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Source: *Journal of Animal Ecology*, Vol. 49, No. 2 (Jun., 1980), pp. 629-642

Published by: British Ecological Society

Stable URL: <http://www.jstor.org/stable/4268>

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LONG-DISTANCE MOVEMENT OF *PIERIS RAPAE*

By

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SUMMARY

(1) Adult female butterflies were bred on artificial diet containing dye so that they laid coloured eggs, and the distribution of eggs was used as an amplifier for the distribution of adults.

(2) The butterflies were released in a 1 km square grid of cabbage plants. The observed pattern of coloured eggs agrees with independent predictions based on Jones's (1977) rules for short-distance movement.

(3) Each butterfly flies about 700 m per day over the ground, and ends the day 250–600 m from where she started.

(4) Each butterfly maintains a preferred direction throughout one day, but the direction changes unpredictably from day to day.

(5) The butterflies in these experiments laid only 10% of their daily complement of eggs, because they could not find enough host plants.

(6) This method of studying animal movement overcomes several flaws inherent in previous methods, but is restricted to distances of a few km at most.

INTRODUCTION

This paper considers whether Jones's (1977) rules for short-distance movement of the cabbage white butterfly can be extrapolated to predict movements over several days. If so, we have a new method for studying animal movement.

The most usual method of studying movement involves the release of marked animals and their recapture by traps or shooting. Used in isolation this method has four flaws.

(1) We have to assume that the few percent of animals recovered (e.g. Finch & Stinner 1975; Parsons & Duncan 1978; Rogers 1977) are typical of the vast majority which are not.

(2) The distribution of traps biases the geographical pattern of recoveries.

(3) We cannot deduce, from the pattern of recoveries, the rules of movement which gave rise to that pattern, and which specify different patterns in different circumstances (Jones 1977).

(4) Animals move about in order to find something, or to avoid something, so we cannot understand the movement process unless we know what the animals are seeking and can measure their success in finding it.

Alternative methods may avoid some, but not all, these problems. Radio tracking, for example, avoids the first three but not the fourth, since it tells us where the animals are but not what they are doing. Radar tracking of flying insects and birds is useful but generally restricted to mass migration. Suction trap catches also give much useful information (e.g. Taylor & Taylor 1977) but are not completely satisfactory

because we do not know certainly where the insects come from, nor whether, in any given case, the trapped insects represent successful migrants or lost souls accidentally displaced and doomed to extinction.

The method used here is the second stage of a two-stage analysis. In the first stage (Jones 1977), direct observation of butterfly behaviour was used to deduce some rules of movement and egg-laying over short distances (less than 100 m) and short intervals of time; these rules were then incorporated into a simulation model which could predict how eggs were distributed within these small areas. Now, in the second stage, we extrapolate this model to produce predictions of how a group of butterflies released within a much larger grid of widely spaced host plants will distribute their eggs over a period of several days, and compare observation with prediction. This method avoids all the difficulties mentioned above. The recovery fraction, i.e. that fraction of the individuals released which contribute to the recoveries, is acceptably high. We automatically allow for the effect of trap (host plant) position in generating predictions, and we are using the releases to test our understanding of the rules of movement rather than to try and deduce them.

In effect, the animals' own reproduction is used as an amplifier.

METHODS

To perform this experiment, we needed to be able to distinguish between eggs laid by released butterflies and those laid by wild butterflies. We used the technique developed and used for similar purposes by Parker & Pinnell (1972), of incorporating a dye into the larval diet so that the resultant females laid coloured eggs. Caged wild females laid eggs on potted cabbage plants. When the larvae had hatched and reached early second instar they were transferred to artificial diet containing Sudan IV or Sudan Black dyes—when adult, the females then laid pink or grey eggs which are easily distinguished from the normal whitish eggs. When the animals pupated, they were weighed and divided into large (> 150 mg) and small (< 150 mg) groups. The average weight of the large individuals was 158 mg, of small, 130 mg. Each release included large butterflies of one colour and small butterflies of the other, to see whether size influenced movement patterns. The colours of large and small alternated in successive releases. The adults were kept in large cages with host plants for oviposition and honey solution for food until they were released. Small samples of the adult butterflies were retained in laboratory cages to check their time-pattern of fecundity; they behaved like wild butterflies.

All but one of the releases were made when the butterflies were six days old, i.e. approaching their maximum rate of lay. To see whether older butterflies might show different movement patterns, one release of 10-day-old butterflies was made.

