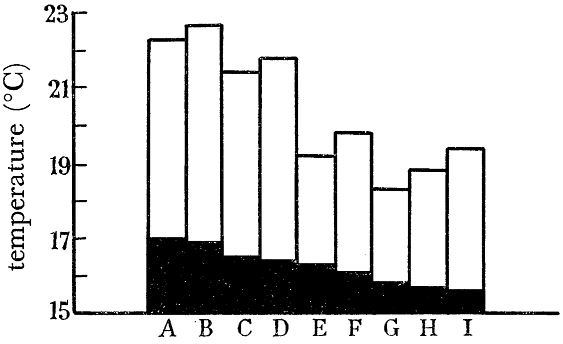

FIGURE 9. Effect of geographical locality on developmental temperature of *P. rapae* larvae. A, Bath; B, Bournemouth; C, Luton; D, Bristol; E, Minehead; F, Rothamsted; G, Manningford; H, Ilkley; I, Newport (Salop). The places are arranged in the order of their 30 year average meteorological station temperature for July (black shading). The developmental larval temperature (open shading) as calculated from pupal weight is corrected for an average date of 15 July. The effect of temperature on size in the field can be detected on a geographical scale.

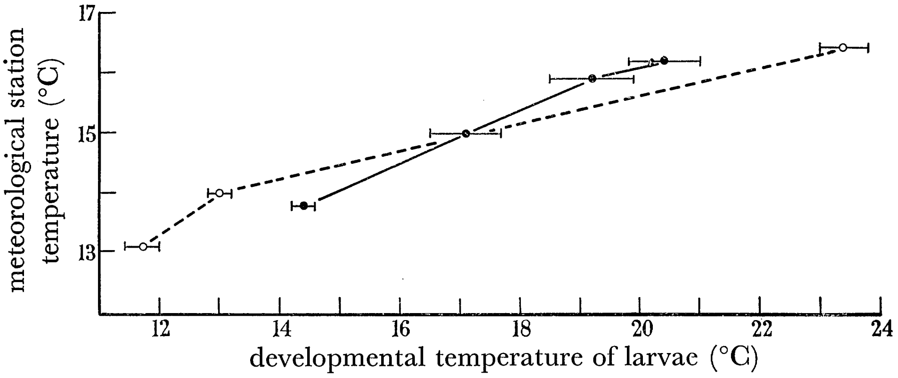

FIGURE 10. Relationship between temperature over a period as measured by a meteorological station and temperature experienced by larvae of *P. rapae* and *P. brassicae* (as calculated from pupal weights) over the same period. ●, *P. rapae*; ○, *P. brassicae*. At higher meteorological station temperatures *P. brassicae* experiences higher temperatures than *P. rapae*. At lower temperatures it experiences lower temperatures than *P. rapae*. This difference is due to the fact that *P. brassicae* spends the whole of its larval life on the outer leaves of the cabbage, whereas *P. rapae* spends the last two instars in the heart.

The few results that were obtained for *P. brassicae* are also included. That *P. brassicae* appears to experience higher temperatures than *P. rapae* at the higher meteorological station temperatures and lower at the lower fits in with the fact that the former spends the whole of its larval life on the outer leaves of the plant, whereas the latter spends half of its larval life in the heart.

(*c*) *Autumn larval development*

P. rapae and *P. brassicae* overwinter only as pupae. Every autumn from 1964 to 1966 there have been some larvae that have failed to reach this stage before the temperature fell to such a level that further development was impossible. The date beyond which no further larvae succeed in pupating varies from year to year and from place to place. In Bristol this date was about 9 November, 1 November and 22 October in 1964, 1965 and 1966 respectively. On average, therefore, there is little opportunity for larval development at Bristol after 1 November.

The screen temperature curve for Bristol (HMSO M.O. 735), the correlation between screen temperature and cabbage temperature (figure 10), and the effect of temperature on rate of development (figure 4) are all known, and from them it is possible to calculate that on average for *P. rapae* it is eggs laid on 3 September that give rise to pupating larvae on 1 November. In fact these dates were about 10 September, 24 August and 3 September for 1964, 1965 and 1966 respectively. These dates were obtained by collecting eggs laid weekly and then following the resulting larvae through their development either on cabbages under nets as in 1964 and 1965 or in glass aquaria maintained outside as in 1966. Only one or two individuals were used for each oviposition date. In figure 11, based on isotherm maps taken from the *Climatological Atlas of the British Isles*, the calculated last oviposition dates of *P. rapae* for successful larval development in England and Wales are shown.

2. *Predictions of the pattern of migration*

It is apparent from the following paragraphs that an exact estimate of the distance travelled by *P. rapae* and *P. brassicae* from emergence to death is not critical in a discussion of the relative selective advantage of different flight directions at different times of year. However, an estimation of distance is necessary to determine the absolute selective advantage of a particular flight angle. The way in which the selective advantage is calculated, however, does not warrant a very precise estimation. Blunck (1954) estimates the distance to be about 180 kilometres for the 'giant' migrations of *P. brassicae*, and, if the adult life span is assumed to be about three weeks, figures obtained by Roer (1961) for marked individuals of the same species give a similar estimate. As *P. rapae* probably does not fly as far as *P. brassicae*, and as the figure needs only to be an approximation, it can be assumed for convenience that, at least in the spring and summer, both species fly about 100 miles from emergence to death.

The selective advantage in flying north is apparent from figure 7. The lower the temperature at which the larvae develop the greater their fecundity when adult. It is now necessary to consider whether there is any selective advantage in flying south and if so to compare this advantage with the advantage in flying north.

Let us consider the first brood of both *P. rapae* and *P. brassicae*. First brood individuals may or may not give rise to a third brood, but more of the offspring of those that go south will give rise to a third brood than of the offspring of those that go north. The selective advantage of going south, therefore, will depend partly on the selective advantage of having a third brood and partly on how many more third brood individuals result from those that go south from those that go north.

It can be assumed that a first brood individual, the offspring of which give rise to a third brood, will have more offspring overwintering than an individual, the offspring of which do not. This increase is therefore a measure of the selective advantage of the third brood. As the offspring of the third brood are larvae and pupae at the same time as the offspring of the latter part of the second brood, it can be assumed that the intensity of predation on the two broods is similar. The selective advantage of the third brood can therefore be determined by the number of individuals that comprise the third brood divided by the number of second brood individuals that gave rise to them. The calculation of this advantage for *P. rapae* has been made in two ways. First, in 1964 the number of eggs laid in a garden were counted every 3 or 4 days throughout the summer. It was found that about 1200 eggs were laid before the resulting pupae showed a 50% diapause. 1200 eggs, at 350 eggs per female (Norris 1935), are equivalent to 3·42 females or 6·84 adults. As a result of sampling throughout the development of these eggs and of the larvae and pupae to which they gave rise, it was calculated that nine adults emerged as a third brood in the garden. This gives a selective advantage of 1·31 for the third brood in 1964. Secondly, if it is assumed that the longevity of an average second brood individual is the same as that of an average third brood individual, the selective advantage of the third brood can be calculated from the curve of seasonal incidence. If the date of oviposition is known beyond which no further eggs give rise to third brood individuals, then the area under the third brood curve divided by the area under the second brood curve up to this date will be a measure of the selective advantage of the third brood. The seasonal incidence curves for 1964 to 1966 for *P. rapae* and *P. brassicae* are illustrated in figure 12, and on them certain critical dates have been marked.

