

## EFFECT OF SPATIAL ARRANGEMENT OF HABITAT PATCHES ON LOCAL POPULATION SIZE<sup>1</sup>

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**Abstract.** The purpose of this study was to examine the effect of the spatial arrangement of host-plant patches on local abundance of the cabbage butterfly (*Pieris rapae*). By considering the movement behavior of adult females, we developed a detailed simulation model of *P. rapae* in patchy habitats. The model was then used to predict effects of cabbage patch spatial arrangement on *P. rapae* egg densities for a specific spatial arrangement of cabbage patches. Field studies confirmed the predictions.

The results of this study are discussed in the context of the effects of dispersal behavior on relationships between patch spatial arrangement and local abundance. The findings are consistent with general simulation results of L. Fahrig and J. E. Paloheimo (*personal observation*) that suggest that large dispersal distances decrease the effect of the spatial arrangement of habitat patches on local population size.

**Key words:** cabbage butterfly; dispersal behavior; dispersal distance; habitat patch; host detection; host-plant patch; local abundance; patch; *Pieris rapae*; simulation modelling; spatial arrangement.

### INTRODUCTION

The breeding habitat of most species is not uniformly distributed over space, but occurs as discrete habitat patches. Populations are therefore divided into sub-populations that are interconnected to varying degrees as a result of dispersal among habitat patches. Several theoretical studies have demonstrated the importance of spatial heterogeneity for overall population persistence (e.g., Roff 1974, Lomnicki 1980, Hastings 1982, Vance 1984) and abundance (e.g., Myers 1976, Taylor and Taylor 1977, Hanski 1982, 1985). The persistence of systems of interacting species such as predator-prey, host-parasite, or competitors, can also depend to a large extent on habitat spatial heterogeneity (e.g., Levin 1974, Shmida and Ellner 1984, Comins and Noble 1985, Holt 1985, Chesson and Murdoch 1986). The reason patchiness can enhance persistence is that, at any particular time, patches in which local extinctions have occurred can be recolonized by dispersers from patches that have not suffered extinctions. If the factors causing such extinctions do not affect all patches in the same way at the same times, then there will always be patches containing colonizers. Over the long term, the survival of the regional population is therefore enhanced.

Models that include spatial patchiness generally do so in one of two ways; either (1) all dispersing individuals are assumed to have equal access to all habitat patches, or (2) individuals dispersing from each habitat patch are assumed to distribute themselves equally

among all nearest neighbor patches. In neither case is there any attempt to model naturally occurring spatial arrangements of habitat patches or realistic dispersal patterns. For the types of questions that these studies address, these simplifications are reasonable. For some questions, however, we may need to examine the effects of particular spatial arrangements of habitat patches. For instance, if we want to study the importance of dispersal corridors among patches, the spatial arrangement of patches is crucial (Fahrig and Merriam 1985, Lefkovich and Fahrig 1985).

The purpose of the present study was to examine the relationship between the spatial arrangement of habitat patches and local population size for a species that does not move through dispersal corridors. We define the spatial arrangement of patches as the matrix of pairwise distances between all pairs of patches. The relative positions of the patches in space are implicitly included in this definition. The species we studied was the cabbage butterfly (*Pieris rapae*). Our approach was to (1) use information concerning the dispersal behavior of *P. rapae* to postulate an appropriate spatial arrangement of habitat patches (i.e., cabbage patches), to examine potential relationships between patch spatial arrangement and local population density; (2) form predictions concerning the effects of the chosen spatial arrangement, through computer simulation; and (3) compare the predictions with field data.

### BIOLOGY OF *PIERIS RAPAE*

Adult *Pieris rapae* are normally first observed in flight at the end of April in southern Ontario (Michaelowicz 1980); emergence from overwintering diapause continues into May (Harcourt 1966). Oviposition usually commences in the beginning of May. There are about 3.5 generations per summer, each of which

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includes eight stages: egg, five larval instars, pupa, and adult.

*P. rapae* females oviposit primarily on plants in the family Cruciferae. Host plants therefore include agricultural crops such as cabbage, broccoli, brussels sprouts, cauliflower, kale, turnip, radish, mustard, and rapeseed, and wild cruciferous weeds such as yellow rocket, shepherd's purse, wild mustard, and poor man's pepper grass (Richards 1940, Parker 1970). Cultivated host plants are much preferred over wild host plants (Twinn 1925, Jones and Ives 1979). Before pupating, the fifth larval instar of *P. rapae* ceases feeding and enters a "wandering phase" (Richards 1940, Harcourt 1961); pupation usually occurs near the periphery of the host-plant patch. *P. rapae* overwinter in the pupal stage (Richards 1940, Harcourt 1966).