The butterflies were released near the centre of a 1 km^2 grid of cabbage plants. The plants, about 30 cm high with 7–9 leaves, were grown in pots and replaced daily. Several different grid arrangements were used. The basic arrangement was that shown in Fig. 1(a), i.e. with 100 m between adjacent plants except for a 7×7 centre section with plants 50 m apart. Four releases were made onto this grid arrangement. Two releases were made onto the same area with a grid lacking the 7×7 centre section on the first day (NC grids), and two were made onto the basic grid with an extra 40 plants at 2 m intervals at the release point. One release was made in a different area on a completely different grid arrangement (Fig. 1(b) NG grid).

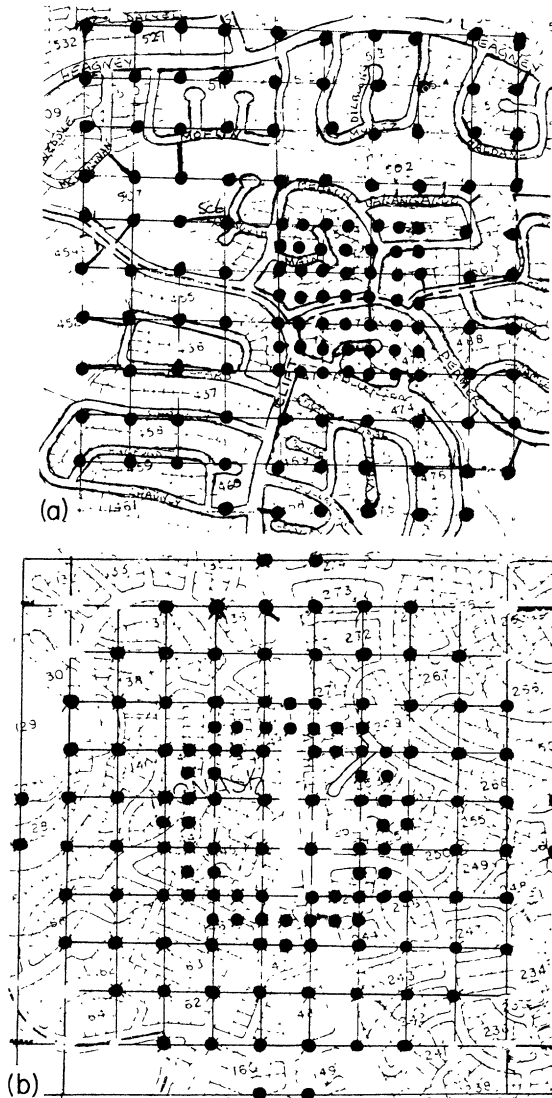


FIG. 1. (a) regular grid; (b) new grid. Distances between adjacent plants, 50 or 100 m.

The grid for all but the last-mentioned release was laid out on a Canberra suburb under construction on a gentle north-south slope, at the site envisaged by Shute (1953): the road network is complete but no houses have been built. The entire area had many wild flowers, notably thistles *Carthamus lanatus* and *Centaurea nigra*, on which the butterflies fed. At the time of the first few releases, there was some mustard (*Hirschfeldia incana* (L.)) growing near one edge of the grid, but this quickly dried out so that the potted cabbages were the only available hosts. The eggs laid each day on each plant were counted after the plants had been returned to the laboratory. Plants were occasionally lost to kangaroos, rabbits, and passing motorists, and there was some damage from grasshoppers, but losses were surprisingly light.

depends, not only on butterfly movement, but on the numbers of eggs laid when a plant is detected. When a butterfly discovers a solitary plant, she lays on it a number of eggs which follows a negative binomial distribution: the variance is three times the mean, and the mean depends on the number of mature eggs which the butterfly has ready to lay (Jones 1977). So the number of eggs laid on one plant depends on the number which the butterfly has previously laid on other plants. All these computations are of the 'Monte Carlo' type, using pseudorandom numbers generated by the computer.

PATTERN OF MOVEMENT

First day's movement

Figure 2 shows a computer prediction of the pattern of eggs laid on the basic grid on the first day after the butterflies are released. Since the pattern is generated with random numbers, a different set of random numbers would give a different pattern in detail: it is the overall distribution and density of eggs that matters. Figure 3 shows the actual field record for one release, which is entirely typical of the series. It agrees very well, both in pattern and average numbers, with the completely independent prediction of Fig. 2. The short-distance movement can indeed be extrapolated, at least for 1 day. The next four paragraphs will examine separate aspects of this daily movement.

