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MOVEMENT PATTERNS AND EGG DISTRIBUTION IN CABBAGE BUTTERFLIES

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INTRODUCTION

Most animals move about to seek food or mates, to avoid predation or for some other reason. Whatever their objectives in moving, their success in achieving those objectives affects their survival or reproductive rate. Thus the population dynamics of a species may depend on its movement patterns; one cannot be completely understood without the other.

To study movement in the field, it is not enough to release animals and observe their positions at some later time, since any distribution of animals may be generated by a variety of movement patterns which would have produced very diverse spatial distributions in other circumstances (see Appendix). To predict the outcomes of movement in all the environments which a species normally encounters, the rules of movement for individual animals must be known, and to understand the biological significance of those rules, it is necessary to know how the resultant distributions affect survival and reproduction.

This paper describes movement and egg-laying of female cabbage white butterflies, *Pieris rapae* L., in Canada and Australia. *P. rapae* was chosen because individual females are conspicuous and easily tracked; their objectives (oviposition sites and nectar) are known; their success in finding those objectives can be observed; and the fate of different distributions and densities of eggs and larvae can be studied in the field.

The behavioural descriptions are built into simulation models. These solve two methodological problems: defining what measurements will adequately describe the behaviour, and putting those measurements together to predict searching success in any particular circumstances. If the behaviour model is realistic, the parameters define its important properties, and the model itself becomes a tool to predict and explain egg distributions.

METHODS

Cabbage butterflies lay eggs singly on the foliage of crucifers, and the caterpillars feed there for five instars. At the end of the last instar, the larvae leave the plant to pupate. When the female emerges, she generally mates on the first day and begins to lay on the second or third day. There are several generations each year, the number depending on the climate. *Pieris rapae* overwinter as diapausing pupae.

Mature females moving from plant to plant were watched in Canberra (Australia) and Vancouver (Canada). Several species and various ages and sizes of crucifer were used to examine host preferences. These observations were incorporated in simulation models. Egg counts on Vancouver field plots (not used for watching butterflies), as well

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as data in the literature, tested the models' ability to generate realistic egg distributions, and the models were then used to examine the egg distributions and densities generated on different distributions and densities of host.

Observations of butterfly movement

Five different plant patterns were used, three in both Canada and Australia:

- (a) a square grid with hosts at 1 m intervals (both places);
- (b) hosts in groups of 4, with 3 m between adjacent groups, and 1 m between plants within a group (both);
- (c) a square grid with hosts at 4 m intervals (Australia only);
- (d) a square grid with hosts at 10 m intervals (Canada only);
- (e) two lines of hosts in groups of 3 or 4, with 20 m between groups (both).

Observations began in Australia in December 1972, on a 20 × 40 m cabbage patch with large plants in the first three patterns. The butterflies were wild ones which flew into the patch. Plant-to-plant moves were recorded by Cartesian co-ordinates. The record for each butterfly began near the centre of the patch and continued until she reached the edge. Since many females were always present, it was not possible to tell whether a particular butterfly laid an egg during a particular visit to a plant. The 1 m and 4 m records were used to build the model and estimate parameter values; the grouped-

Table 1. *Characteristics of kale plants used in 1973 Vancouver flight experiments*

Type	Mean no. leaves per plant	Mean leaf length (cm)	Weeks since seedling transplanted
(1) Large old	15.4	17.6	9-14
(2) Medium old	10.4	8.4	9-14
(3) Medium medium	9.3	9.2	6-10
(4) Medium young	9.5	10.0	4-8
(5) Small very young	5.1	4.3	less than 4

plant records were used as a check. A second set of data from closely-spaced plants was collected in a Canberra market garden in February 1975, on three plots of cauliflower, each 20 × 90 m, which had been planted as seedlings three, seven and nine weeks previously. The seven- and nine-week-old plants were of similar size and their records are analysed together; the three-week-old plants were much smaller and are analysed separately. Few butterflies were present, so it was possible to examine the leaves visited by each for eggs.

In Vancouver, observations on closely-spaced plants (patterns (a) and (b)) were made using kale grown in pots. Five types were used (Table 1). Types 2 and 3 were grown in pots small enough to prevent them growing any bigger than type 4. Cut flowers inserted in each pot provided feeding sites. Both wild and laboratory-reared butterflies were watched; their records are indistinguishable from each other and are analysed together. There were few wild butterflies, so plants visited by each female could be checked for eggs.

The 10 m and 20 m plant patterns used cabbage, kale, and radish in large pots (in Australia, brussels sprouts were also used). The 20 m records were used for parameter estimation, the 10 m for checks. In Canada, each butterfly was watched until she left the field and could not be recovered (about one-quarter of the trials); or until she had

failed to lay an egg, despite having located and landed on hosts, for at least half an hour. Thus one or two animals were watched each day, each being followed through her whole day's egg-laying. The behaviour of the Australian butterflies did not permit this procedure; they were more inclined to leave the field, and to fly away if caught and released again. So, as a female left the field, she was, if possible, caught and dissected to count the number of mature (i.e. chorionated) eggs still present.