The results from several studies suggest the following description of the dispersal characteristics of *P. rapae*. Female butterflies emerge from the pupal stage on or near the host-plant patch where they fed as larvae (Richards 1940, Harcourt 1966); adults live for  $\approx 3$  wk (Gossard and Jones 1977). Male adults are strongly attracted to small white objects, and actively search host-plant patches for females (Jones et al. 1980; L. Fahrig and J. E. Paloheimo, *personal observation*). Consequently, most females are mated within 24 h of emergence; they begin to lay eggs within 24–36 h after mating (Jones 1977). Often this first egg-laying bout will occur on the host-plant patch where the butterfly fed as a larva. During a particular egg-laying bout, females lay most or all of their available mature eggs. However, they spread these over the entire host-plant patch (Root and Kareiva 1984). Females leave host patches almost immediately following an egg-laying bout (Jones 1977). We (Fahrig and Paloheimo 1987) studied the dispersal rate of adult females from a cabbage patch of 450 plants. The daily dispersal rate was 0.74; that is, 74% of females present on the patch on any one day had dispersed by the next. The average daily dispersal distance is 250–700 m (displacement: Jones et al. 1980). Females spend  $\approx 3$ –5 h a day in flight if the weather is favorable. Therefore, since only 15 min is required, on average, to lay the total daily number of mature eggs (Fahrig and Paloheimo 1987), most of the butterflies' time in flight is spent in nonhost patch areas, feeding on nectar, and searching for new host patches. Most or all of a female's daily complement of eggs is laid on the first patch of hosts that she finds on that day (Jones 1977). Although flight direction within a particular day is highly directional (Jones et al. 1980, Root and Kareiva 1984), flight direction changes at random from one day to the next (Jones et al. 1980). When searching for host plants, females fly along close to the vegetation, stopping every few metres to test for the suitability of plants for egg laying (Root and Kareiva 1984). Suitability is determined by testing for the presence of glucosinolates through chemoreceptors located on the tarsi (Renwick and Radke 1983).

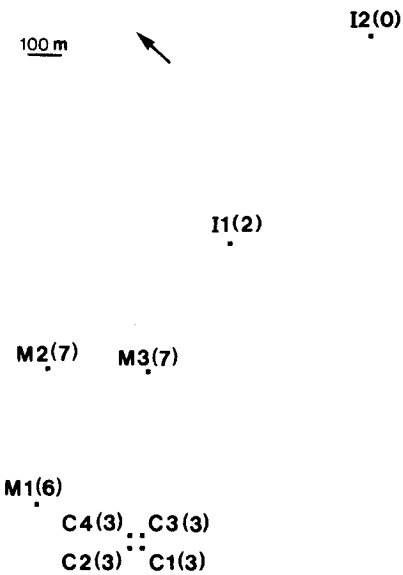


FIG. 1. Experimental layout of nine cabbage patches. Locations of patches and distances among them are to scale, but patches are drawn larger than actual scale for visibility. Numbers in parentheses indicate the number of patches from which the patch is likely to obtain immigrant females that will lay eggs; for further explanation see Experimental Layout. Patch codes indicate their categories: "C" patches had several patches close by, "M" patches were at intermediate distances, and "I" patches were isolated.

Flight orientation is not influenced by the presence of host plants; females discover only those hosts that are directly in their flight paths (Fahrig and Paloheimo 1987). The number of eggs laid on a host patch is independent of the size of the patch (by area or number of plants) (Fahrig and Paloheimo 1987), but depends, to varying degrees, on the weather, the butterfly's age, the length of time since her last egg-laying bout (Gossard and Jones 1977), and the quality of the plants (Ives 1978, Jones and Ives 1979, Myers 1985).