The most remarkable feature of short-distance movement is the high degree of directionality of Australian butterflies (Jones 1977). Different butterflies have different

*	*	*	*	5	*	*	*	*	*			
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				3	14	3	2	20	5	24		
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				2	1	*	5	*	1	8		
*	*	*	*	3	2	*	37	*	*	*	*	*
*	*	*	*	5	*	*	*	*	*	*	*	*
*	*	*	*	*	*	*	*	6	*	*	*	*
			*	1	*	*	*	*	*	*		

FIG. 3. Observed field distribution of coloured eggs from 165 butterflies released at R, 3 January 1979. Mean distance from R to eggs, 147 m; r.m.s. distance, 179 m.

preferred directions, but each individual flies with sufficient directionality to keep her well within an angle of 45° over a distance of 1 km. When this directionality is removed, so that the movement becomes a pure random walk, the computer predicts that no eggs will be laid outside the centre section of the grid (Fig. 4). Even if the distance flown by each butterfly is increased unreasonably, to carry the random walk outside the centre section, the egg distribution is quite unrealistic (Fig. 5). The field results therefore require the butterflies to maintain their directionality throughout the daily period of egg-laying.

Of all the parameters used in the computer prediction, only one is poorly estimated: the distance (700 m) flown over the ground by a butterfly in one day. Originally estimated from observations of flight speed, duration of rests and the times of day when females were observed flying, this value has been checked in two ways. The number of butterflies which reach the edge of the grid on the first day is acutely sensitive to the distance-flown-per-day. The computer predicts that with an overground flight distance of 700 m, most of the butterflies end the first day in a ring between 250 and 600 m from the release point, i.e. mostly just inside the grid. If the distance flown were greater, the ring would spread outside the grid and the number of butterflies crossing the edge of the grid would greatly increase. To test this, on one occasion we put 90 extra plants at 5 m intervals along the middle part of the northern edge of the grid. The computer predicts that, when the average distance flown over the ground is 700 m, eight of these 90 plants should receive coloured eggs; we got seven.

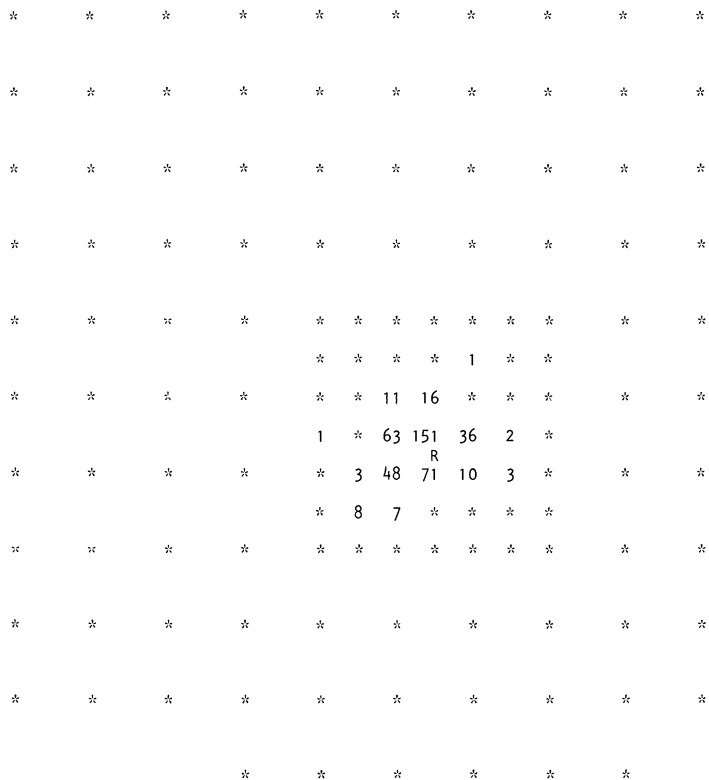


FIG. 4. Computer prediction, as Fig. 2 but undirected random walk. Mean distance from R to eggs, 42 m: r.m.s. distance, 50 m.

