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**EFFECTS OF DISPERSAL BEHAVIOUR ON RELATIONSHIPS
BETWEEN SPATIAL ARRANGEMENT OF HOST PATCHES
AND LOCAL POPULATION SIZE**

Lenore Fahrig

**Department of Zoology
University of Toronto**

**A Thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy in the
University of Toronto**

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Lenore Fahrig

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Room 309, 63 St. George Street

Effects of Dispersal Behaviour on
Relationships Between Spatial Arrangement
of Host Patches and Local Population Size

Committee:

Professor D.A.G. Mickle, Chairman
Professor D.A. Chant
Professor D.W. Dunham
Professor J.E. Eckenwalder
Professor P. Kareiva, External Examiner
Professor J.E. Paloheimo, Supervisor
Professor W.G. Sprules, Internal Appraiser

EFFECTS OF DISPERSAL BEHAVIOUR ON RELATIONSHIPS BETWEEN
SPATIAL ARRANGEMENT OF HOST PATCHES AND LOCAL POPULATION SIZE

An abstract of a thesis submitted in conformity with the
requirements for the degree of Doctor of Philosophy
in the University of Toronto

Lenore Fahrig, 1987

Field studies of the behaviour of adult female cabbage butterflies (*Pieris rapae*) indicated that they do not detect their host plants from a distance. This finding was corroborated by including host finding behaviour in a model of egg abundance and comparing the predictions with egg abundance data found in the literature. Generalised simulations (not related to any particular species) then led to the prediction that, for organisms which do not detect host patches from a distance, the spatial arrangement of habitat patches should have little effect on local population size. This prediction was confirmed for *P. rapae* through computer simulations and a corresponding field study. At this point in the work therefore, a reasonable explanation for the limited effect of patch spatial arrangement on local population size in *P. rapae* was the inability of dispersing females to detect new host patches from a distance. However, the results of a more complete set of general simulations cast doubt on this conclusion, by producing the hypothesis that an organism's dispersal distance is more important than its ability to detect habitat patches, in determining the degree to which patch spatial arrangement affects local population size. To test this hypothesis would of course require much more field work, probably on several different species. The implication of this result for *P. rapae* is that the high dispersal distance of *P. rapae* is the most likely explanation for the low effect of host patch

spatial arrangement on local population size.

BIOGRAPHY - Lenore Fahrig

1959 Born, (Ottawa, Canada)
1977-1981 B.Sc. (Hons.), Queen's University
1981-1983 M.Sc., Carleton University
1984-1987 School of Graduate Studies, University of Toronto

GRADUATE STUDIES

Major Subject:

Ecology Dr. G. Sprules, Dr. N. Collins

First Minor Subject:

Stochastic Processes Dr. J. Paloheimo

Second Minor Subject:

Statistics Dr. Chakravorti, Dr. Shields

PUBLICATIONS

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Fahrig, L. and H.G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66: 1762-1768.

Lefkovitch, L.P. and L. Fahrig. 1985. Spatial characteristics of habitat patches and population survival. *Ecological Modelling* 30: 297-308.

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Fahrig, L., L.P. Lefkovitch and H.G. Merriam. 1983. Population stability in a patchy environment. In Lauenroth, W.K., G.V. Skogerboe and M. Flug (eds.). *Analysis of ecological systems: state-of-the-art in ecological modelling*. Elsevier, New York. pp. 61-67.

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1. Introduction

The habitat of most species is not evenly distributed over space, but is divided into discrete units, or "habitat patches". Populations therefore are divided into a number of subpopulations, which are interconnected to varying degrees through dispersal of organisms between them.

Dispersal in Patchy Habitats: Single Species

Stability

Several theoretical studies have shown that population stability, measured as long-term survival probability of regional populations, can depend to a large extent on the interchange of organisms between subpopulations in a spatially heterogeneous environment (Reddingius and den Boer 1970, DeAngelis et al. 1979, Lomnicki 1980, Hastings 1982, Vance 1984, Urban and Shugart 1986). In fact, the persistence time of a population can increase by several orders of magnitude due to dispersal among subpopulations (Roff 1974a). The essential idea is that there may be a relatively high probability of local population extinction within a patch, but efficient recolonisation of extinct subpopulations from other patches can ensure virtually indefinite maintenance of the regional population.

Empirical studies have corroborated the theoretical prediction of increased stability with increased interchange among subpopulations. Den Boer (1981) studied a species of carabid beetles (*Pterostichus versicolor*) in a patchy habitat. The species was composed of several subpopulations, which fluctuated out of phase with one another. In simulation experiments, the expected survival time of the species was much increased by the fact that it was composed of interconnected subpopulations. In the event that a local subpopulation were to become extinct, the asynchrony in population fluctuations of subpopulations would ensure that some other subpopulations would be relatively abundant; the habitat of the extinct local population would therefore be recolonised readily by dispersers from one or more of the other subpopulations. The probability of regional extinction would therefore be reduced.

For mice inhabiting patches of wooded area, the survival rate of a subpopulation within a woodlot depends on the degree to which the woodlot is interconnected to other woodlots by fence-rows, along which the mice disperse (Fahrig and Merriam 1985). Cappuccino and Karciva (1985) studied the population dynamics of the rare butterfly, *Pieris virginiensis*. They found that part of the reason for the rarity of the species was that it is unable to disperse efficiently among host plant patches. This may be a recent problem caused by an increase in open areas due to deforestation; the butterflies are reluctant to fly across such open areas. Local extinctions therefore are not readily recolonised, and the overall population size remains low. Davis and Jones (1986) found a similar situation in their study of the common rock rose, *Helianthemum chamaecistus*. They discovered that many suitable habitat sites were unpopulated because interchange among subpopulations is a rare event; the overall population size was therefore lower than it would be if all sites were occupied.

Theoretical and empirical evidence therefore generally supports the notion that interchange among subpopulations through dispersal in a spatially patchy environment contributes significantly to the stability and survival rate of the overall population. Theoretical investigations (without reference to specific species) have also revealed a wide range of additional effects of spatial patchiness. Several studies have revealed conditions under which the stabilising effect of dispersal among subpopulations is expected to be greatest. If dispersal among subpopulations is density-dependent, the stabilising influence of dispersal is slightly enhanced (Reddingius and den Boer 1970). However, heterogeneity among subpopulations in population growth rates and dispersal rates had no significant effect on overall population stability. Roff's (1974b) work indicated that, as the number of habitat patches increases, the stability (measured as time to extinction) of the overall population increases. However, Myers (1976), using a similar measure of stability, found that the mean number of habitat patches did not affect overall population stability. This discrepancy can probably be attributed to the different dispersal characteristics assumed by Roff and Myers. Roff assumed that dispersal occurred only between neighbouring patches, while Myers assumed that all patches were

—equally accessible to all others. Myers showed that factors which lead to resource exploitation; such as high fecundity and density dependent dispersal, destabilise the overall population, and cause a reduction in overall population size, whereas factors which lead to the maintenance of resource refuges lead to the stabilisation of the overall population. A population which is unstable on a local scale (i.e., each subpopulation is unstable) can persist for an appreciable time by balancing extinction and recolonisation only if the average number of occupied patches is above a certain threshold (Gurney and Nisbet 1978). For the particular type of model considered by Gurney and Nisbet, this threshold was found to be on the order of magnitude of $3N^{-.5}$, where N is the total number of habitat patches.

Abundance

Theoretical investigations have also indicated that dispersal among subpopulations can have an effect on overall population abundance. Lomnicki (1980) demonstrated that dispersal results in a decrease in overall population density. Roff (1974a,b) found that the number of habitat patches has no effect on subpopulation size, except at very small numbers of patches (fewer than 15), and for low intrinsic population growth rates. As the intrinsic growth rate increases, the sensitivity of the mean subpopulation size to the number of habitat patches decreases. Population size is also a decreasing linear function of the mean number of local population extinctions per time (Roff 1974a,b). Roff suggested that, in a heterogeneous environment, the population size is kept below the carrying capacity of the habitat, because all sites are not equally accessible to all members of the population. This result was also obtained by Taylor and Taylor (1977).

Population Dynamics

Theoretical studies also indicate that the dispersal of organisms among subpopulations can have an effect on the overall population dynamics. For example, Warkowska-Dratnal and Stenseth (1985) found that dispersal can lead to population cycles. Roughgarden and Iwasa (1986) showed that dispersal can lead to several possible steady state population densities.

Hanski (1982) found that a population composed of interconnected subpopulations tends toward one of two possible states. It either becomes regionally and locally common, or regionally and locally rare. If some local sites exist in which a large local population is unlikely to become small, the species may alternate erratically in the rest of the sites between long-term commonness and rarity (Hanski 1985).

Individual Fitness

Attention has also focussed on the question of the adaptive value of dispersal among subpopulations, from the point of view of individual fitness. The aim of such studies is to explain why an individual would "choose" to produce offspring which disperse from a favourable habitat into an unknown area, where the mortality rate may be high, and the probability of finding a new site may be low. This problem is underlined by empirical studies such as that of Pajunen (1986). In this study, three species of *Daphnia* inhabited 507 rock pools. Pajunen found that the distribution of *Daphnia* is maintained by populations in favourable rock pools. From these sources hazardous marginal areas are continually invaded, but with little success. It is not immediately clear what the selective advantage of such dispersal could be. The answer to this problem appears to lie in the fact that, at any time, each subpopulation is subject to the possibility of extinction. Individuals in a patch in which extinction occurs, and which produce no dispersing offspring, face the risk of having no reproductive output. As stated by Taylor and Taylor (1977), "in a doomed habitat, one offspring capable of migrating at the right time may well have more survival value than a litter of more sedentary morphs". Den Boer (1981) used the term "spreading of risk" for this strategy of spreading one's offspring over a large number of habitat patches, thus reducing the risk of complete obliteration of one's reproductive output. The "spreading of risk" strategy may result in a lower mean total reproductive output over the short term, but this is compensated for by the increase in survival probability of one's offspring, and therefore of the dispersal strategy, over the long term. Root and Kareiva (1984, 1986) have used this hypothesis to explain the dispersal behaviour of phytophagous insects among patches of host plants. Horvitz and Schemske (1986) studied a

perennial herb *Calathea ovandensis*; its persistence depends on periodic disturbance by treefalls. They showed through computer simulation that selection favours local dispersal to safe sites.

The conditions for selection for dispersal have also been studied through theoretical investigation of generalised patchy populations. Hamilton and May (1977) and Motro (1982) showed that, for stable habitats composed of a number of habitat patches, individuals which produce dispersing offspring will have a selective advantage, even if dispersers have a high mortality rate. Their result depends on the assumption that each patch can support only one individual; the maximum reproductive output of a nondispersing type is therefore 1. However, this assumption is very restrictive. In fact, selection acts against dispersal when this assumption is not made (Hastings 1983). Hastings modelled dispersal using passive diffusion, and assumed spatial heterogeneity but temporal constancy in the habitat. The work of Holt (1985) supports this conclusion. This indicates the importance of including temporal variability in patch quality, which results in local extinction. Inclusion of such extinctions in Hastings' model would probably have resulted in selection for dispersal. Such is the case in the work of Comins et al. (1980), who found that the optimal dispersal rate is large when the probability of local populations becoming extinct is large. They also found that the optimal migration rate increases as migration is made less perilous. Levin et al. (1984) found that the optimal level of dispersal is an increasing function of the probability that a dispersing individual will successfully attain a new site. Since in the long run in all situations there is a nonzero probability of complete obliteration locally, zero optimal dispersal is never expected to be found in nature. Levin et al. also found that dormancy reduces the optimal dispersal level, and they suggest that the optimal dispersal distance should be positively correlated with patch size and inter-patch distance.

Dispersal in Patchy Habitats: Species Interactions

Predator-prey

The discussion to this point has dealt with the effects of spatial heterogeneity on single species. Several studies have also addressed the ramifications for interacting species. Probably the best known example is the study by Huffaker (1958) of a predator-prey system involving two species of mites in a heterogeneous habitat of oranges which acted as habitat patches. Huffaker showed that increased spatial heterogeneity increased the survival time of the predator-prey system, since the prey were able to disperse among habitat patches to refuge areas without predators. The predator dispersal did not perfectly track the prey, so the prey were able to maintain growing subpopulations in at least some patches at all times. Vandermeer (1973) and Hastings (1977) demonstrated through theoretical studies the stabilising effect of dispersal among subpopulations in predator-prey systems. Holt (1985) studied a theoretical predator-prey system in which there were two patches, one which contained prey and one which did not. He showed that passive dispersal of the predator between the two patches can stabilise an otherwise unstable predator-prey system. An anomalous outcome of this study is that Holt showed that dispersal between the two patches should be selected against. To explain the maintenance of dispersal, he suggested that, over the long term, the system was periodically colonised by a predator, which had a certain tendency to disperse. Since this dispersal tendency would be selected against, eventually the dispersal rate of the predator would be zero, and the predator population would become unstable and die out. Invasion by another predator would then occur, and the sequence would be repeated. However, this scenario is probably only valid for the case of two patches with no random extinction. As stated above, selection will favour dispersal if there is some probability of local extinctions. In this case, the interplay between colonisation and selection against dispersal of predators, as proposed by Holt, would be unnecessary to explain the maintenance of dispersal.

Host-parasitoid

Spatial patchiness favours persistence of host-parasitoid systems. Chesson and Murdoch (1986) divided spatially heterogeneous host-parasitoid models into two categories. In the first category, the parasitoid density is assumed to be perfectly correlated with the host density. Hassell and May (1974) showed that this type of system is unstable if host density does not vary from patch to patch. The probability of the system becoming stable increases as the variation in host density among patches increases. The second type of host-parasitoid model is one in which the spatial pattern of parasitoid aggregation is assumed to be independent of the spatial pattern of host aggregation. Chesson and Murdoch demonstrated that this type of system is potentially more stable than the first type. However, this increase in stability occurs at a cost of decreased parasitoid efficiency. In general, as the risk of hosts being attacked by parasitoids becomes inversely density dependent (i.e., parasitoids aggregate more independently of host density), stability of the host-parasitoid system becomes more likely. Recently, Morrison and Barbosa (in prep.) have shown that large-scale spatial patchiness may be necessary to stabilise host-parasitoid interactions. They demonstrated that the apparent stability of host-parasitoid systems modelled by Hassell (1985), due to the clumped distribution of the host, depends on the fact that in his simulations Hassell allowed the population to reach abundances of much less than one individual. Morrison and Barbosa showed that extinctions readily occur in Hassell's model if this assumption is not allowed. They suggested that inter-patch movements on a large spatial scale are necessary to compensate for such local extinctions.

