

## Interpatch dispersal of the cabbage butterfly

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The purpose of this project was to study the dispersal behaviour of female *Pieris rapae* (cabbage butterfly), with the goal of understanding the relationships between population abundance and dispersal mechanisms. Field studies indicated that (i) female flight orientation is not affected by the presence of a host plant patch, (ii) the number of eggs laid by a female on a patch is independent of patch size, at least within the range 18 to 18 000 plants, and (iii) dispersal rate of adult females from host plant patches is high. A model of egg abundance based on these assumptions was found to explain 85.4% of the variation in log egg abundance data taken from the literature. We suggest that, even though females disperse at high rates and are unable to orient towards host patches, populations maintain generally high abundances because host patches are common and widely distributed, and female flight paths are long. Both of these are expected to increase the probability of host detection.

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L'étude du comportement de dispersion des femelles de la Piéride du chou, *Pieris rapae*, a été entreprise dans le but de mettre en lumière les relations entre la densité de la population et les mécanismes de dispersion. Les observations en nature ont démontré que (i) l'orientation du vol des femelles n'est pas affectée par la présence d'un groupe de plantes hôtes, (ii) le nombre d'œufs pondus par une femelle dans un groupe de plantes est indépendant de l'importance du groupe, du moins entre les limites 18 à 18 000 plantes et (iii) la vitesse de dispersion des femelles adultes à partir d'un groupe de plantes est élevée. Un modèle prédictif de la densité des œufs a été élaboré à partir de ces observations et il peut expliquer 85,4% de la variation du log de la densité des œufs évalué d'après les données de la littérature. Il semble donc qu'en dépit de la dispersion rapide des femelles et de leur incapacité de s'orienter vers des groupes de plantes hôtes, les populations aient toujours une densité assez élevée car les groupes de plantes hôtes sont nombreux et très répandus et les femelles sont capables de voler sur de grandes distances. Ces deux facteurs augmentent la probabilité de détection d'une plante hôte.

[Traduit par la revue]

### Introduction

The ability of a species to disperse successfully can be a major factor affecting its abundance (den Boer 1981; Fahrigh and Merriam 1985; Gould and Stinner 1984; Stenseth and Hanson 1981). Theoretical investigations have shown that there is a selective advantage to high dispersal rate when the environment is variable over time and space (e.g., den Boer 1968; Comins et al. 1980; Levin et al. 1984). However, these studies also indicate that the advantage of a high dispersal rate in a variable environment depends on the ability of the disperser to find a new site (i.e., successful establishment). In fact Levin et al. (1984) found that "the optimal level of dispersal is an increasing function of the probability that a propagule will successfully attain a new site."

The cabbage butterfly (*Pieris rapae*) is a successful and abundant species which spreads quickly. Much is known about the behaviour of egg-laying *P. rapae* females. Root and Kareiva (1984) observed the flight paths of individual females in several fields which contained different densities of host plants. They found that (i) eggs were usually laid singly on plants, (ii) females tended to follow linear flight paths, and (iii) females typically passed over many suitable hosts. Root and Kareiva suggest that the "egg-spreading syndrome" produced by this behaviour may have evolved in response to a spatially variable environment. They suggest that females are "spreading the risk" (den Boer 1968) of offspring mortality over space.

The results of Root and Kareiva (1984) suggest that female *P. rapae* flight behaviour causes egg spreading within a host patch. However, *P. rapae* females have a life-span of about 20 days (Gossard and Jones 1977), and can fly large distances each day (Jones et al. 1980; Yamamoto 1981). A single female is therefore likely to lay her eggs on several different host plant patches during her lifetime. The purpose of the current work is to study the between-patch dispersal characteristics of *P. rapae*.

When combined with the within-patch movement behaviour, this study will provide further insights into the overall strategy of *P. rapae* movement and dispersal behaviours.