Egg distributions in field plots in Vancouver

In 1973, kale plants of various ages were planted in a 6 × 19 m plot at 1 m spacing. As the oldest plants reached fifteen weeks of age, they were replaced with young plants, so that the plot always contained plants of comparable age to those in the flight experiments. I recorded the numbers of eggs laid on the plants through the season. In 1974, to test species preferences and the effects of plant spacing, small plots of radish, kale, and cabbage were planted. The radish and kale were each planted in two contiguous plots; one with 2 m between plants and the other 1 m. Only one plot of cabbage was planted, at 1 m spacing. Each plot contained nine plants. Eggs were again counted throughout the season.

ANALYSIS AND SIMULATION OF BUTTERFLY MOVEMENT

Tables 2–5 summarize all the behavioural observations made during the study. r in the tables is a measure of 'directionality' (Batschelet 1965), estimated from the distributions of movement directions, or of the angles between successive moves. It may take values from 1, when all angles in the distribution are identical, to 0, when the distribution is uniform over 360°. For the distribution of angles between successive moves, r is multiplied by the cosine of the mean angle turned; r (angle) will then be negative (to -1) if the butterfly's average turn is greater than 90°. 'Zero moves' occurred when a female took flight, then returned to the same plant. 'Unit moves' are less than 1.5 m long (i.e. the distance between diagonally adjacent hosts at the closest spacing); 'multiple moves' are longer.

Table 2. *Flight patterns of Australian butterflies among closely-spaced plants, December 1972*

Plant pattern	I (1 m spacing)		II (groups of 4, 3 m apart)		III (4 m spacing)	
	Data	Model	Data	Model	Data	Model
Mean length of non-zero flights	1.39	1.38	2.45	2.38	4.80	5.16
Variance	0.67	0.72	2.37	3.39	2.19	5.27
Proportion of:						
Zero moves	0.32	0.34	0.44	0.46	0.66	0.69
Unit moves						
(a) Straight	0.42	0.42	0.24	0.22		
(b) Diagonal	0.15	0.10	0.03	0.07		
Multiple moves	0.12	0.14	0.29	0.25	0.34	0.38
r for overall distribution of moves	0.28	0.28	0.19	0.24	0.26	0.30
r for distribution of angles between successive moves	0.36	0.40	0.33	0.29	0.53	0.50
No. butterflies	48	200	43	200	29	200

Plant-dependent parameters (other as in Table 6): ZERO = 0.27; STOP = 0.67.

Comparison of Tables 2–4 shows that Canadian and Australian butterflies are very different; most obviously in their directionality, and in the frequency of zero moves. In similar host plant arrangements, Australian butterflies turn less, and have a lower frequency of zero moves, than the Canadians. Tables 2–5 also show that directionality, flight length, the frequency of visits to a plant, the frequency of zero moves, and the number of eggs laid per visit, also vary with the spatial distribution, species, and age of the host plants. The next step is to use these data to establish a set of parameters which will meaningfully describe the butterflies' behaviour, i.e. which will allow prediction of the resultant egg density and distribution for any arrangement or type of hosts, and any density of butterflies. As noted earlier, this required simulation. The model was initially built very simply, then progressively increased in complexity until it would mimic all the available data. In its final form, it uses seven parameters, some depending on the plant, and some on the current fecundity of the butterfly. The following section lists

Table 3. *Movement records of Australian butterflies in a market garden of cauliflowers, 1975, with comparison of predictions of the simulation model; STOP, ZERO and LAY are re-estimated for this set of data; other model parameters as in Table 2*

Plant age	Large cauliflower 7–9 weeks		Small cauliflower 3 weeks	
Mean plant height (cm)	28		20	
Mean plant diameter (cm)	49		31	
	Data	Model	Data	Model
Mean length of non-zero moves	2.52	2.46	4.08	4.15
Variance	4.24	5.02	6.97	9.35
N	456		62	
Frequency of zero moves	0.16	0.15	0.05	0.05
r (directions)	0.16	0.37	0.21	0.44
r (angles)	0.49	0.65	0.66	0.72
Eggs laid per visit	0.28	0.28	0.42	0.41
Parameters of model:				
STOP		0.19		0.09
ZERO		0.12		0.04
LAY		0.28		0.42

them, describes how they are evaluated, the circumstances in which they vary and how they are used.

The model simulates flight and oviposition of an individual egg-laying female as a series of steps across a Cartesian grid with adjacent grid points 1 m apart, i.e. she may move, in one step, only to one of the eight adjacent grid points, where she may or may not land. Every point on the grid is defined as either host (of specified age and species), flower, or simply 'grass'. The parameters of the model must then govern:

- whether a butterfly currently located as in flight at a particular point actually lands there and how often she does so before leaving that point;
- whether, having landed, she lays an egg;
- the direction of travel at each step.