From figure 12 the selective advantage for *P. rapae* can be calculated as having been 1·4 in 1964, which agrees reasonably with the factor obtained by direct observation, and 0·86 in 1966. There was no third brood in 1965 nor for *P. brassicae* in 1965 or 1966. From these figures it can be assumed that the selective advantage of the third brood is about 1·15.

In fact, this figure should probably be lower. There are three reasons for this. First, those first brood individuals that emerge first are most likely to give rise to a third brood. Third brood offspring pupate at the same time as the later second brood offspring and so probably give rise to the individuals that emerge toward the end of the first brood of the following year. These in turn are least likely to give rise to third brood individuals in that year. Secondly, in calculating the selective advantage of the third brood from the curves of seasonal incidence, it was assumed that the longevity of an average third brood individual is the same as that of an average second brood individual. However, because it is subject to lower temperatures, an average third brood individual is likely to live longer than an average second brood individual. The comparison of the areas under the curves of the two broods will therefore tend to exaggerate the number of individuals that comprise the third brood relative to those that comprise the second brood. Finally, it was assumed that the intensity of predation on the offspring of the second and third broods was similar. However, as the larvae that result from the third brood develop at a lower average temperature than those from the second brood, they are subject to predation for a longer period of time than are the latter.

To a certain extent these disadvantages are offset by the fact that the offspring of the third brood undergo larval–pupal ecdysis later than the offspring of the second brood. These pupae, therefore, will be subject to predation for a shorter period of time than the pupae produced by the second brood. Nevertheless, it seems likely from the above considerations that 1·15 is the *maximum* figure for the average selective advantage of the third brood in the Bristol region.

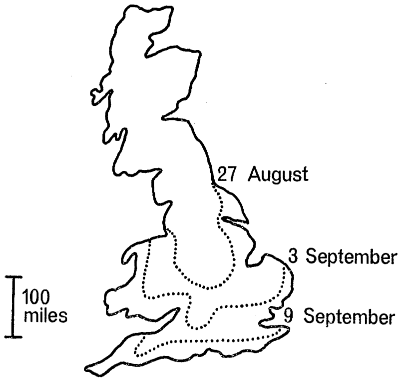

FIGURE 11. Map of England to show last oviposition date of *P. rapae* for successful development to the pupal stage. The isotherms on which the dates are based are taken from the *Climatological Atlas of the British Isles*. If coastal effects are ignored, it can be seen that the isotherms extend more or less from east to west.

A first brood individual that flies south will give rise to offspring that emerge earlier than one that flies north. As these offspring emerge earlier, they will produce more third brood individuals. If it is assumed that oviposition per day remains constant throughout adult life, the *maximum* increase in eggs giving a third brood can be calculated from the number of days earlier that the offspring emerge. If this number of days is represented by d, adult longevity by L, and the selective advantage of the third brood by s then, expressed as a percentage, the *maximum* selective advantage in going south is given by

$$\left(\frac{sd+L-d}{L}\right)100-100.$$

If we assume for the moment that the 'average offspring' of a first brood individual that flies south develops at 1 °C higher than that of an individual that flies north, then for every 1 °C difference throughout the developmental range both the selective advantage in going north and the selective advantage in going south can be calculated. If the advantage in going north is then subtracted from the advantage in going south, the relationships are obtained that are illustrated in figure 13. In this figure are shown the relationships for 1 and 2 °C difference for *P. rapae* and 1 °C difference for *P. brassicae*. It can be seen that as long as larval development occurs above 18·3 °C in *P. rapae* and 19·5 °C for *P. brassicae*, it is an advantage to fly north but below these temperatures it is an advantage to fly south. However, because maximum values have been used throughout the calculation of these curves, these critical temperatures are also maxima. The actual critical temperatures are probably less than those shown in figure 13.

From figures given by Richards (1940), the average oviposition date for first brood *P. rapae* at Slough appears to be about 6 June. From the known curve of Bristol temperature

(HMSO M.O. 735) and figures 4 and 10, it can be calculated that on average larvae from eggs laid on this date will develop at about 18·5 °C. In fact, the average temperature as calculated from the pupal weight of the first brood collections (figure 8) is about 19·3 °C. Therefore it can be calculated from figure 13 that those first brood individuals of *P. rapae* that fly north will have a selective advantage of 0·5 % over those that fly south if the developmental temperature difference of their offspring is 1 °C. In fact the temperature difference, assuming a total individual flight distance of 100 miles, would be about 2 °C (figures 3 and 10). The selective advantage, therefore would be about 1 %.

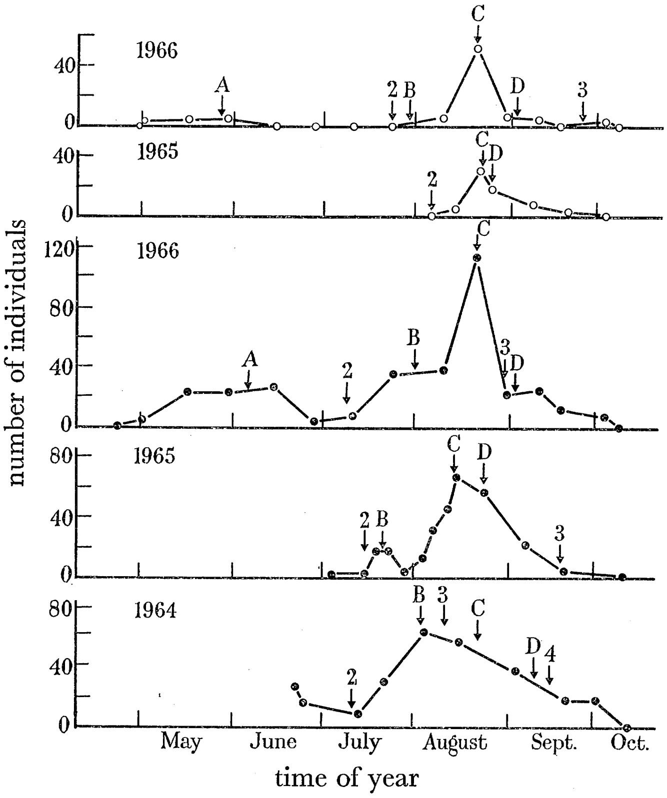

FIGURE 12. Seasonal incidence, 1964 to 1966. ●, *P. rapae*; ○, *P. brassicae*. The number of individuals refers to the total number counted in a garden in 10 counts between 11.00 and 13.00 h GMT. The following dates were determined by collection and observation: A, average oviposition date of first brood; B, date beyond which no eggs laid gave rise to a third brood; C, average oviposition date of eggs that gave diapausing pupae; D, date beyond which eggs laid failed to reach pupal stage; 2, beginning of second brood emergence; 3, beginning of third brood emergence; 4, beginning of fourth brood emergence.

From figure 13 it can be seen that increasing the temperature difference alters the critical temperature very little but does increase the selective advantage for any particular temperature. Therefore the greater the temperature difference the greater the selective advantage. Consequently the greatest selective advantage would result from flying at right angles to the isotherms, i.e. at 159° measured clockwise from south (figure 3).