Jones et al. (1980) studied long-distance movement of *P. rapae* females in a large grid of isolated but evenly spaced host plants. They found that adult *P. rapae* females dispersed about 450 m/day, and their results suggest that movement direction on a particular day was random. To gain further information on *P. rapae* interpatch dispersal behaviour, we conducted field-work to answer the following three questions. First, do ovipositing *P. rapae* females discover new host plant patches by orienting towards them, or must they land on or fly directly over them? Second, once a host plant patch is discovered, does a butterfly lay more eggs on large patches than small ones? Finally, what is the dispersal rate of butterflies from host patches?

### Field studies

#### Host patch detection

From 20 June to 30 August we released 963 wild female *P. rapae* butterflies near cabbage patches at the Cambridge Agricultural Research Station, Cambridge, Ontario. Four hundred and fourteen of these butterflies were collected from a rapeseed plot 14 km from the station, and the remaining 549 were collected from cabbage patches at the station itself. Most of the butterflies were caught while they were laying eggs. The butterflies were released at one of four distances (1, 5, 10, and 20 m) from one of three cabbage patches of different sizes (18, 200, 3600 plants). Each day butterflies were released near one of the three patches; the patches were chosen in sequence, so that approximately equal numbers were released near each patch. Upon capture, the butterflies' wings were marked using coloured markers. The colour combinations indicated the collection site, the release site, and the date of release. Releases were made from all four sides of the patches and occurred no more than 1 h after the butterflies were captured. Captures and releases were made between 1000 and 1400 when egg-laying activity is highest (Jones 1977). A 10% honey

solution (Gossard and Jones 1977) was always present in the cages to ensure that the butterflies would remain more motivated towards egg laying than foraging when they were released. The cages containing the butterflies were placed on the ground at the appropriate distance from the patch for 15–30 min. We then carefully removed the butterflies by hand, one at a time, and waited for them to take flight. The person releasing the butterflies always sat facing the cage and to the left of it relative to the cabbage. Butterflies did show a lower frequency of flying towards the observer. However, this could not affect the butterfly's tendency to fly either towards or away from the cabbage. Also, by positioning the person always to the left, we produced an equal bias toward all four compass directions, since releases were made from all four sides of the patch.

We suggest that our method for releasing the butterflies did not deter them from their normal behaviour. When the same method was followed for butterflies released within a cabbage patch, virtually all immediately resumed egg laying.

When they are "upset," cabbage butterflies show a characteristic behaviour. Instead of flying 1 or 2 m above the ground, they fly straight up to heights of several metres and allow the wind to blow them large distances away (personal observation; Twinn 1925). Ninety-five of the butterflies that we released (9.9%) displayed this behaviour; they were omitted from analyses. Butterflies that landed on flowers, and were therefore clearly not motivated towards egg laying, were also not included; these amounted to 37 (3.8%) of the butterflies. The total sample size was therefore reduced to 831.

We recorded the initial compass direction of flight. We also recorded all sightings of marked butterflies in the three cabbage patches.

The flight direction results were analysed using the following variables. Butterflies were released near one of the three cabbage patches, and were collected from either the rapeseed or the cabbage. Other variables were distance of the release point from the cabbage patch (m), wind speed (km/h), and wind direction (degrees). We also recorded several characteristics of the cabbage patch near which the butterfly was released. These included age of the plants (days) since transplanting, average cabbage plant size (height by width, cm<sup>2</sup>), average number of holes per dm<sup>2</sup> of cabbage leaf area, average plant condition as determined using a scale on which 1 was "very poor condition" (almost dead) and 5 was "perfect condition," average number of *P. rapae* eggs present per plant, average number of young *P. rapae* larvae (instars I and II) present per plant, and average number of old larvae (instars III–V) present per plant.

If we consider two possible responses, flight direction towards or away from the cabbage patch, the overall results indicate no significant tendency for butterflies to fly towards the cabbage. Three hundred and seventy-eight flew towards and 383 flew away ( $\chi^2 = 0.033$ , NS); the remainder (70) flew parallel to the edge of the patch. This result leads to the tentative conclusion that flight direction is random and not directed toward host plant patches.