Table 4. *Flight records of Canadian butterflies among closely-spaced plants, 1973*

Plant pattern	I										II									
	(1 m spacing)										(groups of 4, with 3 m between groups)									
	Data					Model					Data					Model				
Plant type	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Eggs per visit	0.16	0.14	0.25	0.44	0.58	0.18	0.16	0.23	0.42	0.60	0.18	0.13	0.15	0.41	0.64	0.20	0.15	0.22	0.42	0.61
Non-zero visits per plant per butterfly	0.18	0.06	0.10	0.14	0.04	0.22	0.07	0.11	0.14	0.03	0.25	0.09	0.09	0.14	0.08	0.22	0.10	0.16	0.15	0.04
Proportion of zero moves	0.68	0.28	0.32	0.38	0.46	0.63	0.32	0.35	0.41	0.40	0.75	0.42	0.40	0.54	0.55	0.78	0.40	0.52	0.60	0.48
Overall	0.45					0.46					0.60					0.61				
Mean length of non-zero flights	1.76					1.74					2.25					2.19				
Variance	1.21					0.79					9.30					3.80				
Proportion of unit moves																				
(a) straight	0.27					0.22					0.19					0.18				
(b) diagonal	0.11					0.10					0.04					0.07				
Multiple moves	0.17					0.22					0.17					0.13				
r (direction)	0.15					0.16					0.08					0.10				
r (angle)	0.11					0.09					0.22					0.18				
No. butterflies	43					200					48					200				

Parameters of model:
Plant type
STOP 0.67 0.18 0.28 0.36 0.06
ZERO 0.54 0.23 0.27 0.32 0.32
LAY 0.18 0.13 0.23 0.43 0.63

Parameters governing landing

(1) $STOP: 0 \leq STOP \leq 1$

STOP is the probability that a butterfly newly arrived at a grid point will land there. Different grid points may have different values, depending on the plant located there. Initial estimates for particular types of host were obtained from observations of the 1 m plant patterns, by calculating the ratio: unit moves/(unit moves + multiple moves). This estimate is biased; if a female flew 2 m east and 1 m west before landing, its net move would be a unit move and so recorded in the data, i.e. the category 'unit moves' is inflated by multiple moves of this kind. The value of STOP is therefore adjusted in successive runs of the model to find the correct value.

STOP depends on the age, size and species of host. For kale in Canada, it increased with plant size, but decreased with plant age if size was kept constant (Fig. 1). The overall

Table 5. *Comparison of Canadian and Australian movement patterns with host plants in groups of three or four, 20 m apart*

	Canadian	Australian
Mean length of non-zero flights	5.04	7.70
Variance	66.68	142.75
No. flights	453	251
Frequency of zero moves		
Cabbage	0.74	0.65
Kale	0.77	0.69
Radish	0.74	0.43
r (directions)	0.10	0.13
r (angles)	0.05	0.10
Eggs/visit		
Cabbage	0.68	1.00
Kale	0.49	0.50
Radish	0.39	0.43
Non-zero visits per plant per contacting butterfly		
Cabbage	0.45	0.30
Kale	0.44	0.31
Radish	0.22	0.27

consequence of these conflicting tendencies, when the plant grows normally, is that STOP increases linearly with host age. The same effect appeared for cauliflower plants in Australia (Table 3). Comparing host species: butterflies were more likely to land on cabbage and on kale than on radish (Table 5).

Values for grid points defined as 'grass' or 'flower' were first estimated from the 4 m data, by trying a sequence of values until the model reproduced the observed frequencies of visits to grass and flowers. These estimates remained satisfactory for Australian butterflies but, in Canada, observations when hosts were 10 and 20 m apart showed that STOP(grass) varied with the current fecundity and recent history of the butterfly. A female with many eggs was very reluctant to leave hosts; she might fly a metre or so, but then would land in the grass, and her next flight would usually bring her back to the hosts. Consequently she would lay most of her daily egg complement on the first host, or group of hosts, that she found. Subsequent hosts were left more readily. Butterflies with few eggs left hosts readily from the beginning. The 'number of eggs left to lay'

accounts for all the observed differences between individual butterflies, so data for all females were pooled for each host arrangement. These behavioural changes appear in the data as relationships between current fecundity and flight length, directionality and the frequency of zero moves (Fig. 2). Two parameters of the model need to become dependent on current fecundity; attraction toward host plants (i.e. MISS, see (6) below) and STOP(grass) for the first ten moves after contacting a host. The data also required that STOP(flower) vary. Butterflies tended to feed before they began to lay, and after they finished laying, but not to intersperse the two. STOP(flower) was therefore made to increase as the current fecundity decreased, after first contact with a host. Since egg-laying occurs in the middle of the day, this effect might actually be circadian.

(2) $ZERO: 0 \leq ZERO \leq 1$

ZERO is the probability that a female currently landed at a grid point will land again, i.e. hop to another leaf, before her next move. Like STOP, it varies with the host. It was

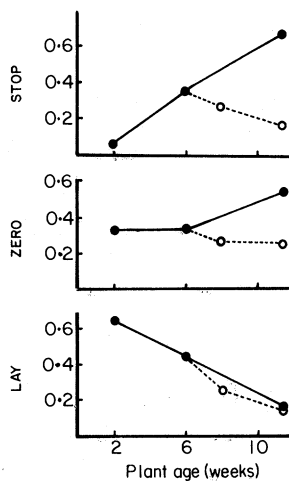


FIG. 1. Effects of size and age of kale on the flight model parameters, estimated from Vancouver females. Stunted plants (○) were about the same size as six-week-old normal plants (●).

estimated from the 1 m data by the ratio: zero moves/total moves, and again like STOP, the estimate is biased and must be adjusted. The largest plants have the highest values (Fig. 1), cabbage and kale have higher values than radish (Table 5).