#### EXPERIMENTAL LAYOUT

The fieldwork was conducted at the Guelph University agricultural research station near Elora, Ontario. Nine patches, each  $10 \times 10$  m and containing 200 cabbages, were in the spatial arrangement shown in Fig. 1. The nearest other cultivated host plants of *Pieris rapae* were at least 1.5 km from any of our cabbage plots. None of the medium between the patches could be considered either a hindrance or a help to *P. rapae* flight. Most of it was planted in various crops, mainly grains. There were also some small fallow areas and grassy and gravel roadways; there were no forested areas in the station. Wild cruciferous weeds, a second source of host plants for *P. rapae*, were scattered throughout the area.

Within the constraints imposed by our field site, we attempted to devise a spatial arrangement of cabbage patches that would be expected to produce a maximal

TABLE 1. Spatial characteristics of the nine experimental cabbage patches (see Fig. 1). Distance is average distance to other patches. Angle is the total angle subtended by other patches between 250 and 700 m from the focal patch.

Patch	Distance (m)	Angle (°)
C1	486	4.00
C2	484	4.33
C3	468	4.24
C4	463	4.60
M1	563	10.83
M2	595	8.74
M3	521	9.58
I1	746	1.56
I2	1388	0.00

effect of patch position on *P. rapae* egg density. The number in parentheses beside each patch in Fig. 1 indicates how many of the other eight patches were likely to be sources of egg-laying females. This number was based on the information on *P. rapae* dispersal behavior described above, particularly on the observations that (1) females tend to lay most or all the eggs for 1 d on one patch, (2) they fly between 250 and 700 m per day, and (3) female flight within a day is largely unidirectional. This behavior results in the prediction that the patches C1 to C4 in Fig. 1 were actually more "isolated" from the point of view of dispersing females than were patches M1 to M3. This is because females that dispersed from C1, for example, would have very few if any mature eggs to lay by the time they reached C2, C3, or C4. Therefore they would pass over these patches without laying eggs. However, by the time they chanced upon M1, M2, or M3 (possibly the next day) they would have a number of mature eggs available to lay. Based on this argument, we expected that the numbers of eggs on patches M1 to M3 would, on average, be slightly higher than those on patches C1 to C4, or I1 or I2.

The spatial arrangement in Fig. 1 was specifically chosen so that patches fell into three categories: "C" patches had several patches close by; "M" patches had most other patches at intermediate distances; and "I" patches were isolated from other patches. To demonstrate that the patches did in fact group into these three categories, we calculated the average distance between each patch and the other eight patches. We also calculated the total of the angles subtended by all of the other patches that were between 250 and 700 m from the patch, for each patch (Table 1). The patches fall into the three groups (C, M, and I) based on these criteria.

Although we expected the egg density in M patches to be higher than that in I or C patches, the difference was not expected to be great, since the dispersal distance from patches is high, thus causing dispersers to be spread over a large area. Also, females do not detect new patches from a distance. Both of these facts mean that the actual fraction of dispersers from a patch that

find any other particular patch within 1 d (the "direct dispersal rate") is expected to be small. In fact, the direct dispersal rate from a patch to all other patches can be calculated as the sum of the angles subtended by the other patches that are between 250 and 700 m from the first, divided by 360°. The average direct dispersal rate for the nine patches calculated in this way is 1.48% of the total dispersers from the patches. However, the dispersal rate from patches (i.e., fraction of butterflies that leave patches) is quite high,  $\approx 74\%/d$  (Fahrig and Paloheimo 1987). Therefore, given the dispersal characteristics of *P. rapae* females, we expected to find some effect (though small) of patch spatial arrangement on population size of *P. rapae* in the cabbage patches. To obtain more fine-tuned predictions for the cabbage butterflies in the experimental setup (Fig. 1), we built a simulation model that includes the specific characteristics of *P. rapae* and applied it to this setup.

#### SIMULATIONS

To model *Pieris rapae* dispersal and population dynamics in the experimental world pictured in Fig. 1, we used a discrete-time simulation model with a time step of 1 d. Only the female population is modelled.

Two important assumptions in the simulations are: (1) all females are mated within 24 h of emergence, and (2) newly emerged females remain on the host patch long enough to complete at least one egg-laying bout before dispersing. The first of these assumptions implies that the males disperse less readily than the females to ensure that at low population densities sufficient males will be in the vicinity of newly emerging females to fertilize them rapidly. Yamamoto (1981) found that male *P. rapae* disperse less readily than females in northern Japan.