Competitors

Theoretical studies of generalised patchy populations have also shown that spatial patchiness enhances the stability of systems of two-species competition (Levin 1974, Slatkin 1974, Shmida and Ellner 1984). Atkinson and Shorrocks (1981) found that coexistence between two competing species can be extended by dividing the habitat into more and smaller patches. Chesson (1985) devised a useful way of describing habitat heterogeneity, and its

effects on the outcome of competition. He defined fixed (over time) spatial heterogeneity (i.e., patchiness) as *pure spatial variation*, variation over time which is uniform over space as *pure temporal variation*, and variation over time which also varies over space (i.e., temporal variation which affects different subpopulations differently) as *spatiotemporal variation*. He found that two-species coexistence is most likely to occur when all of the variation is some combination of pure spatial and spatiotemporal variation. If there is no pure temporal variation, and the population has nonoverlapping generations, the condition for coexistence is that the mean competitive difference between the species, on the log scale, must be less than half the sum of the spatial and spatiotemporal variances. In a spatially variable environment, with each of the two species favoured in different patches, overall positive growth rates can occur for both species at low population densities. Chesson also demonstrated that variation in the ratios of the two species' dispersal rates can favour coexistence. Comins and Noble (1985) also found that spatiotemporal variation in the environment could allow long-term coexistence of competitors. Hanski (1983) showed that the probability of coexistence increases with increasing difference between the time scales of the within-patch (local) dynamics and the between-patch (regional) dynamics. Hastings (1980) studied the effects of spatiotemporal variation on coexistence of several competing species. He showed that an intermediate level of disturbance (i.e., spatiotemporal variation) leads to the largest number of coexisting species.

Importance of Explicit Spatial Pattern

The importance of spatial-heterogeneity (i.e., patchiness) as a factor affecting population dynamics is therefore well established. However, there are several levels of spatial heterogeneity which may be considered, depending on the question one is asking. In the theoretical studies described above, the questions centre on whether the population dynamics differ in the presence and absence of spatial heterogeneity. Therefore, patchiness is included in these models in the simplest way possible; the habitat is either patchy or it is not patchy. The actual spatial distribution of habitat patches is a second level of spatial heterogeneity. To model the various effects of different spatial arrangements of patches, one must explicitly include the

spatial relationships among patches in the model. This renders models mathematically intractable; instead they must be studied through computer simulation.

Dispersal Directionality

Lefkovitch and Fahrig (1985) studied the effect of habitat patch spatial arrangement on population survival through simulation experiments, for the special case in which dispersal between patches depends on the presence of a "dispersal corridor" linking the patches. This system was modelled on the example of white-footed mice (*Peromyscus leucopus*) living in patches of woods, which may be interconnected by fencerows along which the mice disperse (Fahrig and Merriam 1985). Lefkovitch and Fahrig found that, for such groups of interconnected patches, the survival time of a subpopulation depends on the size of the largest geometric figure of which the patch forms a part, through its connections with other patches. These results clearly apply only to species for which dispersal occurs along such "dispersal corridors". This is a highly directed form of dispersal, in which the probability of organisms dispersing from one particular patch to another one is either very low or quite high, depending on whether or not the two patches are linked by a dispersal corridor. The purpose of the present study was to examine the effects of habitat spatial pattern on local population size, for species which do not disperse along dispersal corridors.

Dispersal Directionality of Herbivorous Insects: Host Patch Detection

In the case of herbivorous insect species, dispersal often is not directed from one host plant patch to another, along corridors. This is not to say that insect dispersal is not directional; dispersers may follow wind or water currents, or gradients of light or gravity. However, dispersing insects are generally not channelled specifically between patches. The probability of insects dispersing from one particular patch to another therefore depends to a large extent on the ability of the dispersers to detect host patches from a distance.

In general, the initial (i.e., long-range) detection of host plants by herbivorous insects is usually visual (Feeny et al. 1983), and chemical recognition plays a major role in close-range

recognition. Wiklund (1984) studied the egg-laying behaviour of 51 species of butterflies; species which use visually apparent host plants find their hosts without having to alight on non-host plants. However, those which use hosts that are visually non-apparent frequently alight on non-hosts before finding an appropriate plant for oviposition.

The two main components of visual detection are colour and shape. Colour recognition can generally occur from farther away than shape recognition (Stanton 1983). Butterflies have the widest visual spectral sensitivity (ultraviolet to red) among animals (Silberglied 1984) which is particularly important for those butterflies which lay eggs on the inflorescences of host plants (e.g., Courtney and Duggan 1983, Wicklund and Ahrberg 1978). In some insects, colour recognition is less well defined. For example, boll weevil (*Anthonomus grandis*) adults have a generalised ability to distinguish between blue-green and other colours and therefore between plants and non-plants (Cross 1973). Insects which use a combination of colour and shape in host recognition include the pipevine swallowtail butterfly (*Battus philenor*) (Rausher 1978), the green peach aphid (*Myzus persicae*) (Hodgson and Elbakheit 1985), and the apple maggot fly (*Rhagoletis pomonella*) (Moericke et al. 1975). Douglas fir bark beetles (*Dendroctonus pseudotsugae*) (McMullen and Atkins 1962) and desert locusts (*Schistocerca gregaria*) (Wallace 1958) orient towards black/white boundaries and vertical silhouettes.

Although chemical recognition of host plants is common among herbivorous insects, it appears to function largely for very short range (under 1m) recognition (Jander 1963, Finch 1980, Stanton 1983). Typical distances demonstrated for chemical recognition are 50 cm for the onion fly (*Hylema antiqua*) (Dindonis and Miller 1980), 125 cm for the Colorado potato beetle (*Leptinotarfa decemlineata*) (Visser and Nielson 1977), and 20 cm for the citrus butterfly (*Papilio demoleus*) (Saxena and Goyal 1978). Other insects in which short-range chemical recognition of hosts has been demonstrated include the rice brown planthopper (*Nilaparvata lugens*) (Sogawa 1982), the cherry-oat aphid (*Rhopalosiphum padi*) (Leather 1986), and a diamondback moth (*Acrolepiopsis assectella*) (Lecomte and Pouzat 1986).

Although it appears that initial host orientation is normally visual, which may then be followed by short-range chemical host recognition, the sequence is reversed in one well-documented case, the cabbage root fly (*Delia radicum*) (Prokopy et al. 1983). This fly perceives its host plant through chemical cues from 5-15 m downwind of the plant patch; this is apparently the maximum authentic recorded distance for insect orientation to naturally produced volatiles of host plants in the field. The final landing site for the cabbage root fly is chosen using visual cues, from within 25 cm of the plants.

Most insects seem to be able to improve host detection on a short-term basis through learning (e.g., Rausher 1978). In fact, Papaj and Rausher (1983) state that conditioning of host preference has been observed almost everywhere it has been examined.

Although there is much evidence for short range host recognition in herbivorous insects, Thorsteinsten's (1960) statement that "there seems to be no critical evidence that insects can orientate to plants beyond a few metres" appears to still hold true (Finch and Skinner 1982). On the other hand, herbivorous insect dispersal distances range from tens of metres (e.g., Kareiva 1982) to hundreds of metres (e.g., Cross 1973, Jones et al. 1980), to tens or hundreds of kilometres (e.g., Kennedy and Stroyan 1959, Bateman 1972). Relative to these distances, host detection distances are very small. For insects dispersing among host plant patches, therefore, dispersal can not be considered to be directed from one patch to the next; the probability of dispersers from a particular patch detecting another particular patch must be low for most herbivorous insects.

Purpose and Outline

The purpose of this work was to study the effect of patch spatial pattern on local population size for species which do not disperse through dispersal corridors. In particular, the work was concerned with the question: how does host detection ability in a herbivorous insect affect relationships between host patch spatial arrangement and local population abundance? I studied this question in the context of the cabbage butterfly (*Pieris rapae*).

I conducted field studies on *P. rapae* to determine the host detection ability of adult females. The results of the field studies were corroborated using a model relating dispersal behaviour to egg densities of *P. rapae*. I then conducted computer simulations to form general (i.e., not limited to *P. rapae*) predictions concerning the relationship between patch detection ability and the influence of patch spatial arrangement on local population abundance. Specific simulations of *P. rapae* populations in a spatially explicit patchy habitat were then conducted. These were used to produce specific predictions concerning the effects of host patch spatial arrangement on local abundance of *P. rapae* for a particular spatial arrangement of host patches. Field studies were then conducted to examine the validity of the simulation results. Finally a large set of general simulations was conducted, to study the importance of host detection ability, relative to other aspects of dispersal behaviour, on local population abundance.

2. Life History of the Cabbage Butterfly

Adult *P. rapae* are normally first observed in flight at the end of April in southern Ontario (Michaelowicz 1980); emergence from overwintering diapause continues into late May (Harcourt 1966). Oviposition usually commences at the beginning of May. There are 3.5 generations per summer, each of which includes eight stages: egg, five larval instars, pupa, and adult.

P. rapae females oviposit primarily on plants in the family Cruciferae, and occasionally on plants in the families Capparidaceae, Resedaceae and Tropaeolaceae (Harcourt 1963, Twinn 1924). Host plants include agricultural crops such as *Brassica oleracea* (cabbage, broccoli, brussels sprouts, cauliflower, kale,) turnip (*Brassica rapa*), radish (*Rhaphanus sativus*), mustard (*Brassica hirta*) and rapeseed (*Brassica napus*), and wild cruciferous weeds such as yellow rocket (*Barbarea vulgaris*), shepherd's purse (*Capsella bursa-pastoris*), wild mustard (*Sinapis arvensis*) and common pepper grass (*Lepidium densiflorum*) (Parker 1970, Richards 1940). When given a choice, ovipositing females lay many more eggs on commercial host plants than on wild hosts (Jones and Ives 1979). Adult butterflies feed on the nectar of many deep corolla flowers including dandelion (*Taraxacum officinale*), sweet clover (*Melilotus officinalis*), vetch (*Vicia cracca*), burdock (*Arctium minus*), Canada thistle (*Cirsium arvense*) and wild radish (*Raphanus raphanistrum*) (Twinn 1925). Egg-laying occurs primarily between 10:00 h and 14:00 h, while adult feeding occurs before and after these times (Jones 1977).

Development times of eggs, larvae and pupae are highly dependent on temperature (Richards 1940, Jones and Ives 1979, Michaelowicz 1980). For example, development from egg to adult requires about 53 days at an average temperature of 17 ° C but only 20 days at 27 ° C (Jones and Ives 1979, Michaelowicz 1980). Development times of individual stages at an average temperature of 21 ° C are shown in Table 1. The lifespan of an adult is approximately 20 days (Gossard and Jones 1977). Jones and Ives (1979) also found that larvae on young plants always completed their early instars 20-25% faster than those on older plants.

Table 1. Development times of immature stages of
Pieris rapae at 21 ° C.

Stage	Development Time (days)
egg	4.6
first larval instar	3.4
second larval instar	2.4
third larval instar	2.2
fourth larval instar	2.0
fifth larval instar	4.2
pupa	10.4

Before pupating, the fifth larval instar of *P. rapae* ceases feeding and there is a "wandering phase" (Richards 1940, Harcourt 1961). Harcourt observed that "mature larvae readily migrate from the plants in search of suitable pupation sites, such as fence posts and buildings near the periphery of the field." Richards (1940) found that as the season progressed, the tendency to wander increased so that "in the first brood, many pupae are found on the cabbages whereas in the later broods only a few."

P. rapae overwinters in the pupal stage (Harcourt 1966, Richards 1940). Virtually no pupae of the first generation enter diapause, but the "larvae of the second and third generations produce an increasing number of dormant pupae as the season progresses, till, finally, at the end of the season, all the pupae formed, even if kept warm, refuse to emerge without a diapause" (Richards 1940).

Male *P. rapae* butterflies are strongly attracted to small white objects and actively search host plants for females (pers. obs.). This results in the fact that adult female *P. rapae* normally mate within 24 hours of emergence from the pupal stage, and begin to lay eggs within 24-36 hours after mating (Jones 1977).

Gossard and Jones (1977) studied the factors which affect egg-laying by female *P. rapae*. They found that the number of eggs laid per day depends mainly on the amount of sunlight (solar radiation), the temperature, and the age of the butterfly. Egg-laying rate increases with increasing sunlight and temperature (Gossard and Jones 1977) and peaks at 7-9 days after female emergence (Gossard and Jones 1977, Michaelowicz 1980). Females also lay more eggs on larger plants (Harcourt 1966, Ives 1978, Jones and Ives 1979). Ives (1978) also found that the presence of eggs or larvae did not affect a female's tendency to lay eggs on a plant, but that plants severely damaged by larval feeding received slightly fewer eggs.

There are many factors which influence the mortality rates of the various stages of *P. rapae*. Dempster (1967) estimated that 20-25% of eggs, larvae and pupae were attacked by bird predators and 25-50% by arthropods. Baker (1970) and Harcourt (1966) also found signi-

ficant bird predation and Jones and Ives (1979) and Ives (1978) found wasp predation of larvae.

Parasitism results in from 12-63% mortality in the fourth and fifth larval instars and pupae (Pimentel 1961, Richards 1940, Harcourt 1966, Baker 1970, Michaelowicz 1980). Michaelowicz (1980) found that parasitism was the single most important cause of mortality in the fifth larval instar and the pupae, and that the rate of parasitism increased markedly as the season progressed.

Attack by virus and other diseases is another important mortality factor in the larvae, particularly the fourth and fifth instars (Jones and Ives 1979, Baker 1970). Dempster (1967) estimated that 0.8-4% of all larvae were diseased, while Baker (1970) found that 62% of fifth instar larvae were diseased. Attack by virus and other diseases is probably more important in wet than dry weather.

The only life history stage for which density-dependent mortality has been demonstrated is the egg. Egg mortality increases with increasing number of larvae per plant (Jones and Ives 1979) and with decreasing number of eggs per plant (Kobayashi 1960).

Virtually nothing is known about the factors which influence mortality of adult *P. rapae*. This is because the adults are highly mobile (Jones et al. 1980) and, therefore, it is not possible to keep track of a cohort for its lifespan. Gossard and Jones (1977) determined a survivorship curve for caged adults kept outside. Their results are not likely to be representative of survival rates of butterflies in the wild.

3. Dispersal and Host-finding Behaviour of the Cabbage Butterfly:

Field Studies

As stated in the general introduction, the overall aim of this study was to examine the role of host plant patch detection ability on the relationship between habitat patch spatial arrangement and local population abundance of a phytophagous insect species (*P. rapae*). In this chapter, I report the results of field studies in which I examined the inter-patch dispersal, host detection, and egg-laying behaviour of adult female *P. rapae*.