To further test this, we analysed the data of the butterflies that were observed at a later date (usually 1 day later) in cabbage patches other than the one near which they were released. These were recognized by the coloured wing markings. If the flight paths are generally linear (Jones et al. 1980), then under the assumption of random flight direction, the expected number of observations is calculated as follows. The number of butterflies released at patch *i* is  $n_i$ . The angle whose vertex is at the centre of *i* and which is subtended by patch *j* is  $a_{ij}$ . Therefore, if flight direction is random, the number of butterflies from *i* expected to reach *j* is  $n_i(a_{ij}/360)$ .

A  $\chi^2$  test comparing the expected and observed numbers of observations of marked butterflies indicated no significant difference between the observed and expected values ( $\chi^2 = 2.8$ , *df* = 5; NS). Note that this test is not completely rigorous. If flight paths are not linear, the expected numbers of marked butterflies (Table 1) are probably underestimated. This may be compensated by the fact that we probably did not observe all marked butterflies. Allowing for these reservations, the results support the suggestion that flight orientation of females is not affected by the presence of cabbage.

Because the releases were made under a wide range of conditions,

as indicated by the 12 factors listed above, we analysed the data for the effects of these factors.

First, wind speeds were grouped into five frequency classes. Circular correlations (Batschelet 1981) between wind direction and butterfly flight direction were calculated for each of these frequency classes. At about 17–18 km/h there is a sharp increase in *r*, i.e., in the degree to which the wind "pushes" the butterflies, from 14 to 42%. Gossard and Jones (1977) found that wind speeds over 13–16 km/h inhibit *P. rapae* flight. Therefore, for the remainder of the analysis, we only included the data from the first three wind speed classes (wind speed  $\leq 17$  km/h). For these three classes only, 331 butterflies flew towards the cabbage patch and 317 flew away ( $\chi^2 = 0.030$ , NS).

To determine if any of the remaining 10 factors had a significant effect, each factor was grouped into frequency classes; continuous variables were grouped by examining their frequency distributions. Two-way  $\chi^2$  tests were then performed on the response variable (flight towards or away from cabbage patch) and each of the factors. None of the factors, including distance from the plants, had a significant effect on whether or not the butterflies flew towards the cabbage. This does not preclude the possibility that some combination(s) of the factors might produce a significant effect. However, since there were no significant first-order interactions, it is unlikely that such higher order interactions would account for more than a very small amount of the variation. In any case, most of the factors were highly correlated because they were field measurements over which we had no control. For this reason, we could find no appropriate exact test for effects of such higher order interactions.

In summary, we cannot reject the null hypothesis that flight orientation of female *P. rapae* is not affected by the presence of nearby cabbage patches. This is not to say that females cannot detect host plants from a very short range. The smallest distance from which we released butterflies was 1 m, so we do not know how close to the plant within this 1 m the butterfly must be before detecting it. It is possible that she must actually land on the plant before recognizing it as a host through contact with the tarsi (Traynier 1979). Our result is consistent with that of Renwick and Radke (1983) who found that the presence of cabbage volatiles did not increase the oviposition response of *P. rapae* females. It is therefore unlikely that females can use olfactory detection to find host plants.

#### Number of eggs laid

*Pieris rapae* displays a characteristic egg-laying behaviour. Upon discovering a host plant patch, a butterfly lays several eggs (about 8–10) in succession. Eggs are laid singly, each one normally on a different plant. She then takes a short rest, and then resumes laying. As time goes on, the egg-laying periods become shorter and the rest periods become longer until finally the butterfly takes flight and leaves the patch. We refer to this entire sequence as an egg-laying bout. A bout lasts for approximately 5 to 30 min, and about 5 to 50 (mean = 23.82) eggs are laid during that period.

To determine if the number of eggs laid per egg-laying bout depends on the size of the host plant patch, we observed 33 adult females during oviposition. Each butterfly was observed from the time she discovered a host patch until she left it. Butterflies were observed on patches of a variety of sizes: 18, 200, 450, 840, 1200, and 18 480 plants per patch. There was no relationship between the number of eggs laid per bout and the size of the host plant patch, measured either as number of plants in the patch ( $r = 0.0583$ ,  $p > 0.747$ ), or as area of the patch ( $r = 0.0598$ ,  $p > 0.741$ ) (see Fig. 1).