The simulation model (summarized in Fig. 2) is composed of two main parts: within-patch and between-patch dynamics. Within each patch, the numbers of each of the eight life history stages of *P. rapae* are calculated for each day. Factors that affect recruitment into each stage are the stage development times and survival rates. Both of these vary with the time of the season because development rates increase with increasing temperature (Richards 1940, Jones and Ives 1980), and the survival rates of the later larval instars are influenced by the population densities of parasites, which increase through the season (Michaelowicz 1980; L. Fahrig and J. E. Paloheimo, *personal observation*). Since stage development times are short (3–6 d for fourth and fifth larval instars and 8–15 d for pupae), the stage survival rates were approximated by  $(s_{i,t})^{dt_{i,t}}$ , where  $s_{i,t}$  and  $dt_{i,t}$  are the seasonally adjusted daily survival rate and stage development time of stage  $i$  at time  $t$ .

Only the adult stage (i.e., the butterfly) is involved in the between-patch dynamics, since the other stages are relatively immobile. We assume that butterflies

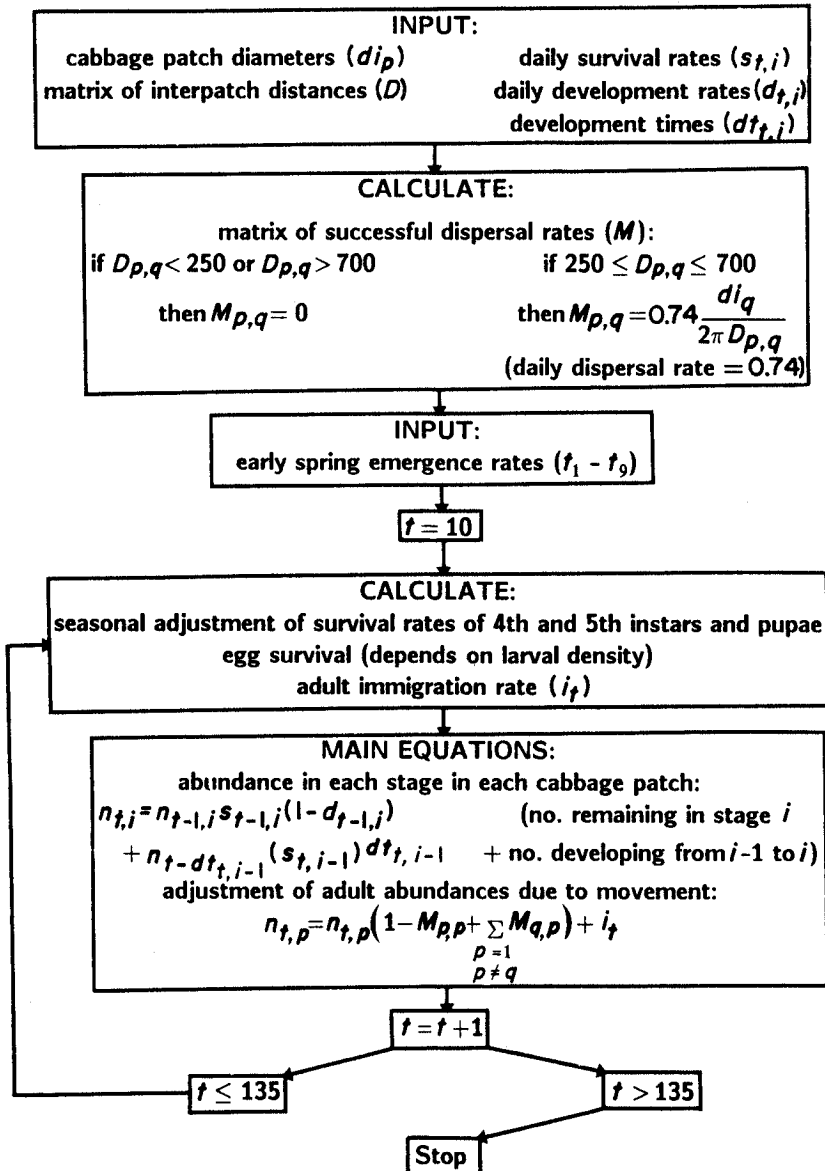


FIG. 2. Flow chart of the simulation model of *Pieris rapae* population dynamics in a series of cabbage patches. *t*: time step in days. *p, q*: cabbage patches. *i*: life history stage. *n*: number of individuals. There are three sets of input values for  $s_{t,i}$ ,  $d_{t,i}$ , and  $dt_{t,i}$  for the periods 15 April–29 May, 30 May–28 June, and 29 June–27 August. To include egg laying, in the second part of the first main equation, for the egg stage,  $dt_{t,i-1}$  (adult development time) is 1 d, and  $s_{t,i-1}$  is 8.73, the mean daily egg-laying rate for female eggs only.

that leave a patch on a particular day do so in all directions with equal likelihood. They fly at least 250 m before laying any eggs, and continue flying for up to 700 m in search of a new host patch. Butterflies are assumed to lay eggs on only one patch per day.