The same arguments apply to *P. brassicae*. The calculated average developmental temperature for this species at Bristol is about 20 °C, and the only collection made, at Bournemouth, gave a figure of 22 °C. Both are above the maximal critical temperature of 19·5 °C.

When we consider second brood individuals, a different set of conditions prevail. As these only give rise to a fourth brood in exceptional years, such as 1964, there is no multiplication factor to consider. Therefore, as long as the temperature is high enough for eggs laid to reach the pupal stage, the selective advantage in travelling north or south will depend on how temperature affects fecundity. The situation for *P. rapae* and *P. brassicae* is illustrated in figure 14. It can be seen that given the above conditions it is always an advantage for second brood *P. rapae* to go north, but only an advantage for *P. brassicae* if the larval developmental temperature is above 16·5 °C. The average oviposition date of those second brood eggs that do not give rise to third brood adults is 19 August for *P. rapae* and 22 August for *P. brassicae* (figure 12). From the known curve

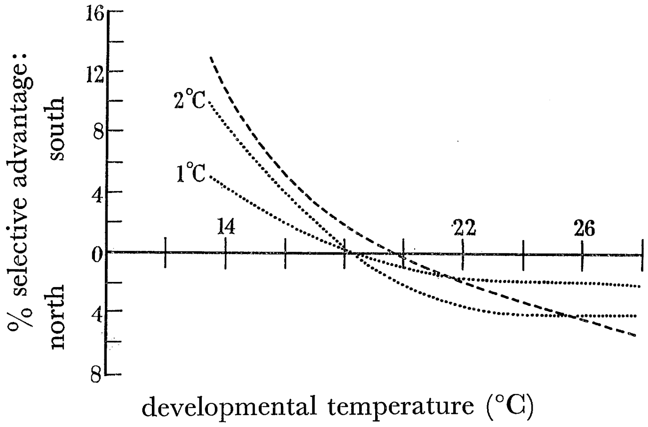

FIGURE 13. Calculated selective advantage of flying north or south for an individual of the first brood, ..., *P. rapae*; - - - -, *P. brassicae*. Above an average developmental temperature of 18·3 °C it is an advantage for *P. rapae* to fly north. The critical temperature for *P. brassicae* is 19·5 °C. If the offspring of two individuals of *P. rapae*, one of which flies south and one of which flies north, have an average developmental temperature that differs by 1 °C, the selective advantage for any average developmental temperature is less than if it differed by 2 °C. The same applies to *P. brassicae* but is not illustrated. The line for *P. brassicae* refers to a difference of 1 °C.

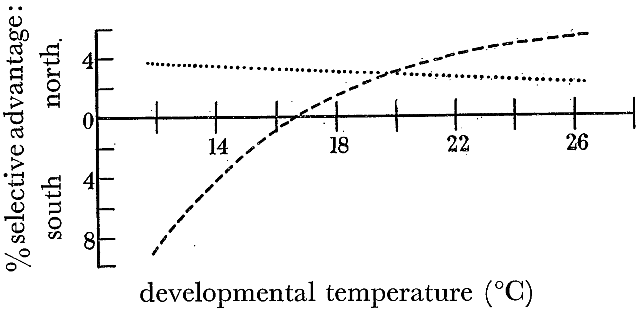

FIGURE 14. Calculated selective advantage in a second brood individual flying north or south assuming there is no fourth brood. . . . ., *P. rapae*; - - - -, *P. brassicae*. Curves are for individuals going north and south, the offspring of which develop at an average temperature that differs by 1°C. It is always an advantage for second brood *P. rapae* to fly north. However, if the offspring of an individual of *P. brassicae* develop at an average temperature that is less than 16·5 °C, it would have been an advantage for that individual to have flown south.

of Bristol temperature (HMSO M.O. 735) and figures 4 and 10, it can be calculated that these oviposition dates should give larvae developing at 17 and 16 °C respectively for the two species. In fact the larval collections made during 1966 gave figures of 15·5 and 12·5 °C. Therefore, from figure 14, it is the second brood individuals of *P. rapae* that fly at an angle of 159° to the sun that are at the greatest selective advantage, whereas it is the second brood individuals of *P. brassicae* that fly at 339° to the sun that are at the greatest selective advantage.

In figure 11 the final oviposition date of *P. rapae* for successful larval development in different parts of England is illustrated. The figure shows that for individuals that have only lived a part of their adult life by 9 September, it is an advantage to be south of Britain by that date. In September adults travel about 2 miles per day (Roer 1961). Individuals at Bristol, therefore, need to start flying south on about 20 August if all their eggs are to have the chance of developing to the pupal stage. However, individuals that have laid nearly all their eggs need not start to fly south until about 3 September (figure 11). It might be expected, therefore, that in *P. rapae* selection would favour the change of flight direction from north to south to occur about half-way between these two dates, i.e. 27 August.

In figure 3 it was shown that in western Europe the July isotherms extend from south-west to north-east. In January they extend from north-west to south-east. The autumn changeover between these two patterns occurs during October, when the isotherms extend from west to east. If coastal effects are ignored, this pattern can be seen in figure 11. Individuals that fly at 0°, i.e. straight toward the sun, will therefore be at a greater selective advantage than those that fly in any other direction.

On the basis of the theory postulated in this paper, it would seem that at Bristol selection favours those individuals of *P. rapae* that fly at an angle of 159° to the sun throughout the summer until about 27 August, when it favours those individuals that fly at an angle of 0°. Selection also favours those first brood individuals of *P. brassicae* that fly at 159°. Throughout the second brood, however, until about 27 August, selection favours those individuals that fly at an angle of 339°, and then after that date those individuals that fly at 0°.

It has to be considered at this stage whether it is within the capabilities of insects in general, and *Pieris* in particular, to show different responses at different times of the year. Fortunately a situation analogous to the one being considered has already been investigated in some detail in *Pieris* and other insects.

The extent to which insects make use of photoperiod is only just being realized (Danilevskii 1965). The phenomena that have been shown to be linked to an appreciation of photoperiod are diapause (Danilevskii 1965), aphid seasonal cycles (Lees 1959; Johnson 1966), and colour and structural polymorphism in certain Lepidoptera and Jassidae (Danilevskii 1965, p. 40).

It is postulated in this paper that the phenomenon of migration in butterflies also involves an appreciation of photoperiod and that it is by this means that *P. rapae* and *P. brassicae* have become adapted to the selective pressures discussed in this section.

3. *Experimental test of theory*

(*a*) *Sun orientation and flight directions*

On the basis of the theory outlined here, it would be expected that quite early in the history of the ancestral *Pieris* the sun was used as an environmental clue during a particular part of adult movement. It was argued that this would have been the most efficient adaptation by which an individual could leave one food or oviposition site and find another. The change in position of the sun during the day was shown to be immaterial in this connexion.

Williams (1958) has pointed out that it is difficult to believe that a butterfly can compensate for this movement of the sun and, because of his concept of migration, he has rejected the possibility that the sun is the environmental clue by means of which migrating butterflies orientate. However, if the course of evolution of the migratory habit in *Pieris* is as suggested here, it would be expected that the sun is used as the environmental clue but that the butterflies do not compensate for its movement during the day (or season). This prediction was tested during the summer of 1966.