The fact that the number of eggs laid per egg-laying bout does not vary with the size of the host field is the most likely explanation for the fact that small fields contain higher *P. rapae* infestation rates (per plant) than large fields (Maguire 1983). It is also consistent with Jones' (1977) results for *P. rapae* in Vancouver. She found that ovipositing butterflies tended to return repeatedly to a host plant or field. Our personal observations confirm that this is also true for butterflies in southern Ontario.

#### Dispersal rate

To determine the rate at which adult *P. rapae* females disperse

TABLE 1. Literature survey of mean *P. rapae* egg densities

Reference	Site location	No. of plants	Field dimensions (m)	Mean no. of eggs/plant	Comments
L. Fahrig, unpublished data	Guelph, Ontario	18	2×2	7.46	
		200	6.1×6.1	4.07	
		3600	27.5×63.0	1.34	
		450	15.0×15.0	1.35	
		450	15.0×15.0	1.43	
		450	15.0×15.0	1.73	
		450	15.0×15.0	1.49	
		450	15.0×15.0	4.06	
		450	15.0×15.0	3.60	
		450	15.0×15.0	3.94	
450	15.0×15.0	2.92			
Jones 1977, pp. 197, 205	Vancouver, British Columbia	9	2×2	7.55	
		36	5×5	6.11	
Lathief and Ortiz 1983, pp. 1032, 1034	Virginia	30	3.42×3.68	6.08	
		30	3.42×3.68	7.17	
		30	3.42×3.68	5.42	
		70	4.6×5.5	3.50	
Maguire 1983, pp. 1416–1418	Utah	4	0.91×0.91	12.60	
		16	2.73×2.73	12.03	
		64	6.37×6.37	9.35	
		9	0.87×0.87	3.65	
		81	4.88×4.88	2.38	
		9	0.87×0.87	6.38	
		81	4.88×4.88	3.06	
Maguire 1984, pp. 465, 467	Utah	4	1.82×1.82	26.82	
		16	3.64×3.64	13.71	
		4	0.87×0.87	14.33	
		4	0.87×0.87	5.92	
		25	2.44×2.44	5.02	
		25	2.44×2.44	1.82	
Michaelowicz 1980, pp. 36, 63, 64	Guelph, Ontario	5852	79.7×53.1	1.78	Read from graphs
		5760	62×53	2.32	

NOTE: Conditions for inclusion of a study in the survey are given in the text.

from patches, we observed a patch of 450 plants for 17 continuous days. All adult females observed laying eggs on the patch were caught, individually marked with coloured markers, and then carefully released. Virtually all butterflies immediately resumed egg laying upon release. Colour combinations of observed butterflies (marked on previous days) were recorded each day. A total of 102 butterflies were marked in the 17-day period. The fraction of butterflies that were not observed on days following their marking was 0.74. Excluding two butterflies that remained on the patch for over 12 days, and calling any fraction of a day a day, the average residence time on a patch was 1.3 days. Since the life expectancy of adult *P. rapae* is about 21 days (Gossard and Jones 1977), only a small fraction of the "missing" butterflies were likely to have died. The results indicate, therefore, that the daily rate of dispersal from host patches is very high.

#### Egg abundance model

The field results indicate that (i) flight orientation of *P. rapae* adult females is not influenced by the presence of host plants, (ii) the number of eggs laid by a female on a particular patch is independent of patch size, and (iii) the rate at which

butterflies leave patches is high, relative to their expected life-span. Although the dispersal rate and distance travelled are high, a new patch appears to be detected only when the butterfly is within 1 m of it. We do not know how near to the plant within this 1 m distance the butterfly must be before she detects the patch.