The group of cabbage patches depicted in Fig. 1 is not a closed system, but is a portion of an area covered by a large mobile population, probably extending over most or all of southern Ontario. Butterflies are constantly flying into and out of the area, and any butterfly found there is likely to be gone within 1 or 2 d, a small

fraction of its lifetime. Butterflies that disperse directly between cabbage patches in 1 d are therefore not the only sources of females arriving on the patches. Other sources include (1) females that fly into the area from outside, (2) females that disperse from a cabbage patch, do not find another patch, and do not leave the area within 1 d, and (3) females that develop from larvae that fed on wild host plants (cruciferous weeds) in the area. The combination of all of these sources is referred to as "immigration" in this study.

The immigration rate was estimated as follows. On

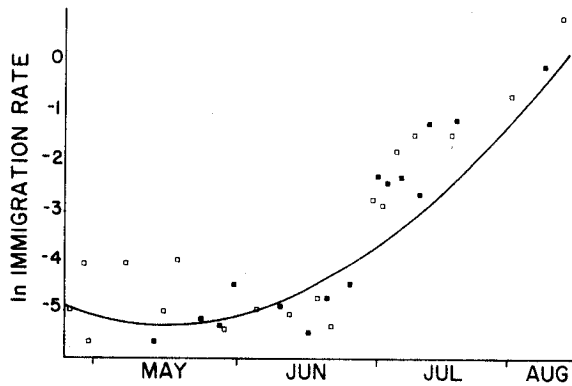


FIG. 3. Immigration rates of *Pieris rapae* butterflies onto cabbage patches (■) and nonhost patches (□).  $\ln(\text{immigration rate})$ :  $\ln\left(\frac{n+1}{t}\right)$ , where  $n$  is the total number of butterflies captured or observed and  $t$  is the observation time in minutes. Regression equation:  $\ln(\text{immigration rate}) = -4.79 - 0.034(\text{day}_1) + 0.00085(\text{day}_1^2)$ ,  $R^2 = 0.848$ , where  $\text{day}_1$  = number of days since 24 April (the first day of observation).

days that were sunny and calm (i.e., appropriate flight conditions for *P. rapae*), we observed either one of patches C3, M1, I1, or I2 (Fig. 1), or one of four areas without host plants, also of dimensions  $10 \times 10$  m. The nonhost areas were 60 m from the host patches, and included sections of a barley field, a grass-covered roadway, a weedy field, and a weedy roadway. Every second day of observation a host patch was observed, and every other day a nonhost area was observed. We attempted to capture all cabbage butterflies that crossed over or landed in the observation area (i.e., the cabbage patch or the nonhost area). The time of capture and sex of the captured butterfly were recorded, and the butterfly was kept in a cage until the end of the day's observation period. We attempted to capture all butterflies, but gave up if the chase took us  $>50$  m from the observation area. The observation time of non-captured butterflies was also recorded, and the sex was entered as "?," unless a positive determination of the sex had been made during the chase. The observations were transformed to  $\ln\left(\frac{n+1}{t}\right)$ , where  $n$  is the number of butterflies captured (or observed), and  $t$  is the total observation time in minutes.

Analyses were performed using SAS (1982). We first found the best-fitting polynomial regression equation ( $\alpha = .05$  for addition of a variable) with independent variable  $\text{day}$  (Fig. 3), where  $\text{day}_1$  is the number of days since 24 April (the first day of observation). The residuals from the polynomial regression were then analyzed for the effects of presence or absence of host plants (class variable *host/nonhost*) and for differences between males, females, and "?"s (class variable *sex*). There was no significant effect of either of these factors or their interaction (Table 2). There were insufficient data to analyze them for the effects of the individual

patch of observation. The regression equation shown in Fig. 3 was used to estimate the rates of immigration onto the cabbage patches. The estimates were multiplied by 68 for the female daily immigration rate because there are an average of 136 minutes of acceptable *P. rapae* flying weather per day in southern Ontario (averaged over the summer), and we assumed that half of the immigrants were females. This assumption is consistent with the result that the immigration rates for females and males were not significantly different (Table 2).