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: (i) eggs were usually laid singly on plants, (ii) females tended fly in straight lines 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. Females "spread the risk" (den Boer 1968) of offspring mortality over space.

The results of Root and Kareiva suggest that female *P. rapae* flight behaviour causes egg-spreading within a host patch. However, *P. rapae* females have a lifespan of about 20 days (Gossard and Jones 1977) and can fly long distances, from 250 to 700 m net distance, in the course of a 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.

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 per day, and their results suggest that movement direction on a particular day was random.

The purpose of the studies reported in this chapter was to gain further information concerning the between-patch dispersal characteristics of *P. rapae*. I conducted fieldwork 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?

Host Patch Detection

Experiment 1

From 20 June to 30 August 1984 I released 963 wild female *P. rapae* butterflies near cabbage patches at the Guelph University agricultural research station, near Cambridge, Ontario. Four hundred and fourteen of these 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. They were kept in a 50x50x50 cm wood-framed cage with a wooden floor and wire mesh on the other 5 sides. The butterflies were released at one of four distances (1, 5, 10, and 20 m) away from one of three cabbage patches of different sizes (18, 200, and 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 one hour after the butterflies were captured. Captures and releases were made between 10:00 and 14:00 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 toward 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 minutes. I then carefully removed the butterflies by hand, one at a time, and waited for them to take flight. While releasing the butterflies I always sat facing the cage and to the left of it, relative to the cabbage. Butterflies showed a lower frequency of flying toward the observer. However, this could not affect the butterfly's

tendency to fly either towards or away from the cabbage. Also, by positioning myself always to the left, I produced an equal bias toward all four compass directions, since releases were made from all four sides of the patch.

I suggest that my 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, 88.4% (i.e., 90 of 102) of them immediately resumed egg-laying.

Cabbage butterflies, when "upset", show a characteristic behaviour. Instead of flying one or two metres above the ground, they fly straight up to heights of several metres and allow the wind to blow them large distances away (pers. obs., Twinn 1925). Ninety-five of the butterflies which I released (9.9 %) displayed this behaviour; they were omitted from analyses. Butterflies which landed on flowers, and were therefore clearly not motivated toward egg-laying were also not included; these amounted to 37 (3.8 %) of the butterflies. The total sample size was therefore reduced to 831.

I recorded the initial compass direction of flight. I 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 in m, wind speed in k.p.h, and wind direction in degrees. I also recorded several characteristics of the cabbage patch near which each butterfly was released. These included age of the plants in days since transplanting, average cabbage plant size (height by width) in cm^2 , average number of holes per dm^2 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 small *P. rapae* larvae (instars I and II) present per plant, and average number of large larvae (instars III-IV) present per plant.

If I 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 ($\chi^2=0.033$, N.S.); 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, I analysed the data of the butterflies that were observed at a later date (usually one day later) in cabbage patches other than the one near which they were released. These were recognised 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 χ^2 test (see Table 2) comparing the expected and observed numbers of observations of marked butterflies indicated no significant difference between the observed and expected values ($\chi^2=2.8$, d.f.=5; n.s.). Note that this test is not completely rigorous. If flight paths are not linear, the expected numbers of marked butterflies are probably underestimated. This may be compensated for by the fact that I 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 is indicated by the 12 factors listed above, I 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. These are shown in Table 3. At about 17-18 k.p.h. there is a

Table 2. Expected and observed numbers of marked cabbage butterflies released near and observed on three cabbage fields (L=large, M=medium, and S=small). See text for method of calculation of expected values.

From Field	To Field	Expected	Observed
S	M	2	1
S	L	9	12
M	S	1	1
M	L	14	12
L	S	1	0
L	M	5	5
$\chi^2=2.8(\text{N.S.})$			

Table 3. Circular correlations between wind direction and butterfly flight direction for 831 cabbage butterflies.

Wind Speed (k.p.h.)	<i>r</i> (%)
0 - 8	16
9 - 13	7
14 - 17	14
18 - 21	42
22 - 27	65

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 k.p.h. inhibit *P. rapae* flight. Therefore, for the remainder of the analysis, I only included the data from the first three wind speed classes (wind speed ≤ 17 k.p.h). For these three classes only, 331 butterflies flew toward the cabbage patch and 317 flew away ($X^2=0.030$, N.S.).

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 contingency table tests were then performed on the response variable (flight towards or away from cabbage patch) and each of the factors. The tables are given in Appendix 1. 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 I had no control. For this reason, I could find no appropriate exact test for effects of such higher order interactions.

Experiment 2

The results of Experiment 1 lead to the tentative conclusion that dispersing egg-laying adult female *P. rapae* do not detect patches of host plants from a distance, but come upon them by chance. This result was considered to be very important, because the main purpose of the thesis research was to determine how host patch detection ability influences the relationships between host patch spatial arrangement and local population size. A second experiment was therefore conducted to test the results of the first.

If dispersing females do not detect host patches from a distance, then the rate of immigration of females into a host plant patch should be similar to the rate of immigration into a

non-patch area of equal size. I therefore decided to measure immigration rates into host and nonhost areas to determine if they differed.

The study was conducted from 24 April to 11 August 1986, on the Guelph University agricultural research station, near Elora, Ontario. On days which were sunny and calm (i.e., appropriate flight conditions for *P. rapae*), I observed either a host plant patch containing 200 to 400 cabbage plants and of dimensions 10m by 10m, or an area without host plants, also of dimensions 10m by 10m. Four different sites were used for both host and non-host areas, to ensure that the results would not reflect an anomalous condition in a particular spot. All non-host areas were within the research station, but at least 60m from the host patches. The non-host areas included sections of a barley field, a grass-covered roadway, a weedy roadway, and a weedy field. Every second day of observation, a host patch was observed, and every other day a non-host area was observed. Each day of observation began just before onset of flight of cabbage butterflies, which normally occurs sometime between 9:30 and 11:30 AM, depending on the temperature. I attempted to capture all cabbage butterflies, both male and female, which crossed over or landed in the observation area (i.e., the cabbage patch or the non-host 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. I attempted to capture all butterflies, but gave up if the chase took me more than 50m 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 data are shown in Appendix 2.

It was considered possible that the initial immigration rates into the cabbage patches would be inflated by any butterflies which remained on the patch from the previous day, and also by any butterflies which emerged from the pupal stage on the patch over the previous night. Therefore, both the total immigration rates (i.e. over the entire observation period), and the immigration rates in the first hour of observation were analysed. In both cases, numbers of males, females, "?"s, and the total of the three were analysed. In all cases the observations

were transformed to $\ln((\frac{n}{t})+1)$, where n is the number of butterflies captured (or observed), and t is the total observation time in minutes ($t=60$ for analyses of results from the first hour only). This transformation accounts for the fact that the total observation time varied depending on the date; it also removes the positive relationship between n and the variance of n .

Analyses of variance were performed on the 8 subgroups of the data described above (i.e. males, females, "?", and total, for each of "total time" or "first hour only"). The class variable "host or non-host area" was included, as well as first, second, and third order terms d , d^2 and d^3 , where d is the number of days since April 24 (the first day of observation). In all cases, the two terms d and d^2 were found to be significant. In no case was there any significant difference between the number of immigrants in host or non-host areas. Figure 1 illustrates the data for the total immigration rates for the total observation period. Figure 2 illustrates the data for the immigration rates of females butterflies within the first hour of observation. The analyses of variance are given in Appendix 3.

The two experiments on host plant detection (Experiments 1 and 2) indicate that flight orientation of female *P. rapae* is not affected by the presence of nearby cabbage patches. This is not to say that females can not detect host plants from very short range. The smallest distance from which I released butterflies in Experiment 1 was one metre, so I do not know how close to the plant within this one metre the butterfly must be before detecting it. It is possible that she must actually land on the plant before recognising it as a host through contact with the farsi (Traynier 1979). The results of the studies of host detection ability are 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.

Figure 1. Ln-transformed immigration rates vs. date in number of days since April 24, 1986.

N : total number of *P. rapae* butterflies. MIN : observation time in minutes. Open squares: immigration rate onto a 10m by 10m non-host area. Closed squares: immigration rate onto a 10m by 10m cabbage patch.

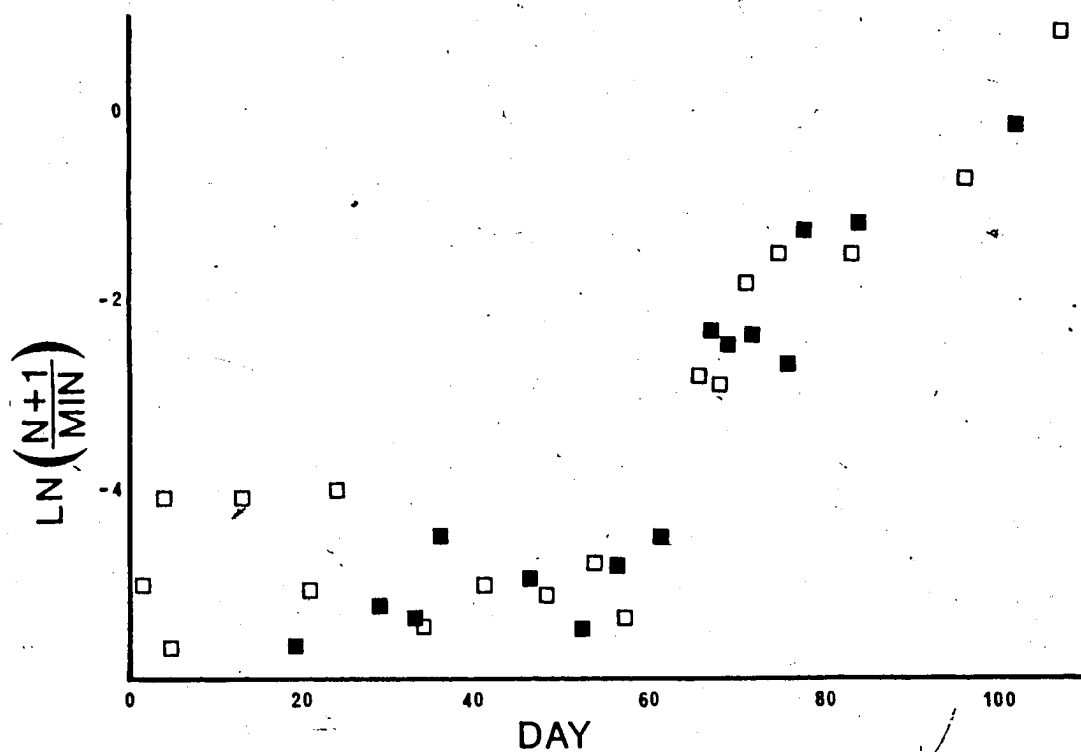
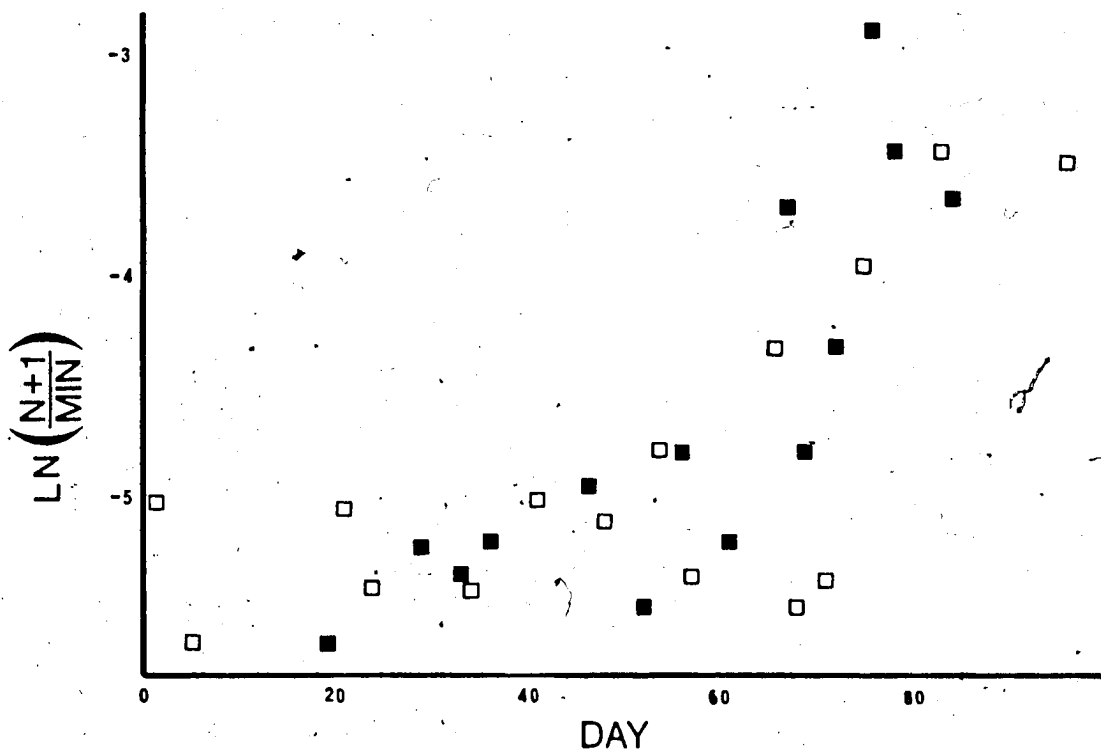


Figure 2. Ln-transformed immigration rates of females in the first hour of observation vs. date in number of days since April 24, 1986. *N*: number of *P. rapae* female butterflies. *MIN*: observation time (= 60 min). Open squares: female immigration rate onto a 10m by 10m non-host area. Closed squares: female immigration rate onto a 10m by 10m cabbage patch.



Number of Eggs Laid

P. rapae display 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. I 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.