A second check on the distance flown is given by the release on 13 February 1979. Heavy cloud prevented flight before 10.00 hours and high winds after 14.00 hours; in between, flight conditions were excellent. The distribution of eggs is abnormal, being concentrated in the centre of the grid. According to the computer, it corresponds to a flight distance of 400 m (Fig. 10). If it takes butterflies 4 h to fly 400 m it will take them 7 h to fly 700 m. This agrees with the general observation that egg-laying females are on the wing between 09.00 hours and 16.00 hours but rarely outside those hours.

The computer model indicates that the first-day recovery fraction is 50%, i.e. 50% of the butterflies lay at least one egg on at least one plant. The other 50% either do not find a plant, or do not lay an egg on it. The recovery fraction could easily be increased by putting out more plants. There is no point in doing so. It is a matter of chance whether any given butterfly finds a plant or not: so the 50% represented in the field samples is a random sample of the butterflies released. The close agreement between observation and prediction, therefore requires that the remaining 50% of butterflies, which chance to be unrecorded, must still behave in the same way. For if 50% behaved in some radically different way, there would be a grave discrepancy between prediction and observation. So the 50% recovery is large enough to assure us that all, or nearly all, females must behave as predicted. But we know nothing of individual variations in distance flown, or intensity of directionality.

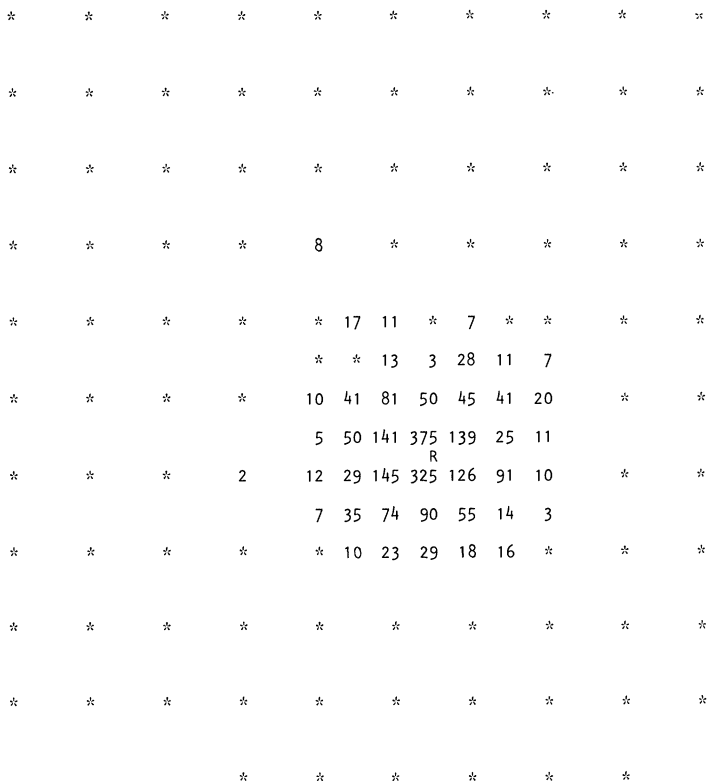


FIG. 5. As Fig. 4, but overground flight distance increased to 3000 m. Mean distance from R to eggs, 72 m; r.m.s. distance, 86 m.

Second day

If each butterfly continued to move in the same direction on the second day, there would be none left in the centre of the grid on the second day. This is not so (Fig. 6). We therefore used the method of Jones (1977) to compare the directions adopted by individual butterflies on successive days, in a Canberra market garden. Figure 7 shows that there is no correlation, i.e. each butterfly adopts a new direction each day. We do not know how each day's direction is decided. In the original short-distance observations made in Canberra in 1972, there are more butterflies with preferred directions North than in any other direction. But in similar observations in 1975, the preferred directions are spread uniformly around the compass. Similarly in the grid experiments: on seven release days the eggs are spread in all directions, as in Fig. 3, but on two occasions there is a large excess of eggs in the northern sector. The mechanism that decides daily directions, therefore, usually produces a uniform distribution of individual directions, but sometimes a northwards bias.