The above method of estimating the immigration rate does not distinguish between immigration as defined above and the females that fly directly between patches within 1 d. However, because of the high mobility of the butterflies and the fact that we expected only  $\approx 1.48\%$  of butterflies on patches to fly directly between patches, immigrants (as defined above) are expected to far outnumber the direct dispersers. The resulting error in the immigration rate estimate was therefore probably small.

At the start of the simulation each patch in Fig. 1 received one adult female per day for 9 d, corresponding to the synchronous early-spring emergence period of *P. rapae*. The population sizes of each life history stage in each patch in Fig. 1 were calculated for 135 d beginning in mid-April and running until the end of August. Fig. 4 illustrates the results of the simulations for the 100-d period corresponding to the field sampling (i.e., 12 May–19 August). Since the model simulates the total number of female eggs on patches of 200 plants, we divided the simulation results by 100 to obtain the number of eggs per plant (Fig. 4). The values were log-transformed to allow visual comparison with field results (below). The predicted population peaks are due to the synchronous early-spring emergence. The main result is that, as expected, patches in category M have the highest predicted population sizes. Populations in C patches are slightly lower, and those in I patches are very slightly lower still. However, the simulations predict that the differences in population sizes due to the spatial locations of the patches are small.

To demonstrate that the predicted effect ( $M > C > I$ ) was due to the dispersal behavior, we conducted further simulations in which alternative ranges of dis-

TABLE 2. Analysis of variance of immigration rates of cabbage butterflies. Data are residuals from the polynomial regression of immigration rates on  $\text{day}_1$  (Fig. 3), where  $\text{day}_1$  = number of days since 24 April. Total degrees of freedom: 98.

Source*	df	Type III ss	F	P
Habitat area ( <i>host/nonhost</i> )	1	0.118	0.36	.551
Butterfly sex ( <i>sex</i> )	2	0.231	0.35	.706
<i>Host/nonhost</i> $\times$ <i>sex</i>	2	0.466	0.71	.495

\* Name of variable is given in parentheses.

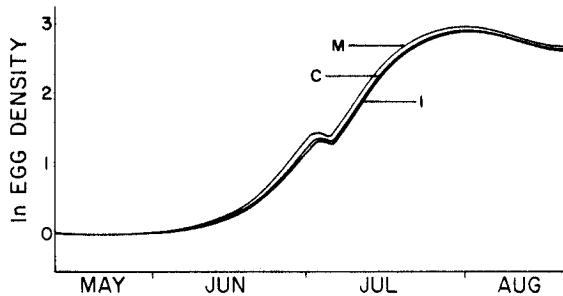


FIG. 4. Simulation results of the number of *Pieris rapae* eggs per plant in three categories of cabbage field. C: C1 to C4 in Fig. 1. M: M1 to M3 in Fig. 1. I: I1, I2 in Fig. 1. Maximum values of egg densities (before log transformation) were 17.85, 17.87, 17.87, and 17.89 eggs per plant for C1 to C4, respectively, 18.23, 18.11, and 18.16 eggs per plant for M1 to M3, and 17.76 and 17.63 eggs per plant for I1 and I2.

persal distances (other than 250–700 m) were assumed. For dispersal distance ranging from 0 to 250 m, the rank order of population sizes predicted by the model was  $C > M$  or  $I$ , for dispersal distance restricted to  $>700$  m the order was  $I > C > M$ , and when any dispersal distance was allowed the ranking was  $C > M > I$ . Therefore, it is clear that the predicted ranking of the local population sizes does in fact depend on the dispersal behavior.

#### FIELD RESULTS

The plots (Fig. 1) were sampled from 12 May to 19 August 1986. Two plantings of cabbage were necessary to cover this period. The second planting occurred on 29 June; seedlings were planted between the rows of the first planting, and there was a transition period of 4 wk during which cabbages from both plantings were present. All eggs on 20 randomly chosen plants from each patch were counted at each sampling. During the period of overlap of the two cabbage plantings, 20 plants from each were sampled (a total of 40 plants) in each patch; population estimates were then taken as the average of the two samplings. The field data on egg density are illustrated in Fig. 5. The data were log-transformed to stabilize the variance.