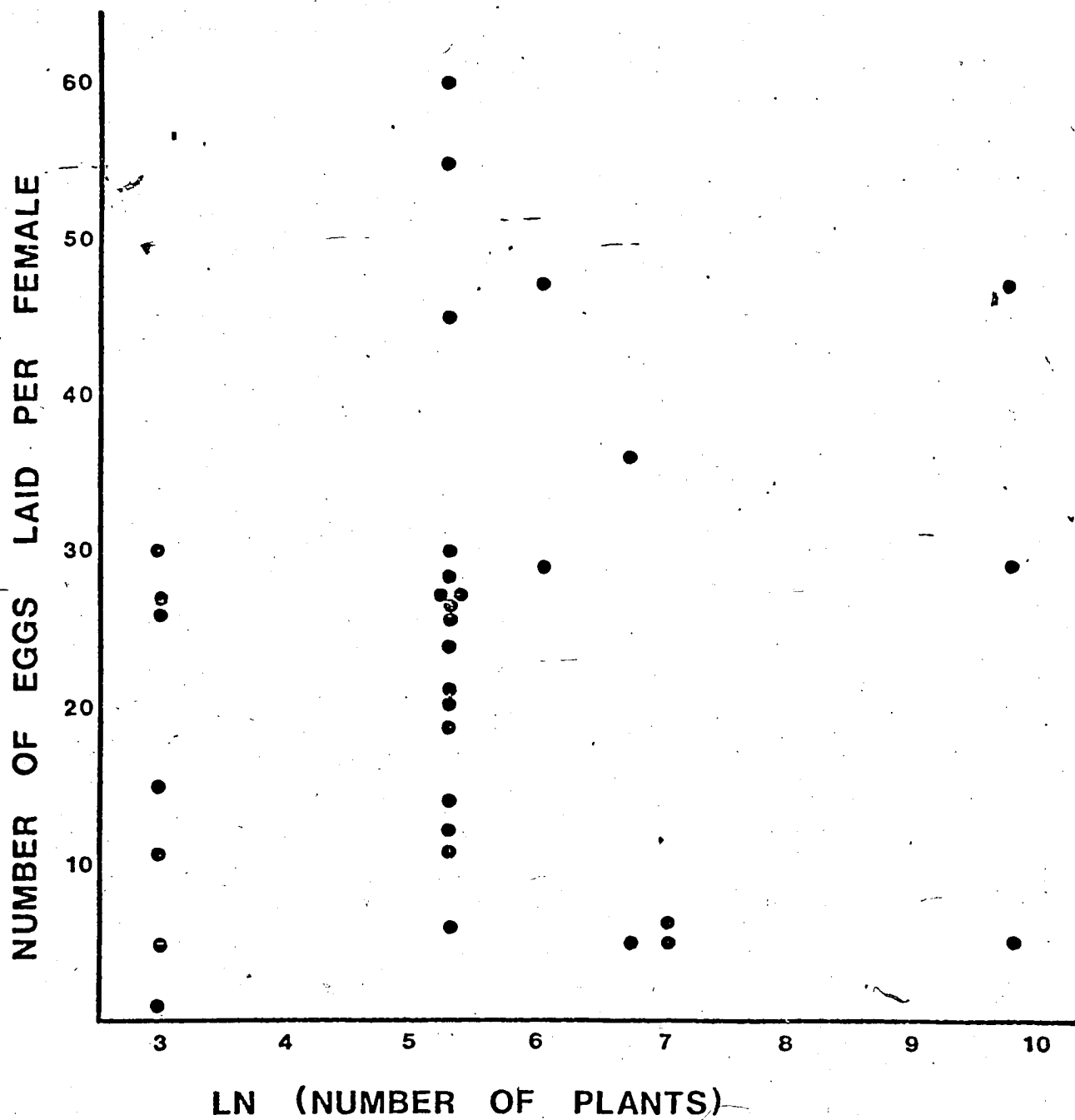
To determine if the number of eggs laid per egg-laying bout depends on the size of the host plant patch, I observed 33 adult females during oviposition. Each butterfly was observed from the time she discovered a host patch until she left it. Butterflies were observed in July 1984 on patches with 18, 200, 450, 840, 1200, or 18,480 plants per patch. The data are illustrated in Figure 3. 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 ($r=0.0598$, $p>0.741$).

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. My personal observations confirm that this is also true for butterflies in southern Ontario. The ability to return to a host plant is most likely facilitated by short-term visual memory (Traynier 1979, 1984, 1986).

Dispersal Rate

To determine the rate at which adult *P. rapae* females disperse from patches, I observed a patch of 450 plants for 17 continuous days from 16 July to 1 August 1985. All adult females observed laying eggs on the patch were caught, individually marked with coloured markers

Figure 3. 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.



and then carefully released. 88.4% of the butterflies (i.e., 90 of 102) immediately resumed egg-laying upon release. Colour combinations of observed butterflies (marked on previous days) were recorded each day. Altogether, 102 butterflies were marked in the 17 day period. The fraction of butterflies which were not observed on days following their marking was 74%. Excluding two butterflies which 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 20 days (Gossard and Jones 1977), only a small fraction of the "missing" butterflies was likely due to mortality. The results indicate, therefore, that the daily rate of dispersal from host patches is very high. The data are shown in Appendix 4.

Summary of Dispersal and Host Detection Behaviour

The results described in this chapter, combined with those of other studies (Richards 1940, Harcourt 1966, Gossard and Jones 1977, Jones et al. 1980, Jones 1977, Root and Kareiva 1984, Renwick and Radke 1983, Ives 1978, Jones and Ives 1979, Myers 1985), 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 and the adults live for about three weeks. Male adults are strongly attracted to small white objects, and actively search host plant patches for females. Therefore, most females are mated within 24 hours of emergence; they begin to lay eggs within 24 to 36 hours after mating. It is likely that in the wild this first egg-laying bout will often 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. Females leave host patches almost immediately following an egg-laying bout; the daily dispersal rate from host patches is about 0.74. The average daily net dispersal distance is 250 to 700 m. Females spend about 3 to 5 hours a day in flight if the weather is favourable. Therefore, since only 15 minutes is required, on average, to lay the total daily number of mature eggs, most of the butterflies' time in flight is spent in non-host 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. Although flight direction within a particular day is highly directional, flight direction changes at random from one day to the next. When searching for host plants, females fly along close to the vegetation, stopping every few metres to test the suitability of plants for egg-laying. Suitability is determined by testing for the presence of glucosinolates through chemoreceptors located on the tarsi. Flight orientation is not influenced by the presence of host plants; females discover only those hosts which are directly in their flight paths. The number of eggs laid on a host patch 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 and the quality of the plants.

4. Dispersal and Host-finding Behaviour of the Cabbage Butterfly:

Modelling Investigation

The field results in chapter 3 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 lifespan. 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. I 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, I built two models of *P. rapae* egg abundance. In the first of these models, I assumed that females do not orient towards their host plants from a distance, but find them by chance, as suggested by the field work. In the second model, I assumed the alternative, namely that females detect their host plants from a distance by some method such as olfaction. I compared these two models against data taken from the literature on egg abundance. The purpose of the modelling 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 field result used as an assumption in the first model. I 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 (pers. obs., Twinn 1924, Root and Karciva 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 Karciva (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 I assume that the host plant patches are rectangular with dimensions greater than 5 by 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 Figure 4). Assuming 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.

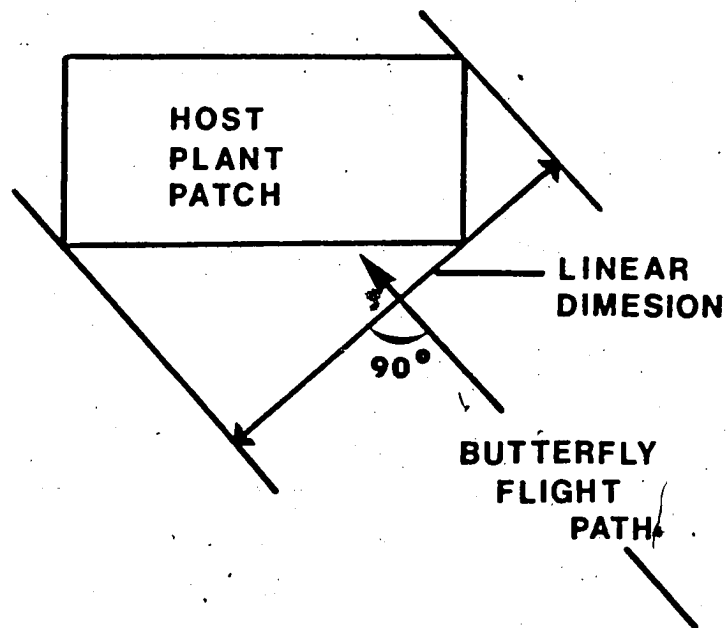
To develop the model let us first assume we have a host plant patch situated in a large region. Jones (1977) and Jones et al. (1980) developed a random walk-type model to describe the movement of *P. rapae* females. For large populations, the probability of detection can probably be estimated by a simple Poisson process with mean patch detection probability q . Under this assumption, the average probability of a butterfly detecting the patch within a time interval (Δt) 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 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 (one 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

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

where n is the number of plants in the field.

Recall that this model is based on the assumption that females can not orient towards host plant patches. If this assumption were invalid, and females were able to detect patches from a distance, perhaps by olfaction, one would expect the detection probability to be more closely related to the patch area than the perimeter. Therefore, I also considered the

Figure 4. Illustration of the "linear dimension" of a rectangular host patch field.



equivalent model in which the probability of detection of a patch is assumed to be proportional to the patch area instead of the perimeter, i.e.,

$$\text{egg density} = dmf(1 - e^{-s(L)})/n, \quad (2)$$

where s replaces p in equation (1) as the constant of detection probability.

Figure 5 illustrates the relative shapes of the two curves, under the assumption that all patches are square. I standardised d , m , f , p and s , thus allowing both curves to be drawn to the same scale. From Figure 5 one can see that the two equations predict similar egg densities for large patches. However, for small patches equation 1 predicts higher densities than equation 2.

The two above models were fitted to data collected from the literature on average number of eggs per patch, and patch dimensions. I used only studies which 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 4 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, I would expect to find different values for d , m , and f in equations 1 and 2 for the different studies. Upon taking logarithms, equations 1 and 2 therefore become

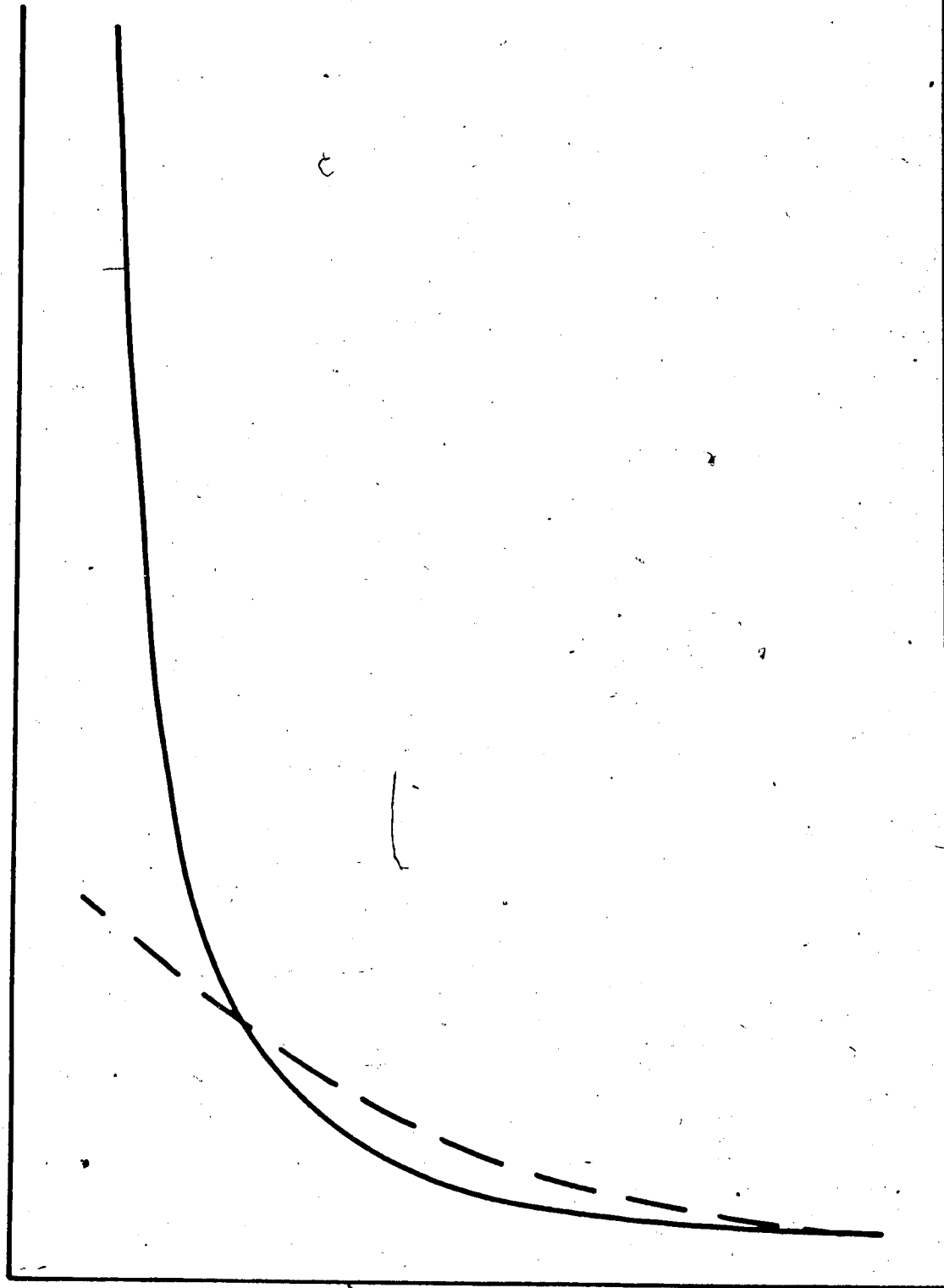
$$\ln(\text{egg density}) = \ln(d, m, f) + \ln(1 - e^{-p(l+L)}) - \ln(n), \text{ and}$$

$$\ln(\text{egg density}) = \ln(d, m, f) + \ln(1 - e^{-s(L)}) - \ln(n)$$

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 $\ln(1 - \exp(-s(L)))$ can be approximated by $p(l+L)$ and $s(L)$. The two models are now

Figure 5. 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 equation 1). Dashed line: host patch detection proportional to patch area (see equation 2). Exact scaling of axes depends on d , m , f , p and s (see equations 1 and 2).

NUMBER OF EGGS PER PLANT



PATCH SIZE

Table 4. Literature survey of mean *P. rapae* egg densities. Note: conditions for inclusion of a study in the survey are given in the text.