To substantiate this finding, we built two models of *P. rapae* egg abundance. In the first of these models, we assumed that females do not orient towards their host plants from a distance, but find them by chance, as suggested by our fieldwork. In the second model, we assumed the alternative, namely that females detect their host plants from a distance by some methods such as olfaction. We compared these two models against data taken from the literature on egg abundance. The purpose of the modeling exercise was to determine how much of the observed variation in egg abundance could be explained by the two postulated behaviour patterns. A stronger relationship between the first model and egg abundance than between the second model and egg abundance would lend support to the

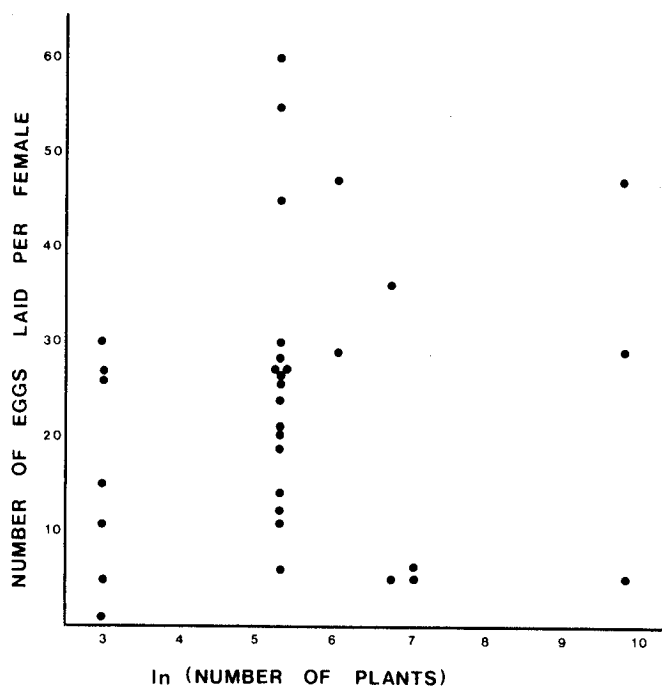


FIG. 1. Relationship between the number of eggs laid per egg-laying bout (for definition see text) by wild females observed on cabbage fields of various sizes: 18, 200, 450, 840, 1200, 18 400 plants.

field result used as an assumption in the first model. We begin by describing the first model; the second model is then obtained by adapting the first.

When searching for host plants, female *P. rapae* characteristically fly along at close to vegetation height, landing occasionally to "test" for the appropriateness of the plants for oviposition (personal observation; Twinn 1924; Root and Kareiva 1984; Renwick and Radke 1983). The search area can therefore be viewed as being two-dimensional from the point of view of the butterfly. Root and Kareiva (1984) found that, in a meadow containing host plants at 7-m spacing, the mean distance between successive landings of *P. rapae* females was about 5 m. If we assume that the host plant patches are rectangular with dimensions greater than  $5 \times 5$  m (as in the case of crop fields), and that butterflies detect the patch by flying directly over it or landing on a plant within it (field result (i)), the probability that a female discovers a particular host plant patch is proportional to the "linear dimension" of the field in the direction perpendicular to the flight path of the butterfly (see Fig. 2). Assuming that the flight angle relative to the field is random, the mean of the linear dimension is  $(l + L)(2/\pi)$  where  $l$  and  $L$  are the dimensions of the field. For rectangular fields, therefore, the linear dimension of the field is proportional to the perimeter of the field.

To develop the model let us first assume we have a host plant patch situated in a large region. Jones (1977) and Jones et al. (1980) developed a random walk-type model to describe the movement of *P. rapae* females. For large populations, the probability of detection can probably be estimated by a simple Poisson process with mean patch detection probability  $q$ . Under this assumption, the average probability of a butterfly detecting the patch within a time interval ( $\Delta t$ ) is  $q(l + L)(2/\pi)\Delta t$ , where  $q$  is a constant whose value depends on the flight behaviour and the size of the region surrounding the patch. The formula