TABLE 1. HOURLY COUNTS OF FLIGHT DIRECTION OF *PIERIS RAPAE*

time of day (h GMT)	numbers flying in each direction W	NW	N	NE	E	SE	S	SW
1 May to 21 August								
09.00 to 10.00	9	9	3	3	2	2	3	4
10.00 to 11.00	8	25	13	14	1	7	7	7
11.00 to 12.00	18	31	26	20	8	6	7	6
12.00 to 13.00	8	21	17	14	4	4	1	5
13.00 to 14.00	7	20	24	18	7	6	3	8
14.00 to 15.00	6	22	16	22	8	8	3	7
15.00 to 16.00	8	11	16	23	4	5	2	5
27 August to 14 October								
09.00 to 10.00	0	1	1	1	1	4	2	0
10.00 to 11.00	0	5	10	3	3	21	18	7
11.00 to 12.00	1	9	13	5	3	15	27	23
12.00 to 13.00	2	4	9	3	4	13	12	16
13.00 to 14.00	3	3	6	4	1	7	11	12
14.00 to 15.00	0	0	2	4	1	4	5	10
15.00 to 16.00	1	1	3	5	0	4	3	9

Throughout the summer, counts were made of unidirectional flights of *P. rapae*, *P. brassicae* and *P. napi*. A note was made of sex, species, time of day and direction of each individual seen flying in a straight line. The method of estimating direction was to point the hour hand of a wrist-watch at the sun and then to find south by halving the angle between that and the 1 on the watch face (the watch was set at BST). This was found to be more convenient than carrying a compass because it meant that observations could be recorded at any time whenever and wherever a butterfly was seen. However, it does introduce an error in that it assumes the sun's azimuth changes by 15° every hour. This is not so and requires correction in the final analysis (in the northern hemisphere the sun's azimuth is the angle subtended to the observer between north and the point on the horizon vertically beneath the sun when measured in a clockwise direction).

Direction was recorded to an accuracy of ±22·5° as either north, north-east, east, etc. The results for *P. rapae* were divided into two lots, one for the northward flight and one for the southward. The number of individuals observed flying in each direction for each hour of the day from 09.00 to 16.00 h GMT is given in table 1. These figures were then plotted as percentages and the best curve drawn by eye for each direction, e.g. figure 15. On the basis of these curves, graphs were drawn such as those in figure 16.

The method of calculation of the peak direction for any hour is best illustrated by an example. In figure 16, 09.00 to 10.00 h, the peak direction obviously lies somewhere between west and north-west (270° and 315° respectively, measured clockwise from

TABLE 2. CORRECTION OF CALCULATED PEAK DIRECTIONS OF *PIERIS RAPAE*

	all angles measured clockwise from north					
	1 May to 21 August			27 August to 14 October		
time of day (h GMT)	calculated peak direction	correction	actual peak direction	calculated peak direction	correction	actual peak direction
09.00 to 10.00	291°	−19°	272°	135°	−10°	125°
10.00 to 11.00	315°	−15°	300°	153°	− 9°	144°
11.00 to 12.00	329°	− 5°	324°	173°	− 4°	169°
12.00 to 13.00	344°	+ 5°	349°	189°	+ 4°	193°
13.00 to 14.00	352°	+15°	7°	198°	+ 9°	207°
14.00 to 15.00	9°	+19°	28°	218°	+10°	228°
15.00 to 16.00	29°	+20°	49°	225°	+ 8°	233°

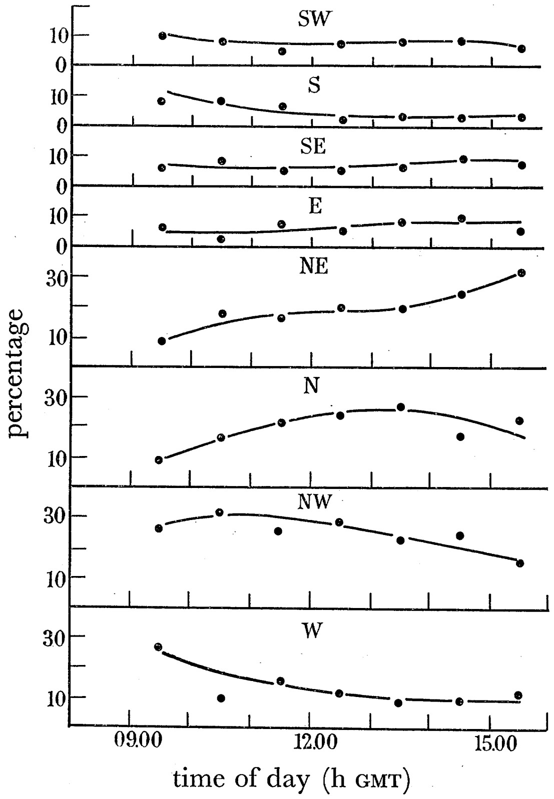

FIGURE 15. Percentage *P. rapae* flying in each of eight directions for each hour of the day from 09.00 to 16.00 h GMT. Observations made 1 May to 21 August 1966.

north). The percentage of individuals going west, south-west, and south add up to 44 and those going north-west, north, and north-east add up to 42. The peak direction, therefore, lies slightly nearer to west than to north-west. The actual angle is given by $270+(42\times 22{\cdot}5)/44$, i.e. 291°.

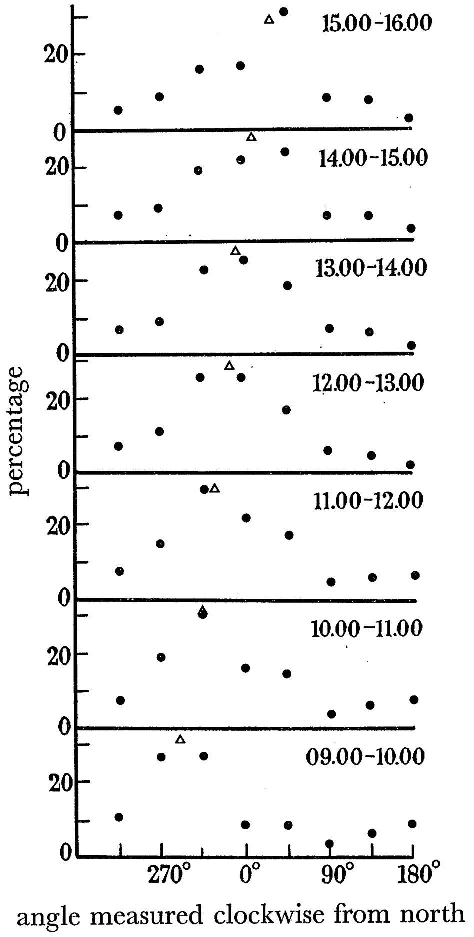

FIGURE 16

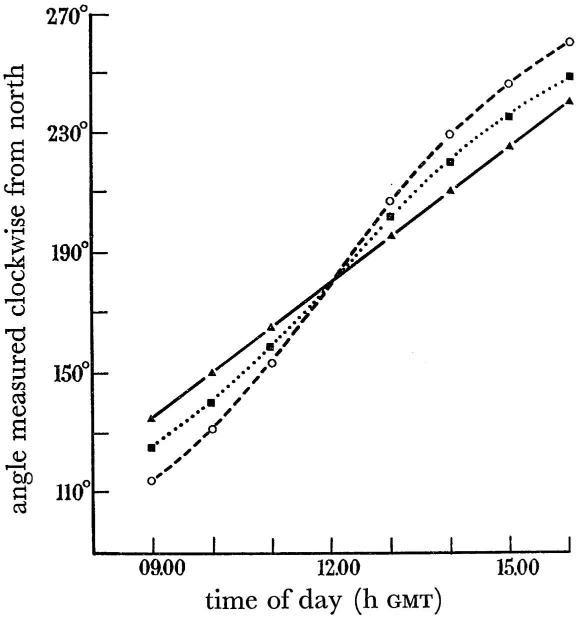

FIGURE 17

FIGURE 16. Percentage *P. rapae* flying in each of eight directions for each hour of the day from 09.00 to 16.00 h GMT. Observations made 1 May to 21 August 1966. △, Peak direction; refers only to angle and is not intended to have significance as a percentage. The peak direction changes throughout the day.