Source	Site Location	Number of Plants	Field Dimensions (m)	Mean Number of Eggs per Plant	Comments
Fahrig, unpublished	Guelph, Ontario	18	2 x 2	7.46	
		200	6.1 x 6.1	4.07	
		3600	27.5 x 63.0	1.34	
		450	15.0 x 15.0	1.35	
		450	15.0 x 15.0	1.43	
		450	15.0 x 15.0	1.73	
		450	15.0 x 15.0	1.49	
		450	15.0 x 15.0	4.06	
		450	15.0 x 15.0	3.60	
		450	15.0 x 15.0	3.94	
Jones 1977 p. 197, 205	Vancouver	9	2 x 2	7.55	
		36	5 x 5	6.11	
Latheef and Ortiz 1983, p. 1032, 1034	Virginia	30	3.42 x 3.68	6.08	
		30	3.42 x 3.68	7.17	
		30	3.42 x 3.68	5.42	
		70	4.6 x 5.5	3.50	
Maguire 1983 p. 1416-1418	Utah	4	0.91 x 0.91	12.60	
		16	2.73 x 2.73	12.03	
		64	6.37 x 6.37	9.35	
		9	0.87 x 0.87	3.65	
		81	4.88 x 4.88	2.38	
		9	0.87 x 0.87	6.38	
Maguire 1984 p. 465, 467	Utah	81	4.88 x 4.88	3.06	
		4	1.82 x 1.82	26.82	
		16	3.64 x 3.64	13.71	
		4	0.87 x 0.87	14.33	
		4	0.87 x 0.87	5.92	
		25	2.44 x 2.44	5.02	
Michaellowicz 1980 p. 36, 63, 64	Guelph, Ontario	5852	79.7 x 53.1	1.78	read from graphs
		5760	62 x 53	2.32	

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

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

Analyses of variance of $\ln(\text{egg density}) - \ln(n)$, as calculated from the data in Table 4 were performed. The six studies were included as a class variable to determine if the term $\ln(dm f)$ varies among studies. Analyses were performed using two models; in one I used the independent variable $l+L$ (as in equation 3) and the other IL (equation 4). For equation 3, both the study ($p < .0054$) and the patch dimensions (i.e. $l+L$) ($p < .007$) were significant, and the R^2 for the whole model was 0.854. For equation 4, again both the study ($p < .002$) and the patch area ($p < .035$) 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 ($r = .954$). To determine if both are actually important, I regressed the residuals from the model in equation 3 (since the R^2 is higher) on patch area. The regression is not significant ($p < .725$).

When the two models were fitted to the data, I obtained lower residual sums of squares at small patch sizes for model 3 than for model 4 (see Table 5). The residual sums of squares for the two models were similar at high patch sizes. This indicates that equation 3 (or 1) is more accurate at low patch sizes than equation 4 (or 2); this difference is important, since it is at the low patch sizes that the two models differ most in shape (Figure 5).

From the analysis, I therefore have some evidence that *P. rapae* egg density can be described by the equation

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

If butterflies were able to detect host patches from a distance through olfaction, I would have expected the equation based on patch area (equation 4 or 2) to reflect reality more accurately than that based on perimeter. Since the model based on perimeter is more accurate, I do not reject the field result which acted as an assumption in equation 1 (or 3), namely that female flight orientation is not affected by the presence of host plants.

Table 5. 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. 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

5. Effect of Detection Radius on Relationships Between Patch Spatial Arrangement and Local Population Size: General Simulations

The results of the field studies on *P. rapae* indicate that the patch detection radius for this species is very small (virtually 0) relative to its dispersal distance. The purpose of the work reported in this chapter was to develop a general hypothesis relating patch detection radius to relationships between patch spatial arrangement and local (in a patch) population abundance. To do this, I developed a general model of populations in patchy habitats, and then varied the value of patch detection radius in the model, to see what effect this would have on the observed relationships. The model is not specific for *P. rapae*, so that the generalities derived from the simulation experiments might have general meaning for populations in patchy habitats. A more specific set of simulations of *P. rapae* populations is described in Chapter 6.

Model Requirements

Developing a model which can be used to find general relationships between habitat patch spatial arrangement and population abundance is not simple. This is primarily because every spatial arrangement of patches in nature is unique; the number of patches, the sizes of patches, and their relative positions in space will all vary among situations. Also, each species differs from all others with respect to those characteristics of inter-patch dispersal which are important determinants of the relationships between patch spatial arrangement and population size. These dispersal characteristics include: (i) the fraction of organisms which disperse from each patch, (ii) the average dispersal distance of dispersers, and (iii) the distance from which dispersing individuals can detect new patches (detection radius).

A model which is to be used to derive general relationships between habitat patch spatial arrangement and population size must therefore be general and flexible enough to encompass most of the possible combinations of patch spatial arrangement, and dispersal characteristics of resident populations.

Because there will be several important parameters in such a model, the generalities derived from it will have to be based on a very large number of simulation experiments. Therefore, it is desirable to work with a model which is as simple as possible, while incorporating enough complexity to derive the required relationships.

The main requirements of the model are, therefore, that it should (i) include the explicit spatial arrangement of habitat patches, (ii) be general and flexible enough to incorporate the majority of spatial arrangements and species, and (iii) be as simple as possible, within the constraints imposed by (i) and (ii).

Models of Patchy Populations

Many of the previously proposed models of patchy populations fall into one of three categories, depending on the assumptions which are made concerning dispersal characteristics. I will refer to these as (i) dispersal pool models, (ii) grid models, and (iii) dispersal corridor models.

Dispersal Pool Models

Dispersal pool models encompass a large number of studies (e.g., Atkinson and Shorrocks 1981, Chesson 1981, 1985, Comins et al. 1980, Hilborn 1975, Levin et al. 1984, Myers 1976, Reddingius and den Boer 1970). Organisms which disperse from patches are assumed to enter a dispersal pool, and are then redistributed among the patches according to a set of rules. The main reason for making the dispersal pool assumption is that it greatly simplifies the model, sometimes allowing for analytical solutions of equations (e.g., Comins et al. 1980). This type of model has often been used to study the role of dispersal in population stability and survival (Lomnicki 1980, Reddingius and den Boer 1970).

Models which contain the dispersal pool assumption, while useful for some types of investigations, can not be used to study the effects of the spatial arrangement of habitat patches on population dynamics. This is because, by assuming the presence of a dispersal pool, one ignores the explicit spatial arrangement of patches. A model which is used to find



relationships between spatial arrangement and population dynamics must therefore be more complex than a dispersal pool model; it must include some explicit description of the spatial distribution of the habitat patches.

Grid Models

A second common approach to including spatial heterogeneity is the grid model (e.g., Kishi and Ikeda 1986, Sawyer and Haynes 1985). This is a simulation model, in which an imaginary grid is placed over the entire region under study, including the habitat patches and the matrix in which they are distributed. The subpopulation within each grid square is explicitly followed through the entire simulation. In the most detailed type of grid model, each individual organism in each grid square is followed (e.g., Kitching 1971).

To develop relationships which can be applied to a wide range of possible spatial arrangements and species, one would need to conduct a large number of simulation experiments, with a wide range of parameter values, corresponding to a wide range of situations. If a grid model is used, detailed information concerning the flow of organisms on the grid is necessary for each simulation. At each time step, one would have to calculate the probabilities of organisms in each grid square reaching each of the other grid squares. Over a very large number of simulations, this type of approach, while possibly successful, would be very expensive and time-consuming.

It would clearly be preferable to find some compromise between the dispersal pool approach, which is too simple to answer the question, and the grid approach, which is probably more complex than necessary to answer the question. A model which includes explicit spatial arrangement of habitat patches, but which does not require that one follow the movements of dispersing organisms through the non-patch matrix is desired.

Dispersal Corridor Models

A model which satisfies both of the above conditions is the dispersal corridor model (Fahrig et al. 1983, Fahrig and Merriam 1985, Lefkovich and Fahrig 1985). In this model,

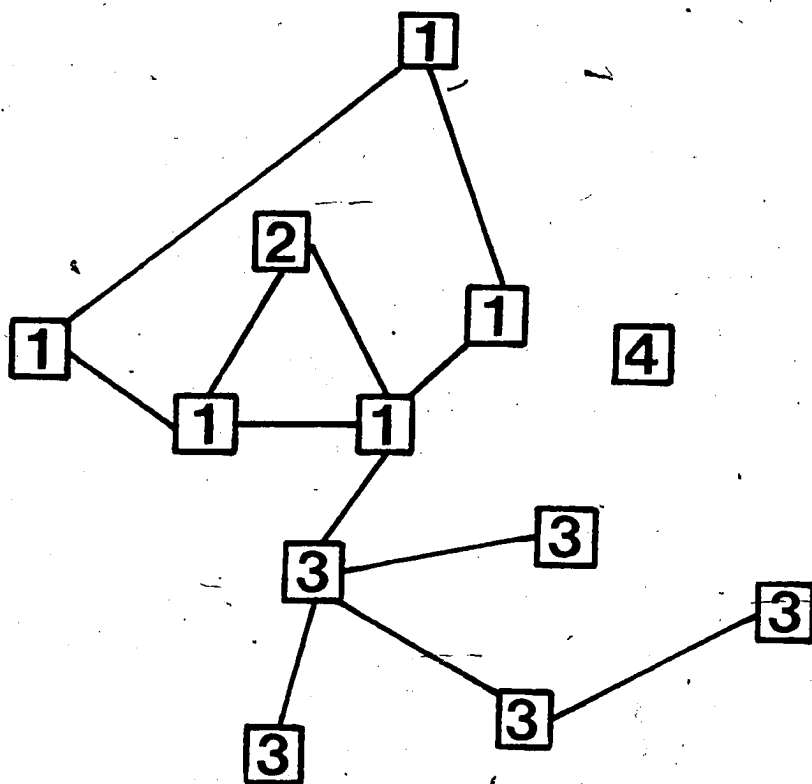
patches in the habitat are represented as nodes, which may be either "connected" or "not connected" to one another. This type of model was shown to be a useful method of modeling populations of small mammals in woodlots, which may be interconnected by fence rows along which dispersing organisms travel (Fahrig and Merriam 1985).

Roff (1974a, b) implicitly included the dispersal corridor assumption by assuming that each of 25 subpopulations was connected by dispersal to its 4 nearest neighbours. However, this assumption renders his model inappropriate for study of the effect of spatial arrangement on population dynamics, because all 25 patches are spatially equivalent.

Lefkovitch and Fahrig (1985) used a dispersal corridor model to find general relationships between the spatial arrangement of habitat patches and population survival. Simulations were conducted of populations in all 34 distinct spatial arrangements of 5 habitat patches. Statistical analyses were then performed on the results. It was found that the probability of survival of a population within a patch depends on two factors. First, populations in patches which are completely isolated have lower survival probabilities than those in patches which are connected to other patches. Second, for those patches which are connected to at least one other patch, the probability of population survival depends on the size of the largest geometric figure of which the patch forms a part. These results are illustrated in Figure 6.

Although the results of Lefkovitch and Fahrig are general relationships between habitat patch spatial arrangement and population dynamics, they are only general to the extent that the concept of dispersal corridors is a general phenomenon in nature. Apart from the example of mammals in woodlots, it is difficult to find other situations in which this assumption applies. Therefore, to derive truly general relationships, one would prefer to use a model which incorporates a much larger proportion of the dispersal characteristics of real organisms. In particular, I wanted to develop a model in which parameter values could be chosen to mimic the situation in which the organism does not detect patches from a distance, as is the case for *P. rapae*.

Figure 6. Illustration of the results of Lefkovich and Fahrig (1985). Squares represent habitat patches, and lines joining them represent dispersal corridors. Numbers in the squares indicate the relative survival probabilities of populations in the patches ("1" is the highest survival probability). See text for further explanation.



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From this discussion, three main criteria emerge for a model which can be used to look at general relationships between habitat patch spatial arrangement and population dynamics. First, it is necessary to include the explicit spatial arrangement of the habitat patches. This precludes use of the dispersal pool assumption. Second, the model should apply to a wide range of species. This precludes use of the dispersal corridor assumption. Finally, the model should be as simple as possible, since a large number of simulation experiments must be conducted. This makes a grid type of model undesirable.

The Model

The model which I propose here satisfies the above criteria. The explicit spatial arrangement of habitat patches is included; distances between all pairs of patches are required to calculate dispersal rates among the patches. The model is not restricted to species which follow dispersal corridors, although it can be modified to include them. Furthermore, it avoids explicit consideration of the spatial locations of organisms in the non-patch matrix, making it much simpler than the grid approach.

The model is a stochastic discrete-time simulation model. It includes within-patch processes and between-patch dispersal in each time step. Within-patch population dynamics are modeled by a discrete approximation to the logistic growth equation. There are six main parameters in the model, which determine the population sizes in each patch at each time step. These are: (i) r : intrinsic population growth rates in the patches, (ii) k : carrying capacities of the patches, (iii) p : fractions of organisms which disperse from each patch in each time unit, (iv) s : dispersal distances relative to the mean distance between patches, (v) d : distances from which dispersers detect new patches (detection radius), and (vi) i : immigration rates. During a particular simulation, the overall value chosen for each parameter is actually the mean of a random variable. The actual values used in the simulation vary stochastically about the means, among the patches and over the time steps.

The simulation does not follow the fate of each organism; instead, calculations are based on the total population sizes in each patch.

Dispersal from each patch is assumed to be, on average, equally likely in all directions, except when a patch is within detection range of the first. The distances which dispersers move are assumed to be taken from a random normal distribution. Patches are assumed to "attract" all those dispersers which would, by chance, fall within a certain detection radius of the patch. Those dispersing organisms which do not successfully find a new patch in a particular time step are not explicitly followed further. They may die, emigrate from the area or successfully detect a new patch at some future time step. The net effect of all these possibilities, plus the possibility of immigration of new individuals into the area from outside it, are accounted for in the immigration term (i). It is this simplifying assumption which allows one to effectively ignore the non-patch matrix.

Figure 7 illustrates dispersal from a particular patch (patch 1). Notice that the fraction of dispersers which reach patch 4 is greater than the fraction reaching either of patches 5 or 6. Figure 8 is a flow diagram of the model.

The Effect of Detection Radius

The purpose for proposing the model described here is, as stated, to address the question: in general, what affect does the detection distance have on the interaction between the spatial arrangement of habitat patches and population size?

To answer this question, I performed a series of simulation experiments using the model described here. Ten habitat patches were randomly distributed in space (see Figure 9), and the values in the model were arbitrarily set as shown in Table 6. The same spatial arrangement was used for each simulation. In each simulation, the population sizes in each of the patches were calculated for 50 time steps. The mean detection radius was varied from 0 to 20% of the mean inter-patch distance. The results of the simulations are shown in Figures 10 and 11. From Figure 10, it can be seen that the population size increases as the detection

Figure 7. Illustration of dispersal assumptions. Organisms disperse from patch 1, in the distribution indicated by the speckled pattern. Recipient patches "attract" all dispersers which fall within the detection radius of the patch (represented by the blank circular areas around the patches). Notice that patches 5 and 6 receive fewer dispersers from patch 1 than does patch 4.