This whole picture—of a fairly strongly marked direction on any one day, but different directions on successive days—may be checked by the rate at which butterflies leave the grid from day to day. A simple simulation predicts that whereas only 16% should leave the grid on the first day, more than 50% should leave on the second, and the remainder at a diminishing rate thereafter. The daily total numbers of eggs laid conform well enough to that prediction. But the comparison cannot be very precise. Those butterflies who leave the grid during the day, lay fewer eggs than those who remain all day. It would therefore

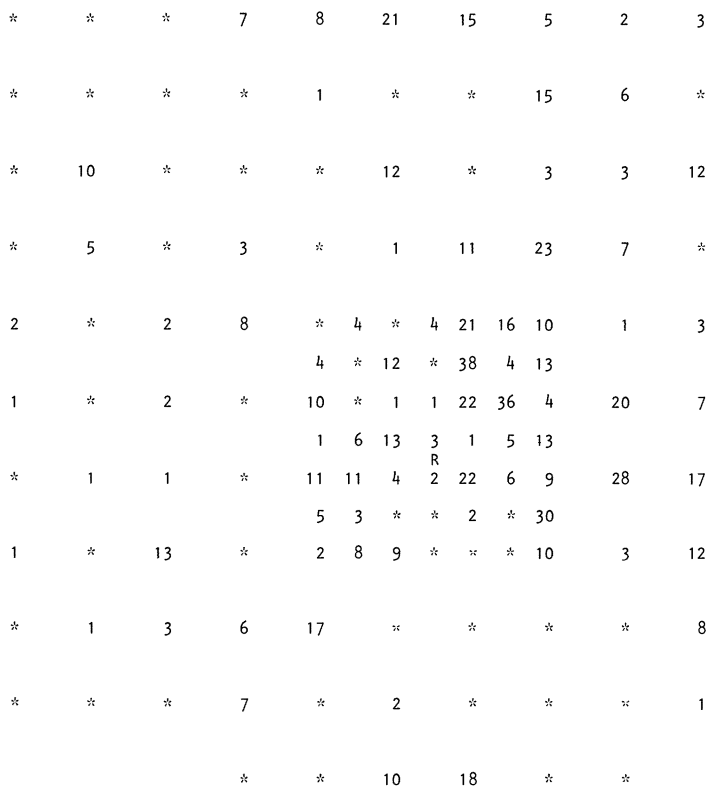


FIG. 6. Observed field distribution of coloured eggs laid on second day, 4 January, after release shown in Fig. 3. Mean distance from R to eggs, 270 m: r.m.s. distance, 314 m.

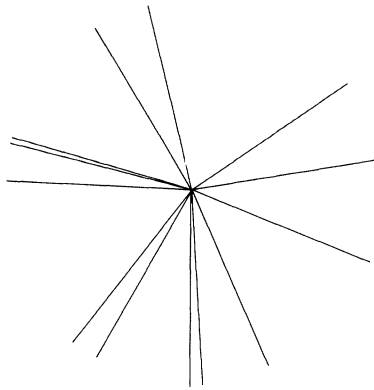


FIG. 7. Distribution of angles between preferred directions on successive days. If the direction of flight on the first day is taken to be towards the top of the figure, the various lines show the preferred directions on the second day. The data exclude any individuals whose preferred directions were not clearly recorded on both days.

take a very complex calculation to predict exact daily totals of eggs. That calculation has not been made, because it would be acutely sensitive to the unknown individual variation in distance flown, and to the effects of temperature and numbers of mature eggs, mentioned below (Fig. 9).

Some checks

This section describes several checks on the methodology. First, there might be something peculiar about the place where we did the trials. The close agreement between observation and prediction makes that unlikely, but we checked with a second grid set in a north-south valley on a neighbouring suburb. The new grid was designed (Fig. 1(b)) to give the most accurate possible estimates of the distribution of directionalities. The release on this grid gave results closely similar to those on the old grid, and the north-south valley did not constrain the butterflies to fly north. The time taken to set the plants out on this grid was almost double that on the old grid, and so the new grid was not used again.

Our first-generation butterflies, reared on artificial diet, might behave differently from wild ones. This too is contradicted by the agreement between observation and prediction. As a check, we released butterflies, reared on cabbage plants in the laboratory, at a time when wild butterflies were scarce. These butterflies laid white eggs. On the day before the release, we made counts to estimate the background density of white eggs being laid by wild butterflies. Allowing for that background, there is no difference between white and coloured distribution patterns.

When we find (say) six eggs on one plant, we do not know whether they were laid by one, two or three butterflies. Consequently the analysis examines the distribution of eggs, not of butterflies. That distribution depends on both butterfly movement, and the number of eggs laid when a plant is discovered. Both are predicted from the short-range behaviour (Jones 1977; Jones & Ives 1979). If the numbers of eggs-laid-per-plant are wrong, the picture of movement will be distorted. We have checked the predicted numbers of eggs laid by single butterflies on each plant, by comparing them with the numbers of coloured eggs actually found on individual plants when only half a dozen butterflies of one particular colour were released.