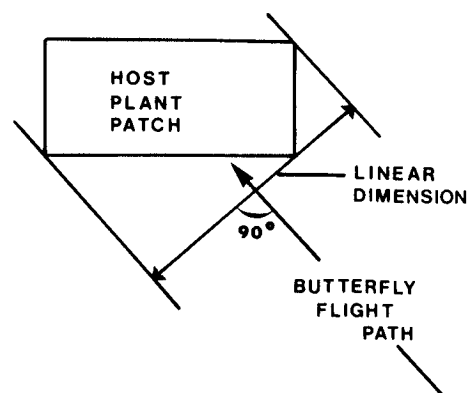


FIG. 2. Illustration of the "linear dimension" of a rectangular host patch field.

can be written more simply as  $p(l + L)\Delta t$ , where  $p = q(2/\pi)$ . If the total number of adult females in the region is  $f$ , then the total number of females laying eggs in the patch in a unit time period (1 day) is  $f(1 - e^{-p(l+L)})$ , and the mean number of eggs laid in the patch per day is  $mf(1 - e^{-p(l+L)})$ , where  $m$  is the mean number of eggs laid per visit;  $m$  is assumed to be independent of patch size (field result (ii)). The total number of eggs in the field at any one time is  $dmf(1 - e^{-p(l+L)})$ , where  $d$  is the development time of eggs. The final model is then

$$[1] \text{ egg density} = dmf(1 - e^{-p(l+L)})/n$$

where  $n$  is the number of plants in the field.

Recall that this model is based on the assumption that females cannot orient toward host plant patches. If this assumption were invalid, and females were able to detect patches from a distance, perhaps by olfaction, we would expect the detection probability to be more closely related to the patch area than to the perimeter. Therefore, we also considered the equivalent model in which the probability of detection of a patch is assumed to be proportional to the patch area instead of the perimeter:

$$[2] \text{ egg density} = dmf(1 - e^{-s(lL)})/n$$

where  $s$  replaces  $p$  in Eq. 1 as the constant of detection probability.

Figure 3 illustrates the relative shapes of the two curves, under the assumption that all patches are square. We standardized  $d$ ,  $m$ ,  $f$ ,  $p$ , and  $s$ , thus allowing both curves to be drawn to the same scale. From Fig. 3 one can see that the two equations predict similar egg densities for large patches. However, for small patches Eq. 1 predicts higher densities than Eq. 2.

The two above models were fitted to data collected from the literature on average number of eggs per patch and patch dimensions. We used only studies that gave results of egg counts averaged over a period of at least several weeks, and for at least two fields of different sizes. Only the host plant species *Brassica oleracea* (cabbage, broccoli, cauliflower, brussels sprouts, kale, collard) was used, to avoid problems of host plant preference (Twinn 1925; Takata 1961; Radcliffe and Chapman 1966). Only those studies for which the number of plants and dimensions of the host field were given, or could be calculated, were included. Table 1 is a summary of the six studies, and the information taken from them. Since the studies occurred in different geographical areas and in different years,

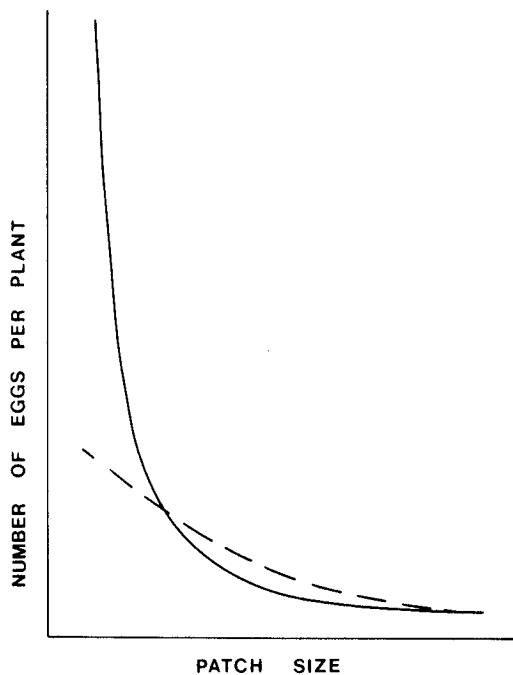


FIG. 3. Two theoretical curves relating *P. rapae* egg density to size (linear dimension) of host plant patch. Solid line, host patch detection proportional to patch perimeter (see Eq. 1); broken line, host patch detection proportional to patch area (see Eq. 2). Exact scaling of axes depends on  $d$ ,  $m$ ,  $f$ ,  $p$ , and  $s$  (see Eqs. 1 and 2).