Parameters governing egg-laying

(3) $LAY: 0 \leq LAY \leq 1$

LAY is the probability that a butterfly currently stopped at a grid point will lay an egg there. It was estimated as: total eggs laid/total visits for each type of host. It decreased linearly with plant age (Fig. 1) but was not affected by plant size. LAY was highest for cabbage, lower for kale, and lowest for radish, when the plants were the same age (Table 5).

Parameters governing direction of travel

(4) $MOVE(1) - MOVE(8): \sum_{j=1}^8 MOVE(j) = 1$

In a homogeneous environment, the frequency with which a butterfly chooses each of

the eight possible moves is given by the values of MOVE(1)-MOVE(8). MOVE(1) takes the highest value, i.e. is the frequency with which the butterfly travels in its preferred direction. If MOVE(1) is high, the female travels in relatively straight lines and the values of r (angle) are high. The frequencies of unit moves in each direction in the 1 m data gave estimates of the values of MOVE.

$$(5) \text{DIR}(1) - \text{DIR}(4): \sum_{J=1}^4 \text{DIR}(J) = 1$$

Different butterflies may have different preferred directions, which are defined to be toward one of the four closest grid points. DIR(J) is the probability that the preferred direction of a particular butterfly is the J th possibility. The distribution of mean directions for each butterfly in the 1 m data provided estimates of these values.

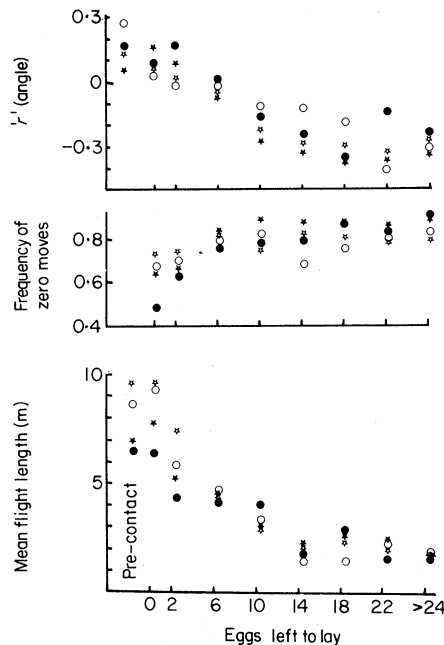


FIG. 2. Effects of current fecundity on flight length, direction and frequencies of zero moves (after contact with a host) in Vancouver butterflies. Solid symbols are for 10 m spacing open symbols for 20 m spacing with plants in groups of three. ●○ data; ☆ ★ values generated by simulation.

$$(6) \text{MISS}: 0 \leq \text{MISS} \leq 1$$

If some of the eight possible moves are toward hosts and some are not, the values of MOVE must be altered to allow for attraction toward hosts. This is done by examining each of the adjacent grid positions in turn; if there is no host plant in the J th position, the value of MOVE(J) is reduced to $\text{MISS} \times \text{MOVE}(J)$. Then, the new values of MOVE are rescaled so that their total is again 1. Like STOP(grass), MISS was first estimated as a constant, then found to vary with the butterfly's current fecundity. It was estimated as follows. Since a female is attracted toward hosts, she is more likely to return to a particular host if there are no others in sight, so producing a higher frequency of apparent zero moves (which are actually multiple moves) when the plants are widely spaced

(e.g. see Table 2). The magnitude of the increase depends on the degree of attraction to hosts. MISS was therefore estimated by trying a sequence of values until the model reproduced the observed increase in the frequency of zero moves.

(7) $CONT: 0 \leq CONT \leq 1$

In the absence of hosts, the directions of successive moves tend to be auto-correlated. $CONT$ is the probability that a butterfly in flight will continue in the same direction as the previous step, rather than choose a direction independently of the previous step. Without auto-correlation, r (angle) would be much higher when the hosts are more widely spaced, i.e. there would then be very little variation in the directions of successive net moves.

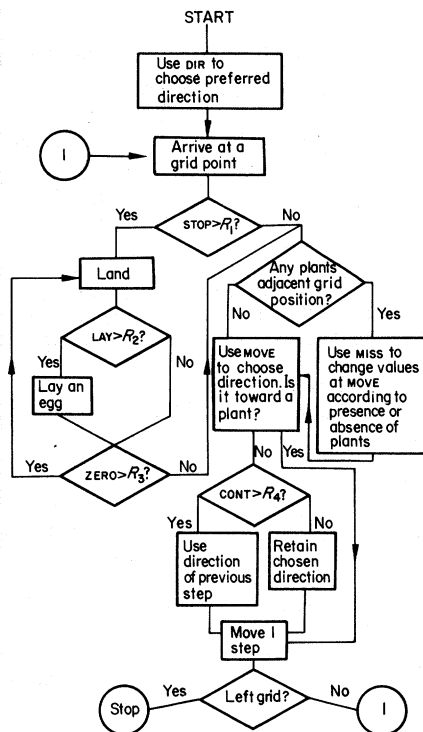


FIG. 3. Flow chart of flight and egg-laying simulation model. R_{1-4} are random numbers selected from a uniform distribution between 0 and 1. Other symbols are described in the text.