The data from one release cover 3–4 days, or about one-sixth of the adult life span. When, on one release, 6-day-olds of one colour were combined with 10-day-olds of another, there was no difference between the distribution patterns.

As noted previously, in each release, large butterflies laid eggs of one colour, while small butterflies laid eggs of the other. As in the laboratory, the large butterflies laid on average 20% more eggs than the small, but there were no other consistent differences between them. The two are plotted separately on Figs 9–11, but corrected where necessary for this 20% differential.

Release densities varied between 80 and 240 females. Within that range, there is no effect of density (apart from increasing *pro rata* the total numbers of eggs laid).

Proportion of eggs laid

The picture so far is of individuals flying across country with considerable directionality, and laying eggs on those host plants which they chance to find. The directionality greatly enhances both the probability that new plants will be discovered, and the dispersal of eggs (Figs 2–5). Each butterfly chooses a different preferred direction on successive days, so that she is not continuously translated over distances of many km. On the grid, suitable host plants are sparse. Not only do 50% of the released animals lay no eggs on the first day, but the average number of eggs laid per butterfly is only 10% of the mature eggs ready for laying: for sub-samples of butterflies, retained in laboratory cages, lay ten times as many eggs per individual as those released in the field. The butterflies do *not* lay large numbers of eggs on the first plants encountered, even when host plants are scarce.

TEMPERATURE AND PLANT SPACING

During the Canberra summer, anticyclones produce long periods of fine, warm weather. Intervening troughs bring clouds and rain for a day or two. The nine releases were all made in anticyclonic conditions. Maximum temperatures on release days ranged from 22 to 38 °C.

Butterflies do not lay in cold, cloudy or windy conditions. The daily number of eggs laid in field cages increases with temperature (Gossard & Jones 1977). The numbers of wild white eggs laid on the grid varied in the same way: fewer eggs were laid on cool days than on adjacent warm days, and high temperatures up to 38 °C did not inhibit laying, except when accompanied by strong winds. Figure 8 plots the ratio of white eggs laid on the second day of each release: those on the first day, against temperature. As expected, there is no clear effect of temperature, because temperatures on the first day were usually similar to those on the second: but wind and cloud on the second day depress the ratio as expected, and one value is inflated in the manner described by Gossard & Jones (1977): when egg-laying is inhibited by cool weather on the first day, the butterflies have more eggs to lay on the next. The remaining four ratios, obtained in excellent conditions, are all close to unity. There was therefore no sharp change in numbers of wild butterflies from one day to the next, i.e. immigrants roughly equalled emigrants: these white ratios record the effects of environmental conditions, and are used as such to compute Fig. 9.

Figure 9 shows the equivalent ratios for coloured eggs. These ratios result from (1) the rate at which the experimental butterflies left the grid, (2) the environmental effects in Fig. 8. They have therefore been divided by the corresponding ratios for white eggs

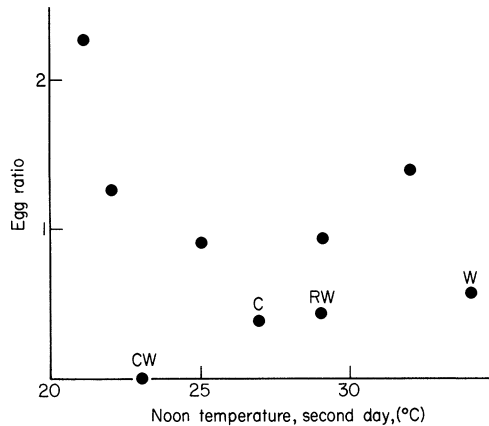


FIG. 8. Ratios of second day: first day totals of white eggs laid on the grid during the first two days of each release, plotted against noon temperatures on the second day. C, second day cloudy; W, second day windy; R, ratio diluted by test release on first day of laboratory-bred butterflies laying white eggs.