we would expect to find different values for  $d$ ,  $m$ , and  $f$  in Eqs. 1 and 2 for the different studies. Upon taking logarithms, Eqs. 1 and 2 therefore become

$$\ln(\text{egg density}) = \ln(d_i m_i f_i) + \ln(1 - e^{-p(l+L)}) - \ln(n)$$

and

$$\ln(\text{egg density}) = \ln(d_i m_i f_i) + \ln(1 - e^{-s(IL)}) - \ln(n)$$

respectively, where  $i$  is the study under consideration. If  $p$  and  $s$  are small (certainly true if the area surrounding the patch is large), then  $\ln(1 - \exp(-p(l+L)))$  and  $\ln(1 - \exp(-s(IL)))$  can be approximated by  $p(l+L)$  and  $s(IL)$ . The two models are now

$$[3] \quad \ln(\text{egg density}) = \ln(d_i m_i f_i) + p(l+L) - \ln(n)$$

$$[4] \quad \ln(\text{egg density}) = \ln(d_i m_i f_i) + s(IL) - \ln(n)$$

Analyses of variance of  $\ln(\text{egg density}) - \ln(n)$ , as calculated from the data in Table 1, were performed. The six studies were included as a class variable to determine if the term  $\ln(dmfi)$  varies among studies. Analyses were performed using two models; in one we used the independent variable  $l+L$  (as in Eq. 3) and in the other,  $IL$  (Eq. 4). For Eq. 3, both the study ( $p < 0.0054$ ) and the patch dimension (i.e.,  $l+L$ ) ( $p < 0.007$ ) were significant, and the  $R^2$  for the whole model was 0.854. For Eq. 4, again both the study ( $p < 0.002$ ) and the patch area ( $p < 0.035$ ) were significant factors, but this time the  $R^2$  was 0.804.

Although both patch dimension and area are important when used in separate models, they are highly correlated ( $r = 0.954$ ). To determine if both are actually important, we regressed the residuals from the model in Eq. 3 (since the  $R^2$  is higher) on patch area. The regression is not significant ( $p < 0.725$ ).

When the two models were fitted to the data, we obtained

TABLE 2. Sums of squares (SS) of residuals using (i) model 1: patch detection proportional to patch perimeter, and (ii) model 2: patch detection proportional to patch area

Patch size (no. of plants)	SS using model 1	SS using model 2
<15	3.918	5.069
>15, <50	2.772	4.883
>50, <100	2.077	2.966
>100	2.895	2.715

lower residual sums of squares at small patch sizes for model 3 than for model 4 (see Table 2). The residual sums of squares for the two models were similar at high patch sizes. This indicates that Eq. 3 (or 1) is more accurate at low patch sizes than Eq. 4 (or 2); this difference is important, since it is at the low patch sizes that the two models differ most in shape (Fig. 3).

From the analysis, we therefore have some evidence that *P. rapae* egg density can be described by the equation egg density =  $dmf(1 - e^{-p(l+L)})/n$ . If butterflies were able to detect host patches from a distance through olfaction, we would have expected the equation based on patch area (Eq. 4 or 2) to reflect reality more accurately than that based on perimeter. Since the model based on perimeter is more accurate, we do not reject the field result which acted as an assumption in Eq. 1 (or 3), namely that female flight orientation is not affected by the presence of host plants.

## Discussion

The apparent finding that *P. rapae* females cannot orient towards their larval host plants from a distance is not inconsistent with current knowledge of butterfly host-finding behaviour. As far as we are aware, it has never been demonstrated that any butterfly can orient towards its host plant from a distance greater than 1 m. However, it has been shown that some species, including *P. rapae*, can learn to visually recognize colours or shapes of host plants from short distances (less than 1 m?) (Rauscher 1978; Stanton 1984; Stanton and Cook 1984; Traynier 1984, 1986). In at least one case (Mackay 1985), short-range visual host plant recognition appears to be innate.