FIGURE 17. Comparison between the change in sun's azimuth and the change that would be observed if the azimuth altered at the rate of 15° per hour. ▲, change of 15° per hour; ■, sun's azimuth (10 September, latitude 50° N); ○, sun's azimuth (21 May and 24 July, latitude 50° N).

The peak directions for each hour were then corrected for the method used in the determination of the direction of flight (table 2). The correction factors for the two lots of results can be calculated from figure 17. The figures for the sun's azimuth were obtained from the *Smithsonian Meteorological Tables 1951*. For the northward flight the average dates were taken to be 21 May and 24 July and for the southward flight 10 September. The azimuth readings are for latitude 50° N.

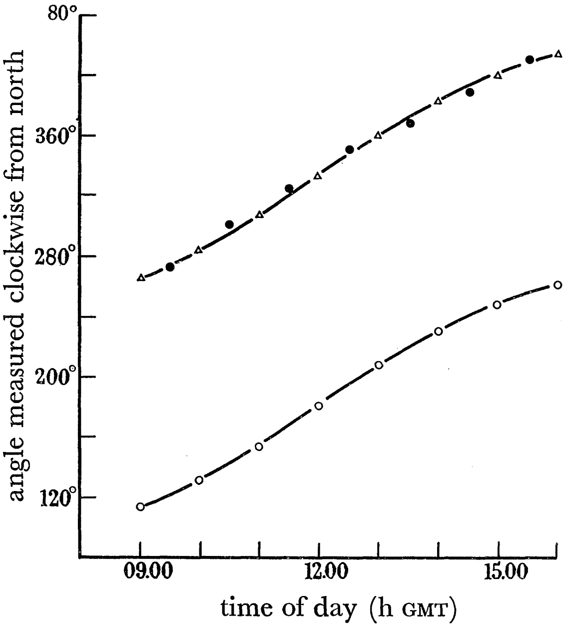

FIGURE 18

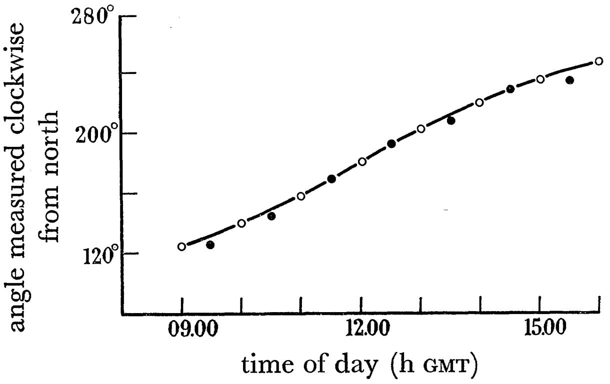

FIGURE 19

FIGURE 18. Comparison of sun's azimuth throughout day (21 May and 24 July, latitude 50° N) and peak flight directions of *P. rapae*, 1 May to 21 August. ○, sun's azimuth; △, sun's azimuth + 153°; ●, peak flight directions of *P. rapae*.

FIGURE 19. Comparison of sun's azimuth throughout day (10 September, latitude 50° N) and peak flight directions of *P. rapae*, 27 August to 14 October. ○, sun's azimuth; ●, peak flight directions of *P. rapae*.

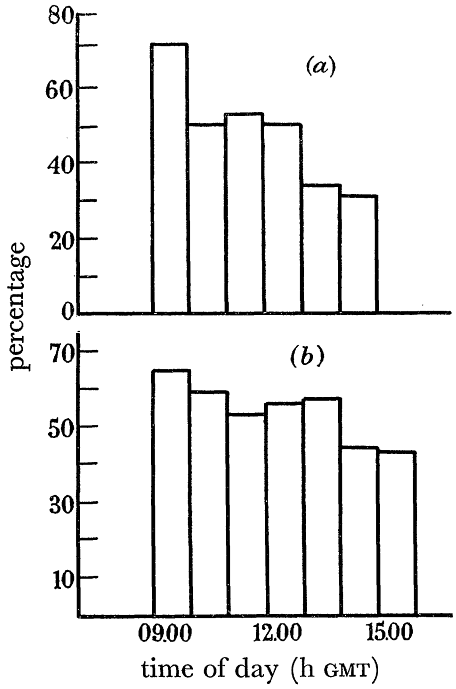

FIGURE 20. (*a*) Percentage *Vanessa atalanta* flying south-east relative to south-west (September and October 1966) and (*b*) of *P. brassicae* flying north-west relative to north-east (1 May to 1 July) at different times of day. In both species direction changes throughout the day.

The peak directions obtained are plotted against time of day in figures 18 and 19 along with the sun's azimuth for the appropriate period. These figures demonstrate quite conclusively that the direction of flight of *P. rapae* alters through the day and season in the same way as does the sun's azimuth. Therefore, unless it can be demonstrated that some other facet of the environment alters in the same way as the sun's azimuth, it would appear that *P. rapae*, and probably other species of butterflies, are using the sun as the environmental clue by which they orientate during migration.

Unfortunately, *P. rapae* was the only species common enough in 1966 for its flight direction to be analysed in much detail. However, sufficient numbers of *P. brassicae* (and *Vanessa atalanta*) were counted for their change in direction during the day to be evident, as in figure 20. This suggests that these species are also using the sun.

TABLE 3. FLIGHT ANGLE OF *PIERIS BRASSICAE* RELATIVE TO THE SUN

number counted flying in each sector (all angles measured clockwise from the sun)						
first brood						calculated peak
22°–66°	67°–111°	112°–156°	157°–202°	203°–248°	249°–294°	
11	27	39	41	27	12	158°
second brood						calculated peak
202°–246°	247°–291°	292°–336°	337°–22°	23°–68°	69°–114°	
2	18	27	24	14	10	338°

The flight directions of *P. brassicae* also have to be calculated in a different way because of the smaller number of observations. Assuming that *P. brassicae* does use the sun (figure 20), every observation of unidirectional flight can be expressed as an angle relative to the sun instead of as a geographical direction. All observations can then be summated to give a large enough sample for an estimate of peak angle to be made (table 3). The peak angle is calculated in the same way as above for the peak flight directions of *P. rapae* at different times of the day. That the difference in direction of southerly flight in *P. rapae* and *P. brassicae* (figure 19 and table 3) is not due to the method of calculation can be seen by recalculating the angle for *P. rapae* in the same way as for *P. brassicae*. This gives an angle of 0·5°.