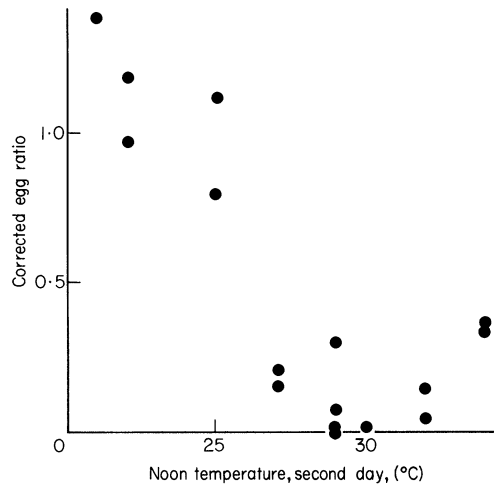


FIG. 9. As Fig. 8, but coloured eggs laid by experimental butterflies. Each ratio has been divided by the corresponding ratio for white eggs (Fig. 8) to correct for environmental disturbances.

(Fig. 8) to correct for those environmental effects. There is a clear residual effect of temperature, so that butterflies leave the grid faster at high temperatures. (The loss of butterflies is unlikely to be due to mortality, for Australian butterflies survive, and lay well in the laboratory up to 40 °C.) The ratio in Fig. 9 is unity at temperatures below 25 °C, but this does not mean that all butterflies were staying in the grid. The coloured butterflies could lay all their eggs when kept in the laboratory before release, but laid only 10% of their mature eggs on the first day of release. Consequently they had 70% more eggs to lay on the second day (Gossard & Jones 1977), but the same is not true of

the wild butterflies (except when weather conditions prevented laying on the first day, Fig. 8). Therefore, if no butterflies were leaving the grid, the ratio in Fig. 9 would be 1.7.

Figure 9 implies that butterflies travel further in warm weather than in cool. No such effect appears in the first-day data. Figure 10 is computed from the average distances from the release point to coloured eggs, for each release day. The computer shows, for any given grid pattern, an almost linear relationship between average distance flown per butterfly, and average distance to eggs. But the relationship differs for different grid patterns, and these differences have been eliminated by converting the average-distance-to-eggs to the corresponding average-distance-flown. There is a possible explanation for the lack of any apparent temperature effect: at temperatures above 25 °C, some cabbage plants began to wilt between 13.00 and 15.00 hours, and wilting inhibits egg-laying. On such days, therefore, the butterflies would stop laying early, but would by then have travelled just as far as they normally do on cooler days, when laying continues until 16.00 hours. Another possibility is that warm evenings permit the butterflies to travel further in search of nectar, after they stop laying eggs.

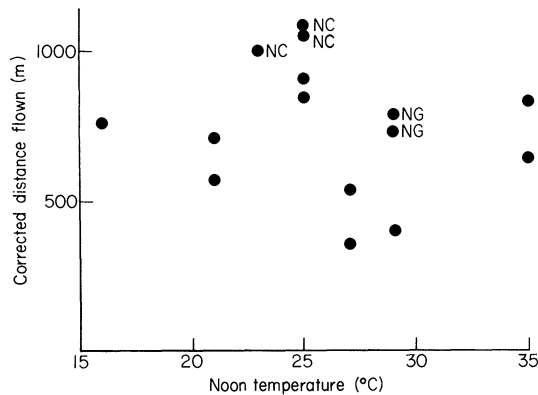


FIG. 10. Estimated average overground distance flown by experimental butterflies on first day of each release, plotted against noon temperatures. NC, 7 × 7 centre of grid absent; NG, new grid (Fig. 1(b)).

Nor is there any firm effect of temperature on the number of eggs laid per butterfly (Fig. 11). The data in Fig. 11 have once again been corrected for differences between grid patterns. Even after this correction, the two releases marked NC, when the 7 × 7 centre patch of the grid was empty, show unusually low numbers of eggs; as does the release on the new grid (NG), which has an empty centre surrounded by a dense ring of plants (Fig. 1(b)). There is therefore some suggestion that the absence of host plants, near the release point, makes the butterflies less likely to lay on more distant plants. There is a corresponding effect of NC, but not NG, on distance flown (Fig. 10). On the other hand, on the two occasions when butterflies were provided with an extra plot of forty plants at the release point (in addition to the regular grid), they laid many eggs on the extra plot before dispersing to lay as usual over the grid. But both these releases were inconclusive, to the extent that on both occasions, bad weather intervened before the second day, so that we have no estimate of day-to-day dispersal from the extra plot in normal conditions. Many butterflies did leave the extra plot within a few hours of release, since many coloured eggs were laid over the grid itself. This contrasts strongly with Canadian experience. We