It is well known that egg-laying rate in *P. rapae* varies with plant quality (Ives 1978; Jones and Ives 1979; Myers 1985), weather, butterfly age, and time since her last egg-laying bout (Gossard and Jones 1977). These factors undoubtedly explain part of the remaining variance from the analysis of variance (i.e., 14.6%). They would also explain the large variability in the data on egg-laying rate and patch size (Fig. 1).

The results from this study, combined with those of other studies suggest the following scenario. A typical female *P. rapae* butterfly emerges from the pupal stage on or near a host plant patch. She mates within 24 h of emergence, and begins to lay eggs within 24 to 36 h after mating (Jones 1977). In the wild this first egg-laying bout occurs on the host plant patch where the butterfly fed as a larva. During this and other egg-laying bouts the butterfly adopts the egg-spreading behaviour described by Root and Kareiva (1984). The butterfly then leaves the patch almost immediately following the egg-laying bout (daily dispersal rate is 0.74). For the remainder of her adult life, she flies about in search of host plants. Her flight orientation is not influenced by the presence of host plants. She discovers hosts which are directly in her flight path. Upon

encountering hosts, she lays a number of eggs that is independent of the size of the patch (by area or number of plants), 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). This scenario results in both within-patch and between-patch egg spreading.

A commonly observed phenomenon in *P. rapae* is that plants at the edge of a patch usually have higher egg densities than those in the centre (Harcourt 1961; Kobayashi 1965; Jones 1977); this is known as the "edge effect," and is consistent with the above scenario. It can be accounted for by the fact that *P. rapae* females have a higher probability of landing first on plants at the edge of a patch than those in the middle. Essentially, therefore, they appear to find a patch by detecting its edge. They then lay a number of eggs, the number being uncorrelated with patch size. If they fly out of the patch before laying all of their mature eggs, they tend to return to complete the egg-laying bout (Jones 1977). These facts combine to ensure that more eggs are laid at the edge of the patch than in the centre. Single isolated plants, which are "all edge," therefore have very high egg densities (Cromartie 1975).

Finally, we come to the question of how the abundance of *P. rapae* is affected by its dispersal mechanism. Although the dispersal rate is high (about 0.74 per day), and the dispersal distance is large (about 450 m/day (Jones et al. 1980)), the ability to detect a new patch appears to be low. Females must fly directly over a patch to detect it. The degree to which this low detection ability depresses population abundance depends on the distribution of host plants. If hosts are in patches that are isolated from one another by large distances, the probability of host patches occurring in the flight path of a butterfly is low, and a high dispersal rate will depress the population abundance. However, if the host plant is common and more evenly distributed, and if the flight path of the butterfly is long, the probability of detecting host patches is increased.

The relationship between host plant distribution and both host-finding behaviour and abundance of butterflies has been noted elsewhere. Mackay (1985) suggested that the current host-finding behaviour of *Euphydryas editha* is more suited to the distribution of its host plant before man's influence on the habitat, than it is to the current distribution of its host plant. Chew (1981) suggested that the wide distribution of both *P. rapae* and *P. oleracea* in New England can be attributed to the wide distribution of their host plants and the high mobility of both species. Finally, Cappuccino and Kareiva (1985) found that the rarity of *P. virginensis* could be partly explained by the patchy distribution of its host plant in time and space. Unpredictable host plant phenology and dissection of the woodland by open habitat across which this species of butterfly was reluctant to fly both resulted in reduced host-finding success.

Although the cultivated hosts of *P. rapae* are generally located in relatively isolated patches, the wild cruciferous weeds that also act as hosts are common and widely distributed (Twinn 1924). This, combined with the long dispersal distance of *P. rapae* females, probably compensates for the low host detection ability. This may result in the species' high invasion rate and generally high abundance.

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