Analyses were performed using SAS (1982). The best-fitting polynomial regression equation ( $\alpha = .05$  for addition of a variable) of all data on time (i.e.,  $day_2$  equalling the number of days since 12 May, the first day of sampling) was calculated (Fig. 5). The effect of each of the different categories of patches was examined by analysis of variance of the residuals from the polynomial regression (Table 3). Categories of fields (i.e., C, M, or I) were designated using the class variable *fldtype*, and individual cabbage patches within these categories (e.g., C1, M3) were designated using the class variable *field*. There was no significant effect of individual cabbage patches within each category of *fldtype*. Categories of *fldtype* were marginally significantly different ( $P = .0595$ ; Table 3A). The levels of egg density

for the categories within *fldtype* were in the order  $M > C > I$ . Two different a posteriori tests revealed that egg density in M was significantly higher than in I, but that in C it was not significantly different from that in either M or I ( $\alpha = .05$ ; Table 3B). The three regression equations for C, M, and I are plotted in Fig. 6.

The large spatial scale of our experiment ( $> 1$  km in extent) created serious logistical problems in terms of planting and sampling the cabbage patches shown in Fig. 1. Unfortunately, as a result, we were unable to establish more than one set of nine patches. This means that our different *fldtype* patches were only pseudoreplicated (Hurlbert 1984). It could be that *P. rapae* eggs were more abundant in patches M1, M2, and M3 because in that particular area soil, or microclimate, or proximity to wild host plants was especially favorable. In fact, however, we observed no consistent differences in these factors that might explain our observed *fldtype* effects. Therefore, we feel that the results of our analysis of variance (i.e., Table 3) genuinely reflect the influence of patch spatial pattern on *P. rapae* egg density.

#### DISCUSSION

In qualitative terms, the model successfully predicted the rank ordering of *Pieris rapae* egg densities among patches occupying different positions in an experimental spatial pattern (i.e.,  $M > C > I$ ). However, the effect of spatial arrangement as predicted by the model (Fig. 4) appears to be smaller than the effect observed in the field (Fig. 6). There are several possible explanations for this. First, in the field data the egg density in M was significantly higher than in I, but C was not significantly different from M or I (see Figs. 5 and 6 and Table 3). This implies that the actual differences may not be as great as they appear in Fig. 6. Second, the model is based on the assumption that butterfly flight dispersal from patches is unidirectional. However, Jones (1977) showed that the degree of unidirectionality in

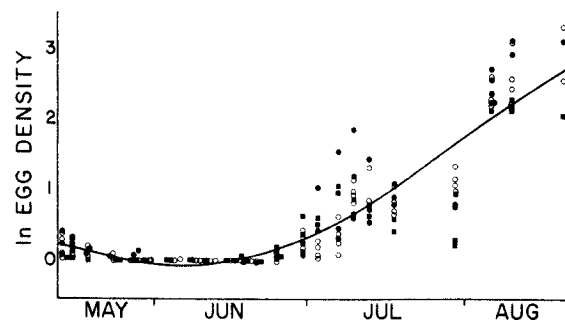


FIG. 5. Log-transformed estimated number of *Pieris rapae* eggs per plant in three categories of cabbage field: ○ field type C (C1 to C4 in Fig. 1), ● field type M (M1 to M3 in Fig. 1), ■ field type I (I1, I2 in Fig. 1). Polynomial regression equation:  $\ln(\text{no. eggs per plant} + 1) = 0.21 - 1.59 \times 10^{-2}(\text{day}_2) + 1.11 \times 10^{-5}(\text{day}_2^2) - 6.95 \times 10^{-8}(\text{day}_2^4)$ ,  $R^2 = 0.863$ , where  $day_2$  = number of days since 12 May (the first day of sampling).

female flight can vary between populations. Deviations from unidirectional flight paths would have the effect of changing the expected probability of females chancing upon cabbage patches. In particular, the daily flight distance would be decreased, which would make patches I1 and I2 less likely to be discovered by dispersers, and patches M1 to M4 more likely to be discovered. This would increase the effect of spatial arrangement on local population size. Finally, it is possible that if stochastic variation were included in the stimulation model, the predicted effect of patch spatial arrangement would be greater. This is particularly likely for this model because it is nonlinear; for example, the survival rate of eggs depends on the density of larvae. Chesson (1981) and Morrison (1986) have shown that biases can be produced by approximating a nonlinear stochastic process by a deterministic model. We did not have estimates of real variability for the parameters in our model, so a deterministic approach was chosen.