(*b*) *Observed dates of change of direction*

From the end of August 1965 to October 1966, counts were made of the flight directions of the three British species of *Pieris* as already described. However, now that it has been shown (figures 18, 19 and 20) that an individual probably maintains a constant angle to the sun, each flight direction may be considered as an angle to the sun rather than as a geographical direction. Whenever twenty or thirty individuals had been counted for any species, the percentage flying toward the sun, i.e. between 270° and 90° to the sun's azimuth, was plotted against the date. The results are shown in figure 21. It can be seen that the date of change of direction of *P. rapae* was 27 August in 1965 and 26 August in 1966 (ignoring for the moment the results for 14 and 15 August 1966), whereas for *P. brassicae* it was around the middle of July.

In table 4 the theoretical predictions of flight angle and date of change of direction are compared with those observed in 1965 and 1966. The close agreement between the two provides good support for the validity of the theory put forward in this paper.

Table 4. Comparison of predicted and observed flight angles and dates of change of direction

		predicted		observed	
		angle to sun	change of direction	angle to sun	change of direction
P. rapae	first brood	159°		153°	
	second brood	159°	27 August	153°	26–27 August
	second and third brood after 27 August	0°		0°	
P. brassicae	first brood	159°	middle of July	158°	middle of July
	second brood	339°		338°	

(*c*) *Photoperiod and migration in* Pieris

It was postulated in §2 that the response of *Pieris* to the selective pressures outlined was possible because of its ability to appreciate photoperiod, and that the phenomenon of change of direction of migration was yet another instance of the use made by insects of this feature of the environment.

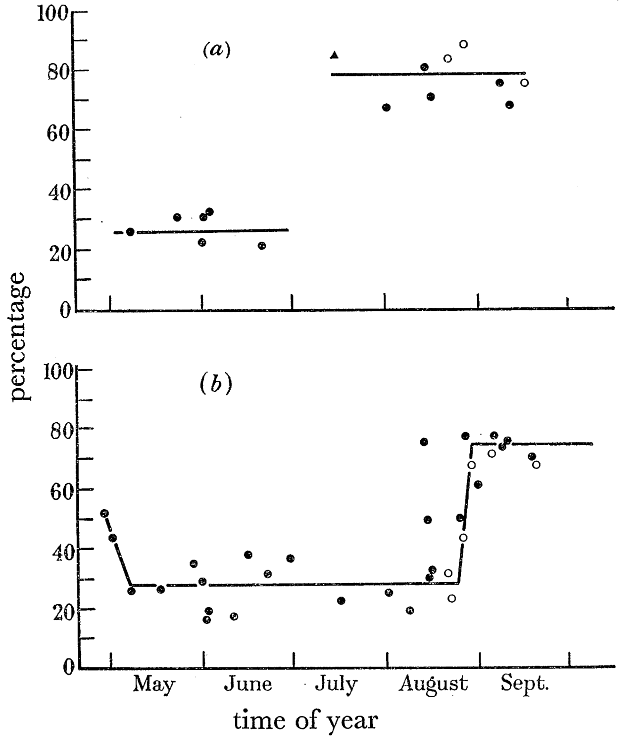

Figure 21. Percentage of (*a*) *P. brassicae* and (*b*) *P. rapae* flying toward the sun, i.e. at an angle between 270° and 90°, at different times of the year. ○, 1965; ●, 1966. ▲, figure from Williams *et al.* (1942). *P. brassicae* reverses its flight direction in the middle of July, whereas *P. rapae* reverses its flight direction on 26 to 27 August.

Figure 21 shows that *P. rapae* changed direction from 26 to 27 August two years in succession. This regularity in itself suggests the existence of a stable environmental clue as to when change of direction should occur. Further, in both years this change of direction cut across a generation, which suggests that it was the same individuals flying north on 25 August that were counted flying south on 28 August. If this was so, the only possible deduction is that it is the adult stage that is sensitive to photoperiod and that the trigger to reverse flight direction is a fall in day length below a certain critical level (or a rise in night length). One further observation adds considerable weight to this deduction. There are two sources of day length variation. One is the orderly seasonal variation and the other is the unpredictable variation that results from the amount of cloud cover at dawn and dusk. When the sky is completely overcast, the day length can be shortened by an hour or more. On 12 and 13 August 1966, the Bristol region experienced two completely overcast dawns and dusks. The effect of this was to shorten the day length to a level that approximated to that usually experienced during the last week of August. Figure 21 shows that a precocious change of flight direction of *P. rapae* occurred on 14 and 15 August, but that the effect of this had disappeared by the 16th. From this observation, two further facts can be deduced. First, that 2 days at short photoperiod are all that are necessary to trigger the change of direction, and secondly that the effects are reversible with the critical period again being two days.

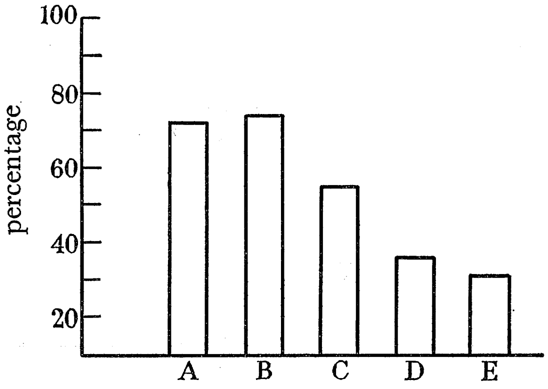

FIGURE 22. Effect of photoperiod during the adult stage on the percentage of *P. rapae* that fly away from the sun, i.e. at an angle between 90° and 270°. A, normal population (1 May to 25 August); B, individuals subjected to 2 days of 17 h photoperiod; C, individuals subjected to 1 day of 12 h photoperiod; D, individuals subjected to 2 days of 12 h photoperiod; E, normal population (27 August to 14 October).

An experiment was carried out to test some of these deductions. From 17 to 21 August collections were made of adult *P. rapae* in the field. The individuals were divided into two batches. One batch was given artificial daylight for an extra $4\frac{1}{2}$ h to give a photoperiod of 17 h, whereas the other batch was covered by black cloth to give a photoperiod of 12 h. These light regimes were continued for 2 days for each batch except for one batch of twenty individuals which was given a photoperiod of 12 h for 1 day only. Except for this last batch, equal numbers of each batch were released on each day to negate any effect of daily variation of wind direction. Half an hour before they were due to be released, the butterflies were placed with a bunch of freshly picked flowers in a large wooden and glass cage in direct sunlight (they had previously been maintained in the shade to avoid unnecessary activity). Once they seemed to be sufficiently active, they were taken out into the middle of a large open field and released. The flight direction across the field was noted for each individual as an angle relative to the sun. The sex of each individual was also recorded.

Eventually 40 individuals were released that had been exposed to a photoperiod of 12 h for 2 days, 40 that had been exposed to a photoperiod of 17 h for 2 days, and 20 that had been exposed to a photoperiod of 12 h for only 1 day. The results are shown in figure 22 and support the deductions made from field observations.

Figure 21 shows that when counts were started on 29 April, *P. rapae* appeared to be just changing its flight direction from south to north, whereas from the photoperiod alone the critical date should have been 19 April. However, the way in which temperature modifies the effects of photoperiod is well known (Danilevskii 1965). It is suggested here that the much lower temperatures of April compared with August raise the critical day length. The change of flight direction from south to north is thus caused to occur later than might have been expected from photoperiod alone.