(In the model, each long move is the resultant of a series of short moves; the greater the number of short moves in the series, the closer to the preferred direction the long move is likely to be.) Decreased variability in r (angle) is in fact apparent in the data (see Table 2) but not to the extent predicted. The model uses a step-length of 1 m. When hosts are 1 m apart, this is likely to be right—the environment gives the butterflies decision-making cues every metre. But at wider host spacings, the data indicate that the butterflies turn less often.

$CONT$ was therefore estimated by trying a series of values until the model gave the correct value of r (angle) when hosts were 4 m apart.

A simplified flow chart showing the use of these parameters is given in Fig. 3. A copy of the Fortran program may be obtained from the author.

Differences between Australian and Canadian behaviour

There were marked differences between Australian and Canadian movement patterns in four of the seven parameters; these are summarized in Table 6. Several possible 'environmental' explanations for these differences can be eliminated. Although Canberra is generally warmer than Vancouver, temperatures in February 1975 were predominantly in the same 21–25° C range as the Vancouver trials. Other weather conditions were also similar.

Shapiro (1970) has found that, at high density, males of *Pieris protodice* Boisd. & Lec., will harass females so much that they become more dispersive. The 1972 Australian

Table 6. Comparison of Australian and Canadian movement patterns, as summarized by model parameters

Parameter	Measures:	Affected by:	Australian	Canadian
MOVE	Directionality of individual females		High directionality MOVE(1) = 0.6	Low directionality MOVE(1) = 0.3
DIR	Preferred directions		Variable DIR(1) < 0.45	Less variable DIR(1) > 0.7
STOP	Probability of landing	Plant species, size, age; current fecundity of butterfly	Values similar for large host plants (0.65–0.75 for cabbage), but after contact with a host: STOP(grass) = 0.015	STOP(grass) = 0.012 + 0.003x
MISS	Responsiveness to host plants	Current fecundity of butterfly	Less responsive MISS = 1 – 0.03x	More responsive MISS = 1 – 0.07x
CONT	Probability of maintaining a flight direction in absence of host plants		Values similar (0.6–0.8)	
ZERO	Probability of repeat visit to host without intervening flight away	Host species, size, age	Lower (0.2–0.3 for cabbage)	Higher (about 0.5 for cabbage)
LAY	Probability of laying an egg during a visit	Plant species, age	Values similar (0.7–0.9 for cabbage; about 0.5 for young kale)	

x = number of mature eggs the butterfly has available to lay.

trials were made in mid-summer, with a cloud of butterflies continuously over the plot; it seemed possible that the high directionality and low attraction to hosts might be a result of high butterfly densities, and that an Australian female by itself would behave like a Canadian. The 1975 market garden trials were made primarily to test this hypothesis. They were carried out in late summer, well past peak population densities, and I seldom saw more than three or four butterflies in a 2-h period, yet they behaved very much as had their predecessors in 1972–73, except that there was even more variability in preferred directions. At this stage, it seems most likely that the observed differences are genetically based.

EGG DISTRIBUTIONS

The simulation model may mimic observed movement very accurately, but this is insufficient; it must also correctly predict egg distributions. This section compares

prediction with observation. None of the following data were used to construct the model or estimate its parameters—they simply check that the model does indeed generate realistic egg distributions.

Plant preferences

The results of egg counts in Vancouver field plots are shown in Table 7. More eggs were laid on young than on old kale, and more on cabbage than on kale or radish. The predicted ratios agree with those observed. Twinn (1924) and Richards (1940) also noted preferences for cabbage over other hosts, but Harcourt (1963) found no clear preferences. P. M. Ives (unpublished) found that caged Australian butterflies laid more eggs on young than on old brussels sprouts.

Table 7. *Egg distributions in field plots*

Host preferences, May–June 1973					
Host plant	Eggs/plant	S.E.	No. plants	Proportion on each type	Predicted proportion (from simulation model)
4–8 week old kale transplanted at 4 weeks old	5.22	1.13	18	0.48	0.40
9–14 week old kale transplanted at 4 weeks old (normal growth)	4.05	0.74	18	0.37	0.46
9–14 week old kale transplanted at 8 weeks old (stunted)	1.65	0.44	18	0.15	0.14
Host preferences, June–August 1975					
Cabbage	7.55	2.61	9	0.49	0.63
Kale	6.11	0.84	36	0.40	0.28
Radish	1.64	0.66	36	0.11	0.09
Effect of plant spacing					
	Predicted ratio*		Observed ratio		
			Kale	Radish	
2-m spacing	0.61		0.68	0.57	
1-m spacing	0.39		0.32	0.43	
Total eggs			171	63	

* Predicted ratio depends on the fecundities of the butterflies encountering the plots. This value used a distribution of fecundities similar to that of the flight experiments.

Plant spacing

The model predicts that, especially at low plant densities, the numbers of eggs laid on a given number of plants should be lower when the plants are closer together (c.f. Fig. 5). Thus the plots planted at 2 m spacings should have received more eggs than those at 1 m spacings. They did so; the predicted ratios agree with those observed (Table 7).