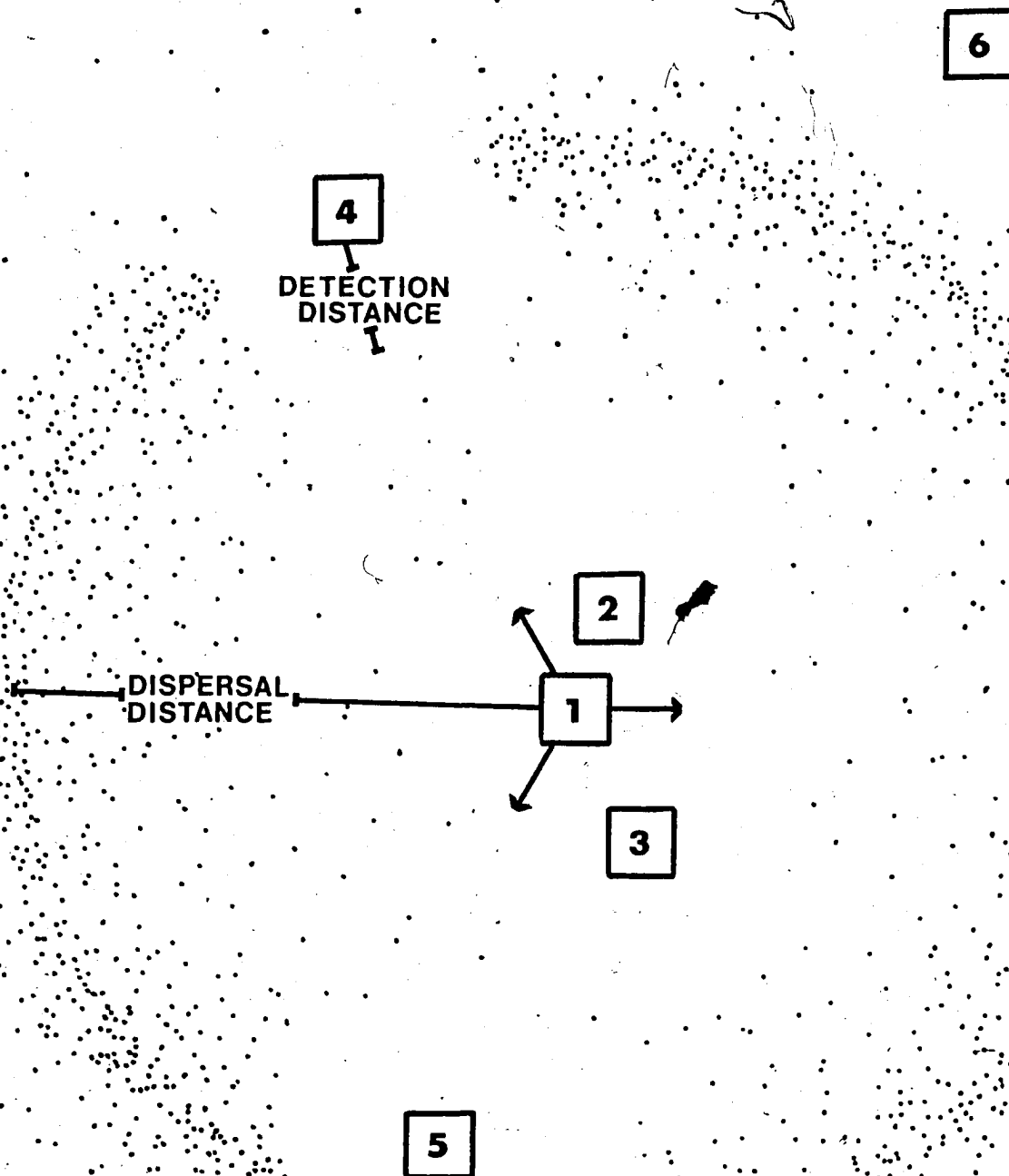


Figure 8. Flow diagram of a general model of a population in a patchy habitat.

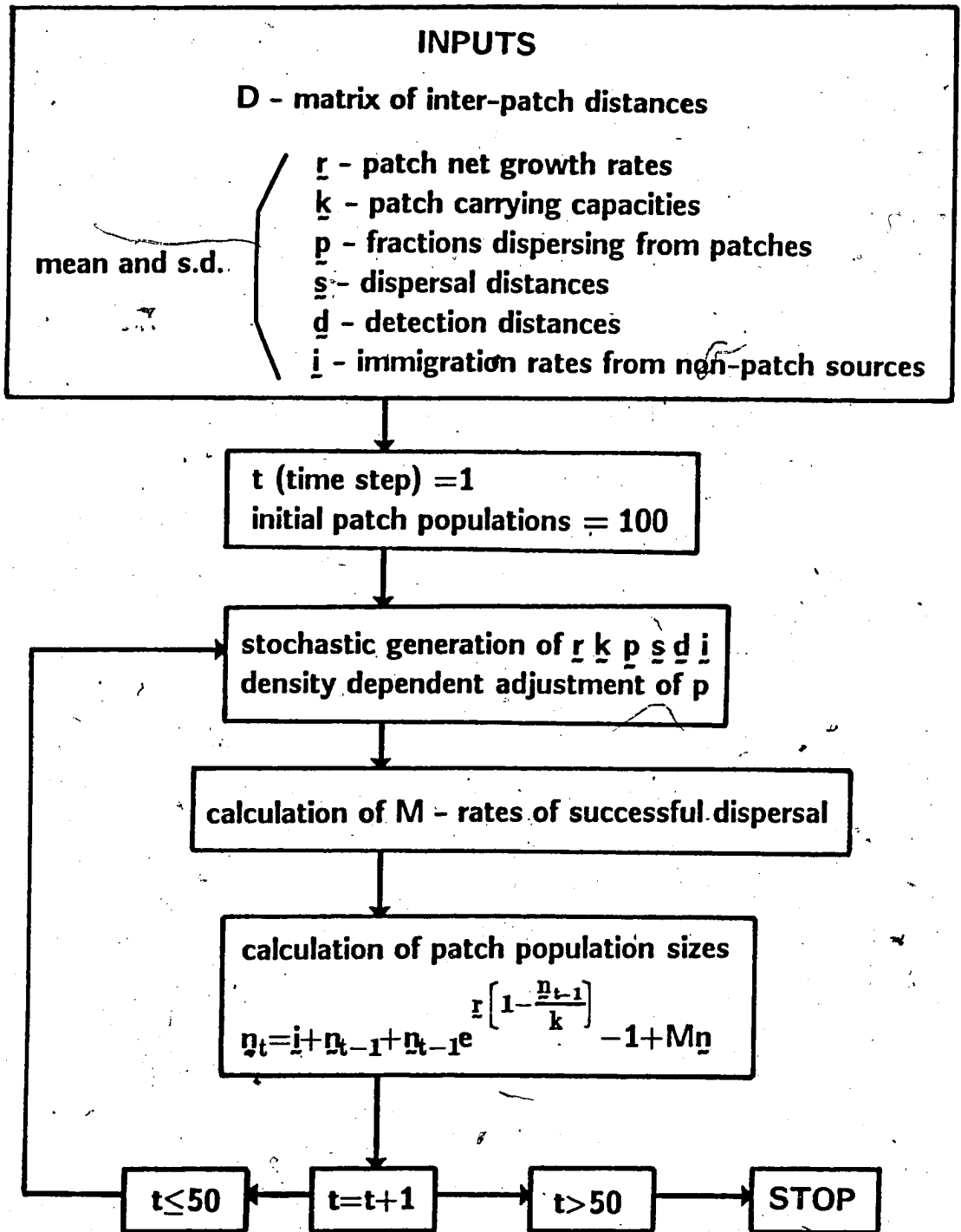
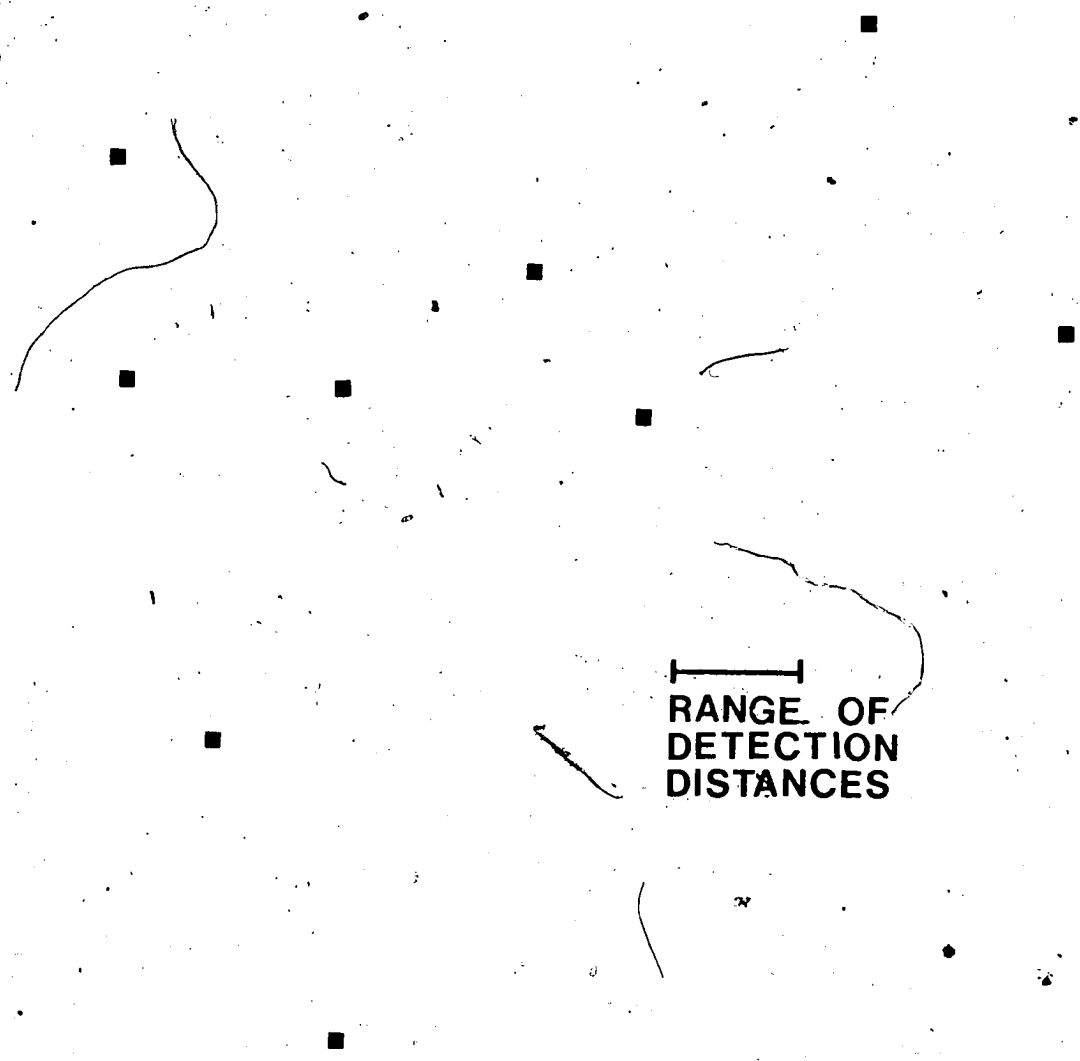


Figure 9. Spatial arrangement of 10 habitat patches used in simulation experiments.



RANGE OF
DETECTION
DISTANCES

Table 6. Parameter values used in the simulation experiments.

Parameter	Mean Value	Standard Deviation
Input Patch	100	0
Population Sizes		
Patch Carrying Capacities	1000	10%
Net Population	.1	10%
Growth Rates (r)		
Dispersal Distance (as a fraction of mean inter-patch distance)	.5	40%
Dispersal Rate	.5	10%
Detection Radius (as a fraction of mean inter-patch distance)	0.2	10%
Immigration Rate	10	10%

Figure 10. Relationship between mean population abundance in 10 patches, and the distance from which dispersing organisms can detect the patches (detection radius), as derived from simulation experiments.