Figure 21 also illustrates the pattern of migration found in *P. brassicae*. If this species uses the same mechanism as *P. rapae* and if, as shown, its change of direction from north to south occurs about 15 July, then its change from south to north should occur on 1 June. Figure 21 shows, however, that *P. brassicae* flies north throughout May. Therefore it cannot be the adult that is sensitive to photoperiod as in the former species. This is consistent with the observation that the change of flight direction coincides with the emergence of the second generation. It is suggested here that in *P. brassicae* it is the larval stage that is sensitive to photoperiod. If this is so, larvae that develop in short day length would produce adults that fly north and larvae that develop in long day length would produce adults that fly south. This possibility has not yet been tested.

To sum up, it seems likely that because of their different responses to temperature, selection has acted on *P. rapae* to cause it to change its flight direction from north to south at Bristol during the last week of August and on *P. brassicae* to cause it to change its flight direction from north to south in the middle of July. As a result, selection has caused the former species to utilize its appreciation of photoperiod during the adult stage and the latter species to utilize its appreciation of photoperiod during the larval stage.

4. *The problem of the return flight*

Previous workers have believed that for migration to exist there must be a return flight (e.g. Williams 1958). Both *P. rapae* and *P. brassicae* fly north at one time of year and south at another (figure 21). However, it was suggested above that this pattern of migration is the result of selection that at one time of year favours those individuals that fly north and at another time of year those individuals that fly south. It is now necessary to consider whether the southward movement also functions as a return flight, i.e. whether it is equal in distance to the northward flight.

In *P. rapae* the northward flight is at 153° to south. The southward flight, however, is not in exactly the opposite direction at 333° but is instead due south (figure 19). In addition it can be assumed from the relative lengths of time of the two flights that the southward flight is not equal in distance to the northward flight but that there is a total yearly shift of about 70 miles.

P. brassicae flies at 158° for approximately the same length of time that it flies at 338° (figure 21 and table 4). At first sight it would therefore appear that in this species the southward movement does function as a return flight. However, experiments on *P. rapae* have shown that the lower the night temperature the more time is spent in flight the next day. It might therefore be expected that first brood individuals in May and June would fly further per day than second brood individuals present from the end of July to the beginning of September. This effect could also be reinforced by the longer day length during the first brood. This possibility is supported by figures obtained by Roer (1961) with marked individuals of *P. brassicae*. His experiments suggest that on average first brood individuals fly approximately 7·5 km per day, whereas second brood individuals fly approximately 2·5 km per day. Assuming a longevity of 25 days for individuals of both broods, these figures suggest that first brood individuals fly 118 miles to the north from emergence to death, whereas second brood individuals fly only 40 miles to the south. There is therefore a yearly shift to the north of approximately $\frac{78}{2}$, i.e. 39 miles.

If the southward movement of *P. rapae* and *P. brassicae* does not function as a return flight, some explanation is required for the persistence of migration in these two species, especially as previous workers, e.g. Williams (1958) have thought that such a situation was unlikely. It is unlikely that the edge of the range moves northwards at the rate of over 40 miles a year. It is also unlikely that the butterflies could evolve the habit of not flying over the edge of their range. Over most of Europe the edge is not marked by sea, as in the British Isles, but by an isotherm which is not detectable to a butterfly. Because of the nature of the interaction of seasonal and latitudinal variation, even photoperiod cannot be used as a clue by which the position of this isotherm can be judged.

It must therefore be assumed that a result of the evolution of the migratory habit in *P. rapae* and *P. brassicae* is that individuals are lost each year at the edge of the range. If the habit is to persist, the selective disadvantage due to this loss at the edge must be less than the selective advantage of the habit over the rest of the range. It is possible to calculate whether this is so from the results obtained during this work.

Three stages in the evolution of the migratory habit are suggested here. In the first of these stages, in which the butterfly remains at its site of emergence, there will be no loss of individuals at the edge of the range. It is suggested that from this situation many butterflies evolved the way of life shown in figure 2. However, as this way of life must involve the loss of some individuals at the edge of the range, it must be assumed that the extra production of individuals at the centre as a result of this way of life is greater than the loss at the edge. The selective advantage of the migratory habit should therefore be calculated relative to the stage shown in figure 2 and not relative to the stationary stage.

Let us consider 100 individuals at the centre of the range of the species. A percentage (x%) of these 100 individuals fly north and y% fly an equal distance south. Let us also suppose that the next year x% of those that flew north also fly north and y% fly south, and that x% of those that flew south fly north and y% fly south. The distribution of the offspring of these 100 individuals after n years will be given by:

$$x^n; \quad nx^{n-1}y; \quad n\left(\frac{n-1}{2}\right)x^{n-2}y^2; \quad n\left(\frac{n-1}{2}\right)\left(\frac{n-2}{3}\right)x^{n-3}y^3; \ldots\ldots y^n.$$

The distance between each of these groups will be the distance flown north each year plus the distance flown south.

This formula may be used to calculate the loss of individuals from the edge of the range each year. This calculation can be made for the pattern of migration determined by the shape of the temperature/fecundity curve, for the pattern of migration containing a return flight, and for the way of life shown in figure 2. If the relative selective advantage of each pattern is known, it is then possible to calculate which has an overall advantage.

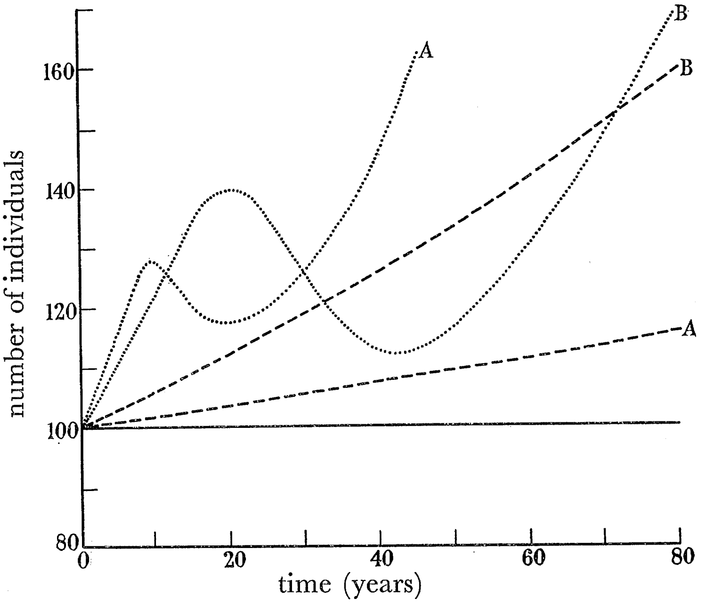

Figure 23. Relative increase with time of number of individuals that possess three different patterns of movement. . . . . ., individuals that possess the pattern of migration determined by the shape of the temperature/fecundity curve; - - - - -, individuals that possess a pattern of migration that contains a return flight; ——, individuals that disperse equally in all directions. A, *P. rapae*; B, *P. brassicae*. In both species the pattern of migration determined by the shape of the temperature/fecundity curve is at the greatest selective advantage even although it is a pattern that does not contain a return flight. The calculation begins for each pattern of movement with 100 individuals at the centre of the range (about 500 miles from the edge).