The 'edge effect'

Perhaps the commonest observation in the literature on *P. rapae* egg distributions, is that more eggs are laid on the edge of plots than in the centre (Harcourt 1961; Kobayashi 1965). Harcourt (1963) suggested that this was because butterflies were continually

leaving the plot to feed and then returning to lay more eggs. Vancouver and Canberra butterflies did not do this, and the model in fact separates feeding and laying periods. Nonetheless, it does generate an 'edge effect', whose intensity depends on MISS and MOVE. As a butterfly leaves a group of hosts, a low value of MISS makes her more likely to return, so plants on that edge accumulate more visits and therefore more eggs, than other plants. If she is very directional (i.e. MOVE(1) is high), she will tend to leave again immediately, so that only edge plants receive more visits. (This behaviour was very obvious in Australian butterflies.) But if less directional, she may wander back through the plot, so that the difference between centre and edge is reduced.

Distribution on the central plants of a field

Harcourt (1961) in Canada and Kobayashi (1965) studying *Pieris rapae crucivora* Bdv. in Japan, both found that the eggs on the inner plants of a field were clumped, with the variance increasing slightly faster than the mean. The model gives a similarly clumped

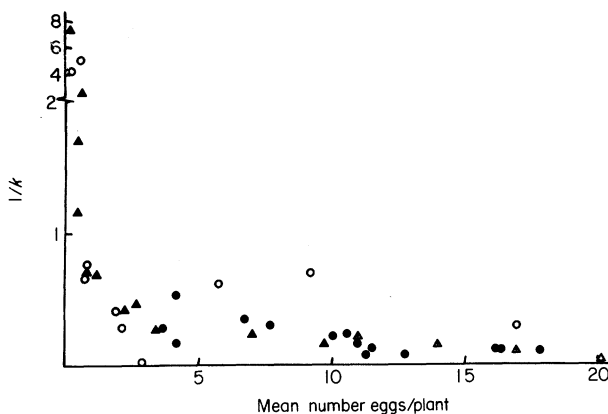


FIG. 4. Aggregation indices (negative binomial k) on the central plants of a closely-planted field; a comparison of values generated by the simulation model, with values estimated by Kobayashi (1965). ● Kobayashi field plot; ○ Kobayashi cage experiment; △ simulation model. The values of LAY and ZERO in the model were set at 0.7 and 0.4 respectively (i.e. at appropriate values for *Pieris rapae rapae* on cabbage plants. The value of ZERO is intermediate between estimated Canadian and Australian values.)

distribution. The precise relationship between mean and variance is determined by ZERO and LAY (which jointly determine the number of eggs a butterfly lays on a host before leaving it); higher values of either give more clumped distributions at a particular egg density. Figure 4 compares Kobayashi's data with egg dispersion indices generated by the model for a range of butterfly densities. Because these indices changed with egg (and butterfly) density, Kobayashi suggested that females changed their behaviour at high densities so as to produce more uniform egg distributions. No such changes are incorporated in the model, yet it predicts results very like Kobayashi's, indicating that the changing indices reflect a statistical rather than a behavioural phenomenon.

EFFECTS OF MOVEMENT PATTERNS ON EGG DISTRIBUTION AND DENSITY

This section uses simulation to compare the egg distributions which would be produced

by Australian and Canadian females over a range of host densities. The models were set to run in 100×100 m plots containing between 4 and 1000 plants. STOP, ZERO and LAY were set to values appropriate to attractive hosts (e.g. cabbage) — 0.65, 0.3, and 0.7 respectively for the Australian model, and 0.65, 0.5, and 0.7 for the Canadian. At each host density, hosts were arranged uniformly, randomly, or in groups of four. Then 120 hypothetical females were flown through the plot, each one starting near the edge which its preferred direction made it most likely to encounter first. The results are shown in Figs 5–7 and Table 8. Random and uniform plant distributions gave similar results, and are treated together.

Table 8. *Within-clump and between-clump variation in eggs/plant, in simulations of Canadian and Australian butterflies*

Number of groups of plants in the 100×100 m plot (4 plants/group)	Canadian model			Australian model		
	Between- group M.S.	Within- group	F	Between- group MS	Within- group MS	F
4	5862	1424	4.12	25.4	34.2	0.74
9	2424	303	8.01	332	183	1.81
16	2449	596	4.36	172	180	0.96
25	1878	422	4.45	187	73	2.56
225	220	46.4	4.74	30.1	35.0	0.86

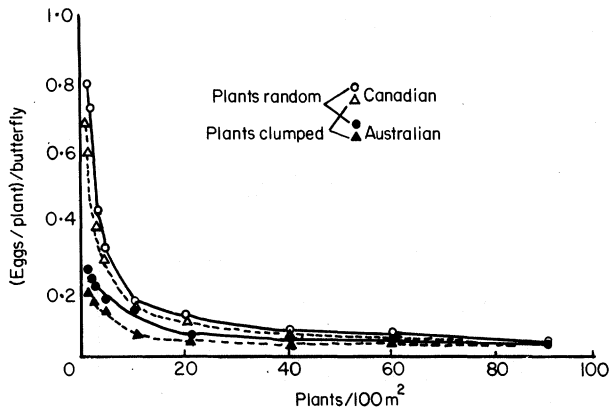


FIG. 5. Egg densities generated by 120 simulated Australian and Canadian females on different host densities and distributions in a 100×100 m plot.