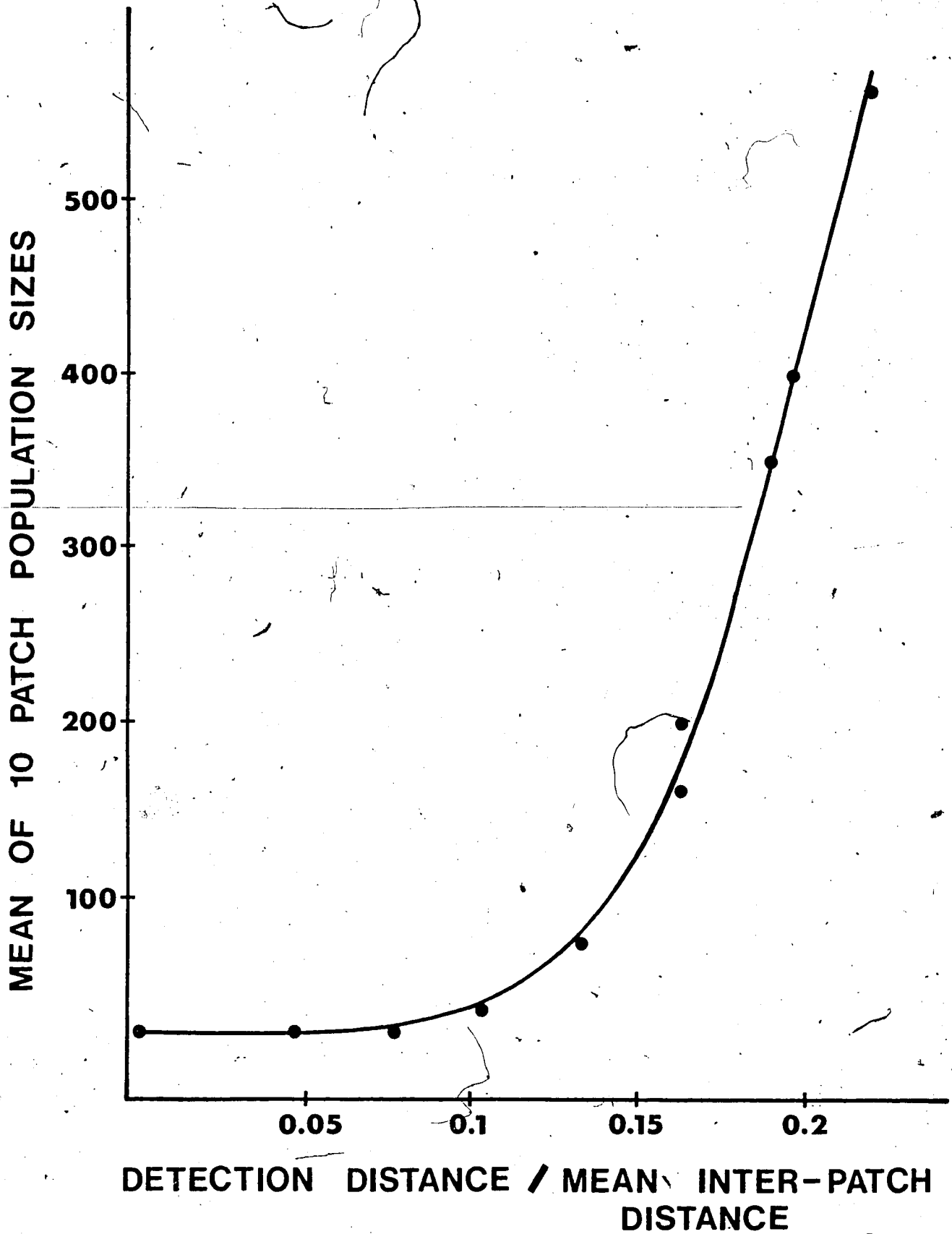
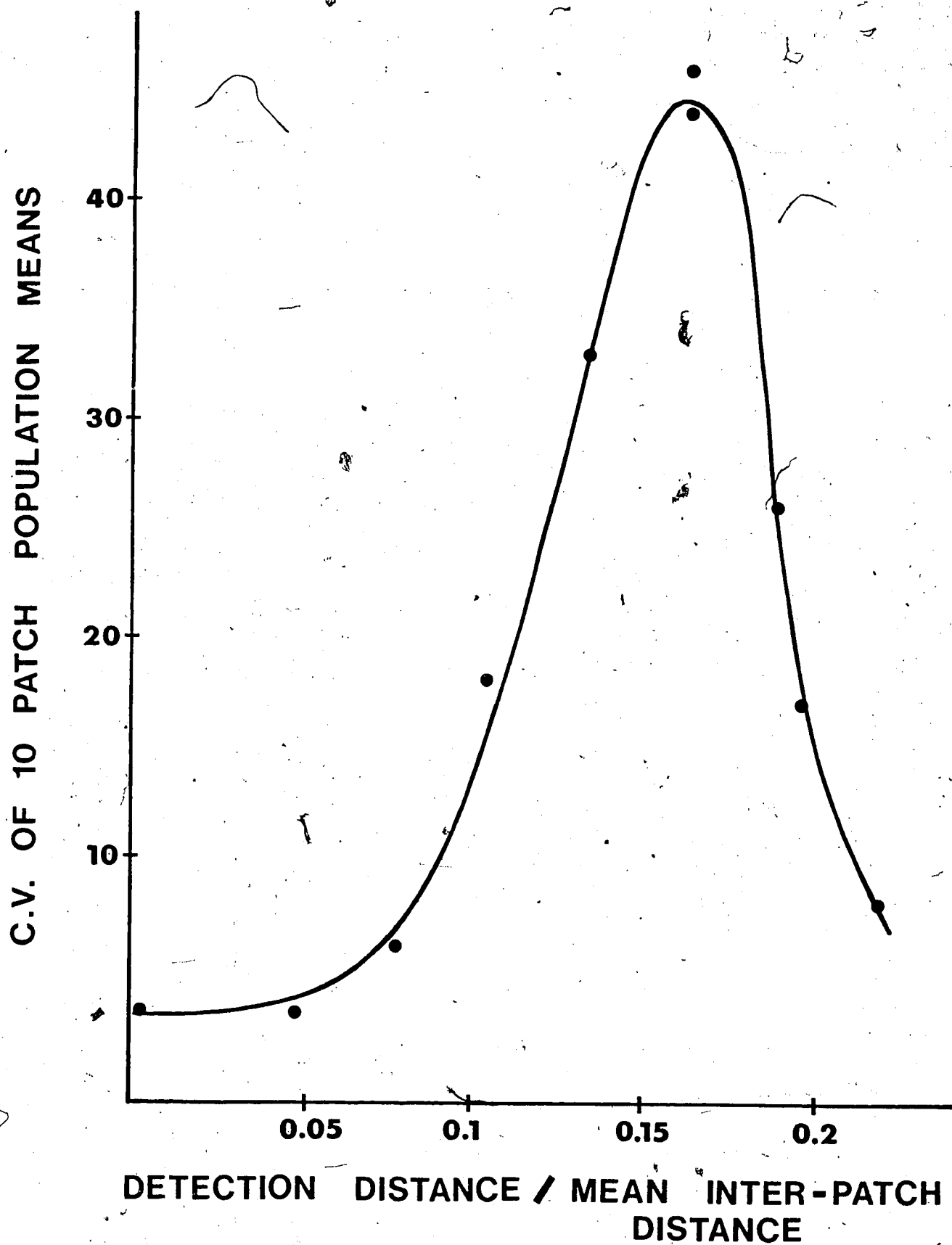


Figure 11. Relationship between coefficient of variation among the mean population sizes in 10 patches, and the detection radius, as derived from simulation experiments.



radius increases. This is expected because more dispersers are successful in finding patches, when the detection radius is increased. However, this result does not reveal anything about relationships between the spatial arrangement of habitat patches and local population size.

From Figure 11, however, one can see a marked effect of the spatial arrangement on population dynamics. This figure illustrates the relationship between the detection radius and the coefficient of variation (C.V.) among the mean population sizes in the 10 patches. The C.V. is low for very low detection radii, increases as the detection radius increases, and then decreases again for higher detection radii. This can be interpreted as follows. At low detection radii, very few of the dispersing organisms successfully reach new patches. Therefore, the population dynamics in the 10 patches are essentially independent. Any differences among them are due to the effects of stochastic variation in their within-patch population processes. As the detection radius increases, however, a higher proportion of dispersers actually reach new patches. Those patches which are situated at distances near the mean dispersal distance from the other patches will receive more dispersers than those which are not. Therefore, added to the variation due to within-patch processes, the population dynamics in the patches are influenced by their relative spatial locations. This causes an increase in the C.V., which measures the degree to which the populations in the 10 patches differ. Finally, at higher detection radii, the level of interchange among the patches is high enough that any differences caused by the spatial distribution of the patches are damped out. The swamping effect of high dispersal rates was also noted by Hastings (1982).

For the specific case of the cabbage butterfly, the results here (Figure 11) indicate that it is unlikely that the spatial arrangement of host plant patches has an important impact on local population dynamics. Since the detection radius for cabbage butterflies is 0 (Chapters 3 and 4), the coefficient of variation among local populations is expected to be relatively low. Direct flight of butterflies from one patch to another will be a rare event, and the main source of immigrants is instead expected to be from those butterflies which are "milling about" in the between-patch area. This will tend to decrease the importance of relative spatial location of a

particular patch on its immigration rate. This will be reflected in a lowered C.V. among patch population sizes.

6. Host Patch Spatial Arrangement and Local Population Size in the Cabbage Butterfly

The results of the field studies reported in Chapter 3 and the modelling in Chapter 4 indicate that the host patch detection radius for *P. rapae* is very low, virtually 0 when compared to its large dispersal distance. The general simulation study reported in Chapter 5 indicates that, for species with very low patch detection radii, the spatial arrangement of patches should have little influence on local population abundances. The combination of these two results leads to the hypothesis that the spatial arrangement of host plant patches (e.g., cabbage patches) should have little if any influence on local population sizes of *P. rapae*. The purpose of the work described in this chapter was to examine the validity of this hypothesis.

Experimental Layout

To examine the effects of the spatial arrangement of habitat on the population dynamics of *P. rapae*, I used the above information on dispersal behaviour (Chapter 3), to set up an experimental series of cabbage patches. I attempted to devise the spatial arrangement which would be expected to produce the maximal effect of patch spatial arrangement, given the spatial constraints imposed by the field site. The spatial arrangement of patches is shown in Figure 12. In the figure "C" indicates patches which are "close" together, "I" refers to patches which are most "isolated" and "M" patches are located at "medium" distances from other patches. The sizes of the patches and the distances among them are to scale. The number in brackets beside each patch indicates from how many of the other patches the patch may obtain immigrants, within one day of dispersal from the other patches. This number is based on the facts that (i) females tend to lay most or all of their eggs for one day on one patch, and (ii) they fly about 250 to 700 m per day. This behaviour results in the prediction that the patches C1 to C4 in Figure 12 are actually more "isolated" from the point of view of dispersing females than are patches M1 to M3. This is because females which disperse from C1, for example, will have very few if any mature eggs to lay by the time they reach C2, C3 or C4.



Figure 12. Experimental layout of nine cabbage patches. Sizes of patches and distances among them are to scale. Numbers in parentheses indicate the number of patches from which the patch can obtain immigrants, within one day of dispersal from the other patches; for further explanation see text.

100 m



I2(0)

I1(2)

M2(7)

M3(7)

M1(6)

C4(3) C3(3)

C2(3) C1(3)

Therefore they will pass over these patches without laying eggs. However, by the time they reach M1 to M3 (possibly the next day) they will have a number of mature eggs available to lay. Based on this argument, I 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. However, the difference was not expected to be great, since females do not detect new patches from a distance. This means that the actual fraction of dispersers from a particular patch which find any of the other patches within one day is expected to be small. As stated above, the results of Chapter 5 suggest that, if dispersers do not detect new habitat patches from a distance, then the spatial arrangement of patches should have little if any effect on population dynamics within patches. To produce more exact predictions for the experimental setup (Figure 12), I built a simulation model of *P. rapae* population dynamics in a patchy habitat, and applied it to this setup (Figure 12).

Simulations

The underlying structure of the cabbage butterfly model is similar to the general model described in Chapter 5. However, it is more complex because it incorporates detailed aspects of population dynamics and inter-patch dispersal specific to *P. rapae*.

The model is a discrete-time simulation model; the time step is one day. Only the female portion of the population is modelled. This is justified on the bases that (i) adult females are responsible for inter-patch population exchange, through dispersal and egg-laying, (ii) males are extremely successful at finding and mating with females, almost immediately after their pupation, so dispersing females are almost all mated, and (iii) there is no evidence that the sex ratio is biased in any of the life history stages.

Two important assumptions in the simulations are that (i) all females are mated within 24 hours of emergence and (ii) 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. This is necessary to ensure that,

at low population densities, males will be in the vicinity of newly emerging females. Yamamoto (1981) found that male *P. rapae* disperse less readily than females, in northern Japan.

The model 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 the *P. rapae* population are calculated for each day. Factors which affect recruitment into each stage are the stage development times and mortality rates. Both of these vary with the time of the season because development rates increase with increasing temperature (Richards 1940, Jones and Ives 1979), and the mortality rates of the later larval instars are influenced by the population densities of parasites, which increase through the season (Appendix 5, and Michaelowicz 1980). The specific values of the parameters in the *P. rapae* model were chosen by combining published information on *P. rapae* with information gathered through field work conducted in 1985. Details of the estimation of the parameters which determine within-patch population dynamics are given in Appendix 5.

Only the adult stage (i.e., the butterfly) is involved in the between-patch dynamics since the other stages are relatively immobile. Information on dispersal and host detection in *P. rapae* (see Chapter 3) was used to make the following assumptions. Butterflies leaving 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. Females lay eggs on only one patch per day.

In the field, butterflies which disperse directly between cabbage patches are not the only sources of immigrant females into each patch. Other sources include (i) females which disperse from a patch and do not find another patch within one day, but remain in the study area, (ii) females which develop from larvae which fed on wild host plants (cruciferous weeds), and (iii) females which immigrate into the area from outside. Since, when given a choice, ovipositing females lay many more eggs on commercial cabbage than on wild hosts (Jones and Ives 1979), I expect that the population density on the cabbage will be higher than

in other parts of the study area. However, the rate of immigration of adult females from the sources stated above is expected to be quite high. This was accounted for in the model in an immigration term; the immigration rate was assumed to increase through the season. Details of the estimation of the immigration rate are given in Appendix 5.

A summary of the simulation model is given in Figure 13. The computer code is in Appendix 6.

The simulation began with equal numbers of adults in each cabbage field. The population sizes of each stage in each patch in Figure 12 were calculated for 135 days, beginning in mid-April and running until the end of August. Figure 14 illustrates the results of the simulations for the 100-day period corresponding to the field sampling (i.e., May 12 to August 19, 1986). The main result is that, as expected, patches M1 to M3 had the highest predicted population sizes. Populations in patches C1 to C4 were slightly lower, and I1 and I2 were slightly lower still. However, the simulations predict that the difference in population sizes due to the spatial locations of the patches are minimal. This is in agreement with the prediction in Chapter 5, for organisms which do not detect habitat patches from a distance.

Field Results

The field work was conducted at the Guelph University agricultural research station near Elora, Ontario. Nine patches of 200 plants each were planted in the spatial arrangement shown in Figure 12. The only other cultivated host plants of *P. rapae* which were present on the station were three plots of rapeseed, all of which were at least 1.5 km from any of my cabbage plots.

The plots were sampled from May 12 to August 19, 1986. Two plantings of cabbage were necessary to cover this period. The second planting was planted between the rows of the first planting, and there was a transition period of 4 weeks during which cabbages from both plantings were present. All eggs on 20 randomly chosen plants on each patch were counted at each sampling. During the period of overlap of the two cabbage plantings, 20 plants from

Figure 13. 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, j : life history stages. n : number of individuals.