The effects of patch spatial arrangement on local population abundance in *P. rapae* can be explained as follows. The high dispersal distance and low host-detection ability of this species tend to reduce the potential effects of patch spatial arrangement. This is because females dispersing from a particular patch quickly become spread over a very large area. This reduces the potential effects of exact spatial relationships among patches on the population size within a particular patch. The contribution of dispersers directly from other patches is therefore low relative to the contributions from butterflies that are "milling about" in the inter-patch area. This results in similar immigration rates in all patches, and reduces the effect of spatial arrange-

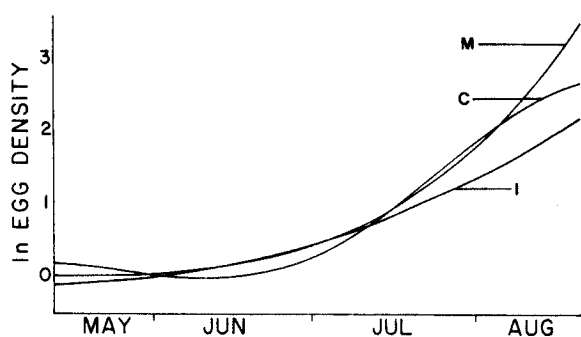


FIG. 6. Separate polynomial regressions of log-transformed egg densities in three categories of cabbage field. Regression equations, where  $day_2$  = number of days since 12 May (the first day of sampling).

- (1) M:  $\ln(\text{no. eggs per plant} + 1) = -0.00594 + 3.52 \times 10^{-6}(day_2^3)$ ;  $R^2 = 0.868$ .
- (2) C:  $\ln(\text{no. eggs per plant} + 1) = 0.179 - 9.48 \times 10^{-4}(day_2^2) + 2.78 \times 10^{-5}(day_2^3) - 1.57 \times 10^{-7}(day_2^4)$ ;  $R^2 = 0.923$ .
- (3) I:  $\ln(\text{no. eggs per plant} + 1) = -0.109 + 2.30 \times 10^{-4}(day_2^2)$ ;  $R^2 = 0.777$ .

Note: the curves for M and I are significantly different ( $P < .05$ ), but the curve for C is not significantly differently from either M or I (Table 3B).

TABLE 3. Analyses of field data of *Pieris rapae* egg densities on nine cabbage patches.

A) Analysis of variance of residuals from polynomial regression of egg density on $day_2$ . See Fig. 5 legend for regression equation. Total degrees of freedom: 223.				
Source	df	Type III ss	F	P
<i>fldtype</i>	2	0.5373	2.86	.0595
<i>field (fldtype)*</i>	6	0.2853	0.51	.8035

B) Means tests for significant differences among <i>fldtype</i> categories ( $\alpha = .05$ ). Mean is the mean value of the residuals from the regression.				
<i>fldtype</i>	N	Mean	Tukey†	Scheffé†
M	74	0.0572	a	a
C	100	-0.0046	ab	ab
I	50	-0.0755	b	b

\* *field (fldtype)* is the individual field (e.g., C1) within the *fldtype* category (e.g., C).

† *fldtype* categories having the same letter are not significantly different.

ment on population abundances. The result is that there is a significant, though relatively small, effect of host-patch spatial arrangement on local abundance in *P. rapae*. This argument is consistent with general simulation results of L. Fahrig and J. E. Paloheimo (*personal observation*) that, for species with high dispersal distances, the spatial arrangement of habitat patches has little effect on local population size.

The results of the present study indicate that it is important to have a good understanding of the dispersal behavior of an organism before one can determine whether the spatial arrangement of habitat patches is likely to have an important impact on population density. If the organism disperses along dispersal corridors, then the spatial relationships among habitat patches are important (Fahrig and Merriam 1985, Lefkovich and Fahrig 1985). However, if the organism disperses large distances in random directions from patches, and does not detect patches from a distance, as in this study, then the spatial arrangement of habitat will have less effect on population dynamics.

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