A given number of plants distributed uniformly or randomly through the plot always received more eggs than the same number distributed contagiously; the effect is most pronounced at low plant densities (Fig. 5) and, as one might expect, the more hosts there are in a plot, the fewer eggs are laid on each plant (though more are laid in the plot as a whole). In all cases, the models produce highly contagious egg distributions—much more so than when hosts occupy every grid position (c.f. Fig. 4).

There are striking differences between Canadian and Australian results. The Canadian model gives higher egg densities, especially at low host densities, and the eggs are more aggregated (Figs 5 and 6). When plants are in groups, between-group variation is much higher than within-group variation for the Canadian eggs but not the Australian, i.e.

Canadian distributions show high geographic as well as between plant aggregation (Table 8). Thus different patches of plants may receive very different numbers of eggs, not because they differ in quality, but as a chance consequence of the female's behaviour.

The two search patterns also differ in efficiency (Fig. 7). If we define 'efficiency' as the number of encounters with hosts per metre flown (not counting true zero moves as encounters or as adding to the length of the flight path), then at high host densities, the Australians are more efficient, but at low, the Canadians do better. (Average crucifer densities over large areas would almost always be in the lower range.) If hosts are clumped, the range of densities over which the Canadians are more efficient is much

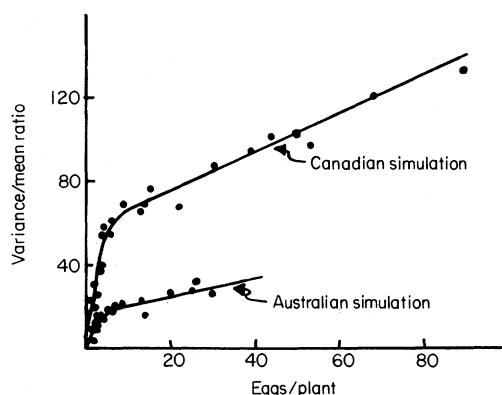


FIG. 6. Variance-mean ratios generated by simulation on uniform and random host distributions.

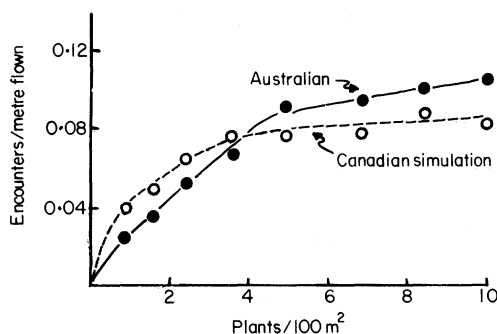


FIG. 7. Search efficiencies on random plant distributions. True zero moves, i.e. in which the female does not leave the grid point, do not increase the flight length or score as an 'encounter'.

increased. This 'advantage' is not because a Canadian female finds more hosts—in fact, she finds fewer—but because she finds the same hosts repeatedly.

In summary, then, the Australian butterflies produce a less aggregated egg distribution at the cost of longer flight paths. The Canadians produce a much more aggregated distribution, but need not fly as much.

DISCUSSION

It is clearly possible to describe and analyse the movements of *Pieris rapae* females, and

to use the results to predict and explain egg distributions. In this way, different behaviour patterns can be precisely compared, and their ecological consequences can be examined.

Australian and Canadian females behave quite differently, and as a result distribute their eggs in different ways—Australian butterflies lay fewer eggs in any given area, i.e. disperse their eggs more widely and generate a less contagious egg distribution, at greater cost in flight time, than do Vancouver butterflies. The two populations are recently derived from European stock (though those in Australia arrived via New Zealand), and the differences therefore imply different selective pressures in the two places. The probable explanation for these differences is discussed elsewhere.

None of the peculiarities of *P. rapae*'s egg distribution arise from behavioural characteristics which are likely to be unique to this species. Indeed, other studies of movement patterns (most are of predators searching for prey, e.g. Banks 1957; Chandler 1969; Dixon 1959; Fleschner 1950; Smith, 1974a,b; Brunner & Burts 1975; Wratten 1973; Murdie & Hassell 1973) show clear tactical similarities; in particular, an increased turning rate after contact with the resource sought. Holling (1966) showed that mantid responsiveness to prey increased with hunger, in a fashion analogous to the way *P. rapae* increases in responsiveness to hosts when it has many eggs to lay. (This phenomenon is certainly not universal, however; when *P. rapae* caterpillars are obliged to search for a new food plant, their responsiveness *decreases* with hunger, possibly because they trade off increased speed for reduced perceptual ability (Jones 1976).)