It can be calculated from figures 3, 10, 13 and 14 that those individuals of *P. rapae* that fly north are at a 7% selective advantage relative to those that fly either east or west. Similarly, those that fly south are at a 7% selective disadvantage. As Britain is at the edge of the range of *P. rapae*, and as figure 21 shows that from May to August 70% fly north and 30% fly south, it can be assumed that individuals that fly north produce offspring of which 30% fly south. The number of individuals that result from 100 individuals of *P. rapae* each year can be calculated to be

$$\frac{107 \times 70}{100} + \frac{93 \times 30}{100},$$

i.e. 103. The yearly selective advantage of the migratory habit in *P. rapae* is therefore 3%. A similar calculation for *P. brassicae* suggests a yearly selective advantage of 2%.

It can be calculated from figures 13 and 14 that if these two species had a return flight, the yearly selective advantage would be much less, i.e. 0·2% for *P. rapae* and 0·6% for *P. brassicae*.

The distance from Northern Ireland to the Alps is about 1000 miles. Although the range of both species extends much further south than this, an estimation of the importance of the remainder of the range is complicated by the presence of the Mediterranean Sea. Therefore it is assumed for the present calculation that the distance from the centre of the range to the edge is about 500 miles.

The following figures are known: the yearly selective advantage of the pattern of migration determined by the shape of the temperature/fecundity curve; the yearly selective advantage of the pattern of migration with a return flight; the yearly shift that results from the migratory habit; the distance from the centre of the range to the edge; and the percentage of individuals that fly north and south. Therefore, if it is assumed that, in a population that distributes randomly, 50% fly north and 50% fly south, it is possible to calculate how many individuals are lost yearly at the edge of the range as a result of the migratory habit. Then, starting at the centre of the range with 100 migrants without a return flight, 100 migrants with a return flight, and 100 non-migrants, it is possible to plot the number of individuals of each against time. This is done for both *P. rapae* and *P. brassicae* in figure 23. In this figure it is assumed that the number of non-migrants remains constant at 100. The other numbers are calculated relative to this constant. This demonstrates that in these two species the selectively most advantageous pattern of migration is that which appears to be determined by the shape of the temperature/fecundity curve (figure 7). This is so even although it is a pattern that does not include a return flight.

One further point arises from this calculation. If 100% of the offspring possessed the selectively most advantageous pattern of migration, the habit would quickly die out. However, if only 50% of the offspring possessed this pattern, the habit would have no selective advantage, e.g.

$$\frac{107\times 50}{100}+\frac{93\times 50}{100}=100.$$

Therefore it would be expected that in both *P. rapae* and *P. brassicae* selection would favour those individuals which produce offspring of which about 75% fly north and then south and of which about 25% fly south and then north. Figure 21 shows that this is in good agreement with the ratio observed in the field.

However, in those species in which selection happens to favour a southward flight equal and opposite to a northward flight selection might also be expected to favour those individuals which produce offspring 100% of which possess the most selectively advantageous pattern of migration. It is suggested here that this could be the situation found in *Danaus plexippus* (Urquhart 1960).

The increase in number of individuals of *P. brassicae* was shown in figure 23 for a ratio of 70 individuals that do possess the favoured pattern of migration to 30 that do not. It was shown that after a period of about 70 years, the pattern of migration which contained a return flight was at a disadvantage relative to the pattern favoured by the form of the temperature/fecundity curve. If this calculation is repeated for a ratio of 100 to 0 for the pattern containing the return flight, it is found that the pattern still becomes a disadvantage after about 200 years.

Discussion

The way in which the theory of migration suggested here conflicts with the previously accepted theory can now be discussed.

There were probably three main reasons for the origin of the concept that populations of migratory species consist partly of residents and partly of migrants. First, the resident-migrant concept fitted in with the suggestion that migration is the result of overcrowding. Secondly, the observation that flight direction was often distributed about a certain peak fitted in with the picture of a swarm of migrants flying in a constant direction through a resident community, the individuals of which were engaged on trivial flights in all directions. Finally, there could have been a failure to distinguish between the status of a species relative to a country and the status of a species relative to itself. For instance, in Britain *Colias croceus* is only a migrant, whereas *Pieris brassicae* is both a resident and a migrant. This is not the same as describing *Colias croceus* as a migrant and *Pieris brassicae* as both a resident and a migrant.

However, it is suggested here that in *P. rapae* and *P. brassicae* selection has favoured a pattern of migration that only superficially resembles the resident-migrant situation. As the selectively most advantageous pattern of migration is one that does not contain a return flight, selection has favoured that not all individuals should fly in the same direction but that their flight directions should be distributed about a certain peak (figure 16).

One of the consequences of the resident-migrant concept was that it interfered with the demonstration that the sun was being used for orientation. For instance, if butterflies had been observed flying north-west in the morning and north-east in the afternoon, it would have been considered that two different swarms were involved with two different points of origin. Each swarm was considered to keep a constant geographical direction throughout the day.

It now seems likely that many species of butterflies, at least in temperate regions, will be found to orientate by means of the sun. However, there are problems to this method of orientation at some times of the day and season in the tropics (Williams 1958). How prohibitive these are can only be decided by investigation. Certainly there is a large part of the year when the sun can be used as an environmental clue for orientation.

The idea of emigration, transmigration, and immigration is also not strictly compatible with the picture of migration outlined here. In *Pieris* the situation appears to be one of emergence, migration, and death. This would also be expected to be true of those species with a period of sexual immaturity in the adult stage, e.g. *Vanessa atalanta*. The only difference seems to be that in these species oviposition is restricted to the last part of the migration and thus gives the appearance of 'settling-down'. As with the resident-migrant concept, therefore, the terms 'emigration' and 'immigration' are perhaps only valid relative to a country.

The association between sexual immaturity and migration (Johnson 1966) obviously does not apply to *Pieris* and seems unlikely to be of general importance in butterfly migration. Although many butterflies do migrate while they are sexually immature, there is no reason to suppose that the two are invariably related. The only time that the two seem likely to interact will be when the selective advantage in migrating further results in an even greater extension of the pre-oviposition period.

One of the problems that Johnson experienced with his theory was that it was difficult to explain migration in males on the same basis. Although throughout most of this present paper reference has been made mainly to females, the same arguments can be applied to males. Whereas a female distributes eggs along her flight path, a male distributes sperm. The result in terms of selection is the same.

The occasional occurrence of giant swarms of butterflies and the suggestion that migration was the result of overcrowding were probably the main reasons for the idea that migrations have a point of origin. However, if migration is considered to be an individual response as suggested here, the midsummer movement of *P. brassicae* cannot 'originate' in southern Scandinavia (Williams 1958). Instead it seems that throughout Europe 70% of all individuals begin to fly south after they emerge and thus give the appearance of a movement that originates in the area of the Baltic basin. The giant swarms seem likely to be the chance result of mass emergence rather than the result of an organised aggregation of adults. Further, if migration has evolved in the way outlined, individuals cannot be 'caught-up' in swarms of their own or other species.

Finally, previous considerations of the problem of the return flight have been of the form: 'can migration exist if there is no return flight?' In this paper the problem was approached differently by a consideration at the species level of the relative selective advantage of migration with and without a return flight. It was shown that in *P. rapae* and *P. brassicae* a pattern of migration which does not contain a return flight is at the greatest selective advantage. However, there seems to be no reason why this should be so in all species.

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