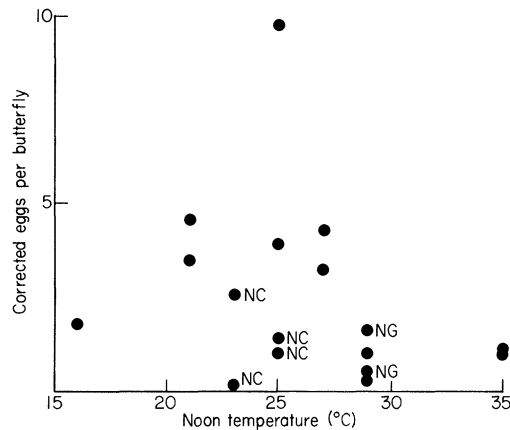


FIG. 11. Average eggs laid per experimental butterfly on first day of each release, corrected for pupal weights and grid patterns, and plotted against noon temperatures. cf. Fig. 10.

made one release of fifty 'coloured' female butterflies on a similar grid at Vancouver, complete with an extra plot of fifty plants at the release point. On the first day after release, more than five times as many eggs were laid on the central plot by each butterfly than were laid by Australian butterflies, and even after two weeks, some coloured eggs were still being laid on the central plot. Many fewer eggs were recovered from the outer grid than in Australia, but while coloured eggs disappeared from the Australian grids by about 4 days from the release, in Vancouver, the numbers of eggs in the outer grid remained about the same for more than a week. These differences support the short-distance observation that Vancouver butterflies are less directional, and more strongly attracted to host plants, than Australians (Jones 1977).

CONCLUSION

On any one day, the movement of Australian butterflies is highly directional but the direction itself has no ecological relevance; it is merely a mechanism for covering more ground, confirming exactly the interpretation of orientation in *Plusia gamma* made by Taylor, French & Macaulay (1973). The distribution of eggs is consequently more broad than that expected from a pure random walk (Figs 2–5). If a butterfly chances not to find enough host plants in one day, she does not lay that day's full complement of eggs, but retains some for the next day. Day-to-day movement is a random walk with a step-length of (on fine days) about 450 m per day. Consequently, a female who lives for 16 days will on average die 2 km from her birthplace: our study covers a significant part of her total movement.

While this is a respectable rate of travel, and some females may go several times as far, it is not nearly fast enough to account for the rate at which *P. rapae* originally spread through Australia (summarized by Peters 1970). From an original appearance in Melbourne in 1939, the butterflies had reached the West Australian coast in 3 years, i.e. at most, 25 generations—despite a ban on the importation of brassicas to W.A. Many insect species have a pre-reproductive migratory phase, but *P. rapae* females do not—they generally begin to lay on the day they emerge. We are inclined to believe, therefore, that

the spread of *P. rapae* in Australia occurred with human help. When larvae are full-grown, they leave their host plant and find a vertical or overhanging surface on which to pupate. Consequently, vehicles used to transport brassica crops may carry pupae and release adults at whatever place they happen to be when the adults emerge weeks (or months if the pupae are in diapause) later.

By contrast, males patrol a 'home range' and mate with females who mature within that range (W. G. Wellington, personal communication). So a male does not mate with females produced at the same place and time, but with the progeny of females who enter his 'home range'.

This method of studying long-distance movement avoids the inadequacies of previous methods. It is the most rigorous method possible, short of following each animal cross-country—precluded in this case by the number of observers required; by the difficulty of recording current position accurately; and by some very prickly stands of thistles. The greatest advantage is that the recovery rate can be made as close to 100% as may be desired. But the method cannot be used to study migrations over distances of more than a few km; it is restricted to species whose local movements can be observed and analysed; it has been greatly simplified by the knowledge that female butterflies search for two things only—nectar and host plants. The method is therefore restricted to a fairly narrow range of species. Within these limitations, the most difficult aspect of population ecology—animal movement—can indeed be studied rigorously. We need not rely on untested assumptions and incomplete evidence.

ACKNOWLEDGMENTS

We are much indebted to Dr D. F. Waterhouse, F.R.S. and other members of C.S.I.R.O. Entomology Division for use of their research facilities: and to Department of Capital Territory for use of their suburb. The study received financial support from an N.R.C. grant to N.G., and an A.R.G.C. grant to R.J. Ms E. Scheermeyer helped grow potted cabbages, and Mr T. Gossard helped with the Canadian release.

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(Received 7 September 1979)