Case studies of the type developed here will enable us to evaluate and expand the applicability of theoretical models of dispersal and spatial heterogeneity. As an example, Gadgil (1971) suggests that isolated patches of habitat should have smaller populations than less isolated patches, since they may lose emigrants at the same rate, but are less likely to receive immigrants; this, as he points out, appears to be true of the citrus mites studied by Huffaker (1958), and of eucalyptus psyllids (Clark 1962). The psyllids, for example, never reach population numbers as high on widely-spaced trees as on those planted more closely. Precisely the opposite is true of juvenile populations of *P. rapae*—widely spaced plants, and plants in smaller groups, receive more eggs. (Further experimental confirmation of this result has recently been given by Cromartie (1975).) This effect—a greater frequency of encounter with more isolated hosts—may occur whenever dispersal distances are large relative to patch size (i.e. in a fine-grained environment) and mortality during dispersal is low. The reason for the effect is simply that if a searcher locates a patch by perceiving its 'edge', then since isolated plants have more 'edge' than the same number of plants in a dense group, they will be encountered more frequently. The effect will be lessened if the searcher tends to aggregate around its resource; an examination of Fig. 5, for example, shows that clumping plants in groups of four may reduce the number of eggs laid on them by up to 40% for Australian butterflies, but by no more than 20% for the Vancouver butterflies, whose tendency to aggregate near hosts is much more pronounced. Avoidance behaviour, i.e. behaviour which tends to produce a negative correlation between the densities of two organisms, would, of course, *increase* the frequency of encounters with isolated *v.* aggregated hosts. Still stronger aggregative behaviour could reverse the effect if, for example, the edge of a dense patch could be perceived at a much greater distance than could an isolated host (Hassell & May (1973) cite a number of examples of this). However, it is notable that not even the strongly aggregative behaviour of the Vancouver butterflies suffices to eliminate the effect when, as in this case, the same host may be found repeatedly by the same butterfly. This implies that a positive correlation between the densities of searcher and

resource, which is produced in predator-prey relationships by very similar types of behaviour, and which, as Hassell & May (1973) and Murdoch & Oaten (1975) point out, has a stabilizing effect on the exploitation relationship, may be very much harder to achieve in a herbivore or a non-discriminating parasite than it is in a predator.

It seems likely that the same effect may make isolated prey populations more susceptible to a highly mobile predator; for example, populations of herbivorous insects on isolated plants may be at greater risk to mobile predators, than similar populations on less isolated plants, in circumstances where the predator must first find the plant and then search it for prey.

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SUMMARY

(1) The movement patterns of Canadian (Vancouver) and Australian (Canberra) cabbage butterfly females searching for hosts are described, and the descriptions incorporated in stochastic simulation models. Some of the parameters of the model (those dealing with probabilities of landing and laying) depend on host plant quality and particularly on the age and species of host plant. Other parameters, and particularly the degree of attraction toward hosts, depend on the current fecundity of the butterfly.

(2) The models correctly predict observed behaviour patterns, characteristics of *Pieris rapae* egg distributions described in the literature, and egg distributions produced in field trials during the study.

(3) Vancouver females are quite different from Canberra females. The behavioural differences result in less dispersal, a more aggregated distribution of eggs and more efficient search at low plant densities.

(4) The two are nonetheless affected in qualitatively similar ways by changes in resource distribution. At any given host density, fewer eggs are laid on more contagiously distributed hosts and egg distributions are more aggregated at low host densities than at high. The effect of contagious host distribution means that more eggs are laid on isolated plants than on plants in small groups, and more on plants in small groups than on plants in large groups.

(5) Thus butterfly density tends to vary inversely with host density, despite aggregative behaviour identical to that which, in predator-prey systems, leads to a direct correlation between the densities of searcher and resource. The difference occurs because the butterfly can find the same host repeatedly, and indicates that such a direct correlation (with its

stabilizing properties) is much more difficult for a truly non-discriminating parasite to achieve than it is for a predator. (*P. rapae* can be regarded as a non-discriminating parasite whose prey happens to be a plant.)

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APPENDIX

BY N. E. GILBERT

This appendix uses random-walk theory to prove that the detailed movements of a group of animals during some time period cannot, in principle, be deduced from the positions of those animals at the end of the period. Suppose that an animal moves in two dimensions in a series of n steps, each of fixed length s . The first step may be taken in any direction. The angles θ between successive steps are random variables with a circular normal distribution with mean zero, i.e. turns to right and left are equally probable. After n steps, the animal is at a distance r from the start. It is convenient mathematically to consider the distribution of r^2 rather than r itself. It can be shown (c.f. Skellam 1973) that the average value of r^2 will be:

$$s^2 \frac{1+z}{1-z} n - \frac{2z(1-z^n)}{(1-z^2)}$$

where z is the average value of $\cos \theta$. The expression for the variance of r^2 is far more complicated and will not be quoted here; but both the mean and the variance may be computed for different values of the step-length s , the number of steps n , and the average cosine, z . It is easy to find quite different sets of conditions which arrive at the same answers. For instance, the values $n = 4$, $s = 1.28$, $z = 0.29$ and $n = 64$, $s = 0.093$, $z = 0.91$ both give an average of 10 and variance of 50 for r^2 ; and a 'Monte Carlo' simulation shows that although the movements are quite different in the two cases, the final geographic patterns of animals are practically indistinguishable. No sober animal is known to move in this purely random fashion, but this purely theoretical argument is enough to prove the point. The animals which take sixty-four short steps cover a greater distance than those which take four long steps, yet the final distribution is the same.

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