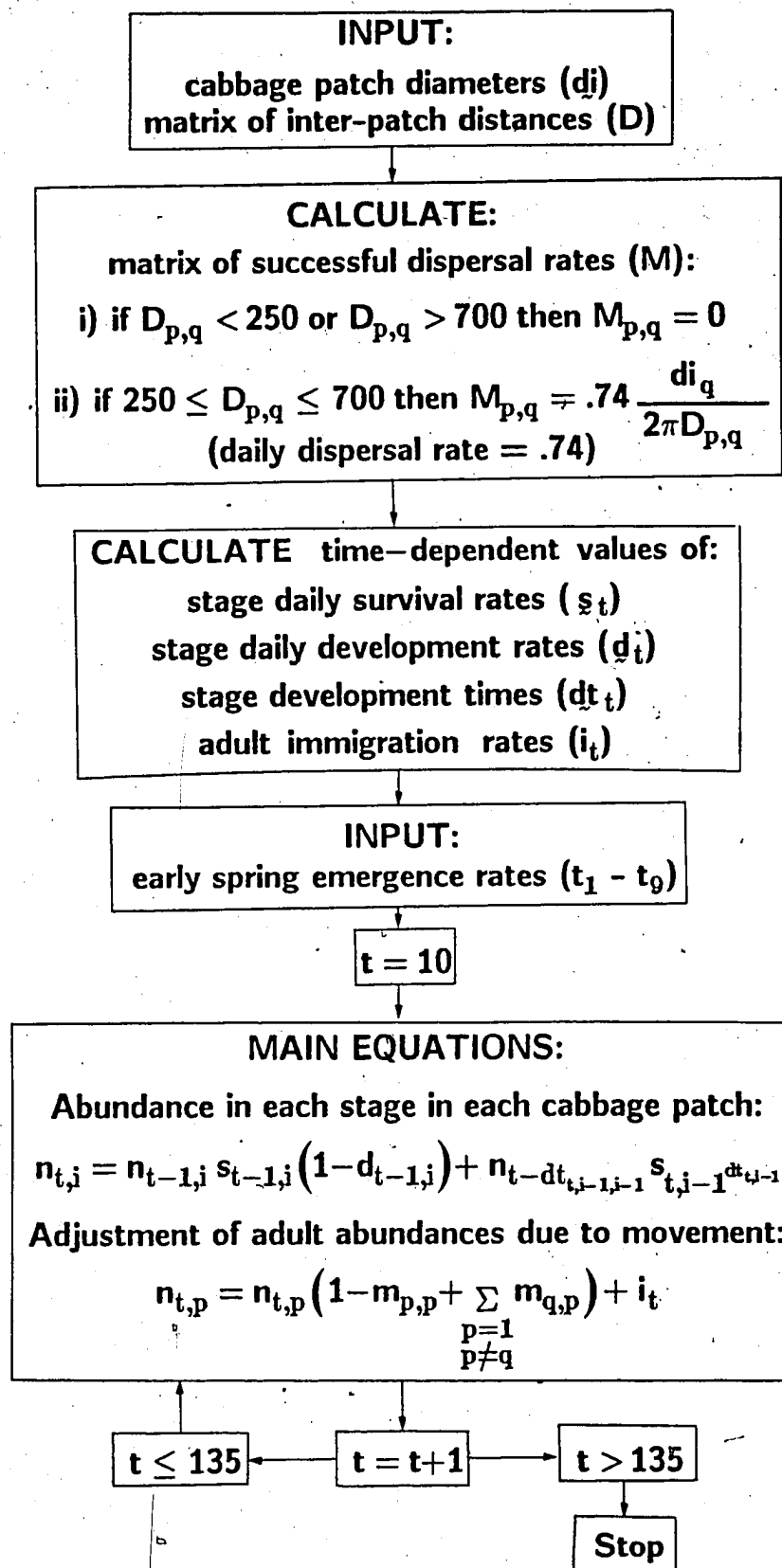
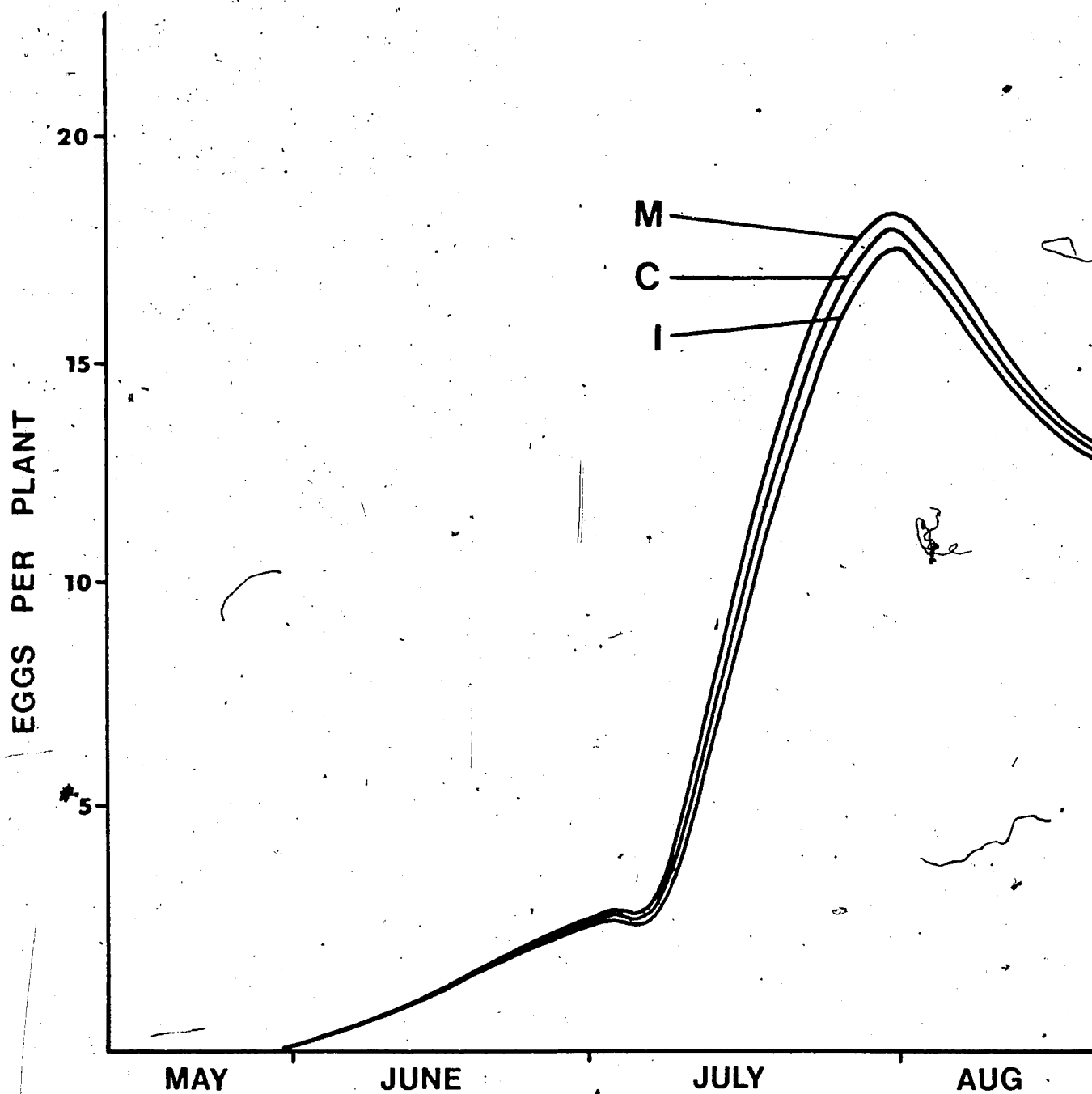


Figure 14. Simulation results of the number of *Pieris rapae* eggs per plant in three categories of cabbage field. C: C1-C4 in Figure 12. M: M1-M3 in Figure 12. I: I1, I2 in Figure 12.



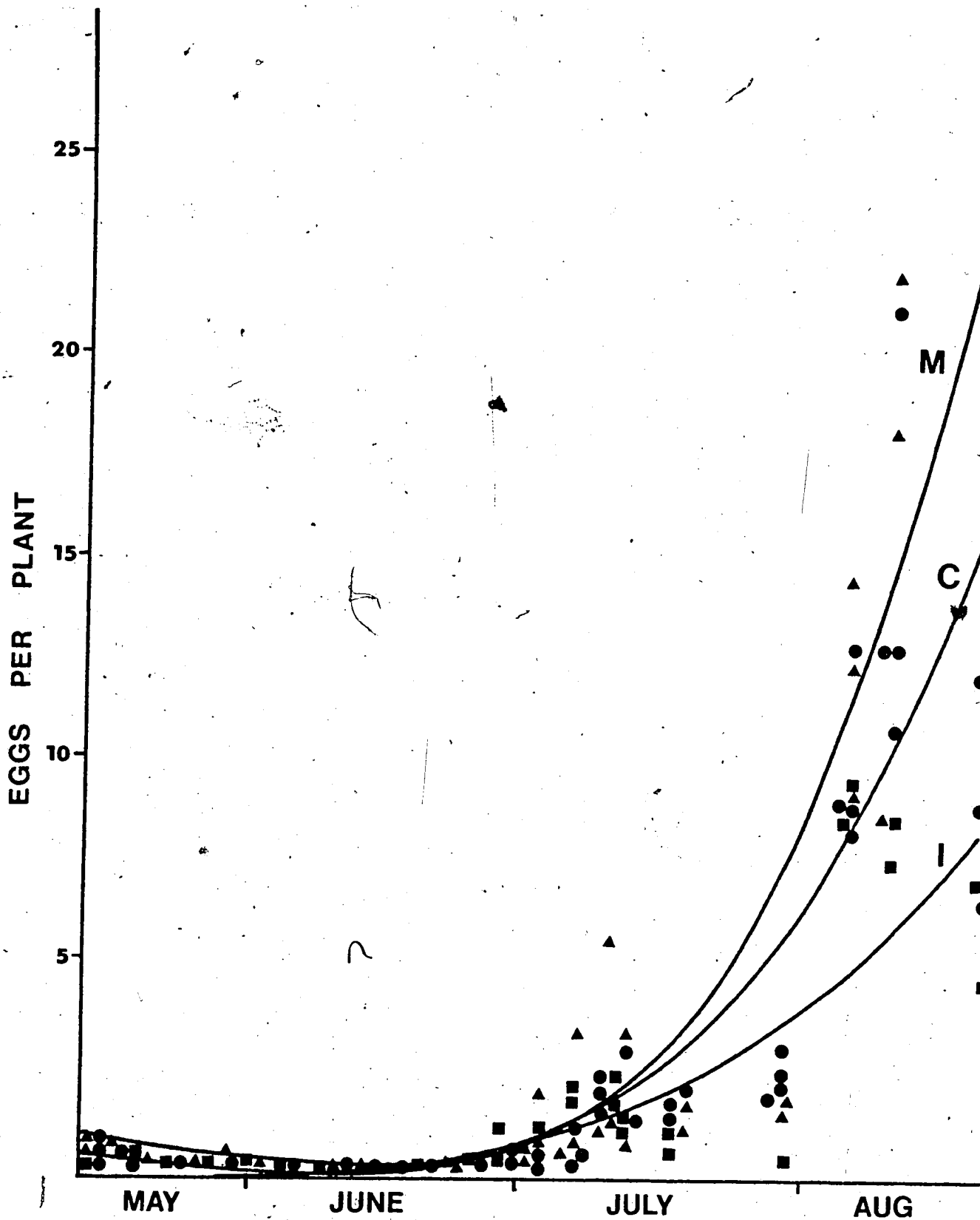
each planting were sampled (a total of 40 plants) in each patch; population density estimates were then taken as the average of the two samplings. The field data are given in Appendix 7, and are illustrated in Figure 15.

Analysis of variance was performed on the egg density data. The variables included variables day , day^2 and day^3 , and the class variable was $field$; the three categories or types of $field$ were C (C1 to C4), M (M1 to M3) and I (I1 and I2) (see Figure 12). Significant effects were found for day^2 ($p < .0001$), day^3 ($p < .0001$), and $field$ ($p < .05$). The fact that there was a significant effect of $field$, indicates that there was an effect of patch spatial arrangement on population densities within cabbage patches. Therefore, to further examine the effect of $field$ on egg density levels, I conducted analysis of variance of residuals from the regression using day^2 and day^3 . There was no significant effect of individual cabbage patches within each category of $field$. The levels of egg density for the categories within $field$ were in the order $M > C > I$. A posteriori tests revealed that the egg density in M was significantly higher than I, but that the density in C was not significantly different from either of M or I. The three regression equations, for C, M, and I, on day^2 and day^3 are plotted on Figure 15. The analyses are given in Appendix 8.

The results of the field study support the predictions of the simulations. *P. rapae* egg densities in the three categories of field occurred in the same order for both simulation and field data (i.e., $M > C > I$). The fact that in the field data, the egg density in M was significantly higher than I but C was not significantly different from M or I (see Figure 15), supports the expectation that there would be only a small effect of spatial arrangement on the population dynamics of *P. rapae*.

The spatial arrangement of patches in this experiment was specifically chosen to produce as large as possible an effect on local *P. rapae* population size, within the constraints of the field site. Given the small effect found in this experiment, it is likely that the population size in most naturally occurring or cultivated host patches of *P. rapae* will be unaffected by spatial relationships with other host patches.

Figure 15. Estimated number of *Pieris rapae* eggs per plant in three categories of cabbage field. Circles: field type C (C1-C4 in Figure 12). Triangles: field type M (M1-M3 in Figure 12). Squares: field type I (I1, I2 in Figure 12). Regression equations for the three types of field, on day^2 and day^3 are shown. Note: the curves for M and I are significantly different ($p < .05$), but the curve for C is not significantly different from either M or I.



7. Determinants of Local Population Size in Patchy Habitats

The results of the study to this point can be summarised as follows. In Chapters 3 and 4, I demonstrated that the radius of detection of host plant patches by *P. rapae* females is very low. In Chapter 5, I presented simulation studies which suggest that, for species with low detection radii, the spatial arrangement of habitat patches should have little influence on local population size. In Chapter 6 I showed, through simulations and field study, that this suggestion is valid for *P. rapae* populations in cabbage patches. A possible implication is that the spatial arrangement of host plant patches has little influence on local *P. rapae* population size because the host patch detection radius of females dispersing among host patches is very low.

The purpose of the work reported in this chapter was to examine the effect of detection radius in conjunction with other aspects of dispersal behaviour and population growth, through simulation experiments. The aims were twofold. First, I wanted to determine whether the small detection radius of *P. rapae* females is the most likely reason for the small influence of host patch spatial arrangement on local population size. Second, I wanted to conduct general simulation experiments to develop hypotheses concerning the types of species for which the spatial arrangement of habitat patches is most likely to have a large influence on local population size.

Methods

The method I used for this portion of the study was to extend the preliminary set of simulations reported in Chapter 5 to a more comprehensive set. Instead of looking only at the effects of changing one parameter (detection radius), I simultaneously varied all important parameters in the model, to determine their relative influences on the patch population sizes.

The Model

The model is a slightly more complicated version of the one proposed in Chapter 5. The area under consideration is assumed to consist of discrete patches of breeding habitat in a "matrix" of ~~non~~-breeding habitat. The explicit spatial arrangement of breeding habitat is included; distances between all pairs of patches are required to calculate dispersal rates among the patches.

As in Chapter 5, the model is a stochastic discrete-time simulation model. It includes within-patch processes and between-patch dispersal in each time step. Within-patch population dynamics are modelled by a discrete approximation to the logistic growth equation. There are six main parameters in the model, which determine the population sizes in each patch at each time step. These are: r , intrinsic population growth rates in the patches; k , carrying capacities of the patches; p , fractions of organisms which disperse from each patch in each time unit; s , dispersal distances relative to the mean distance between patches; d , distances from which dispersers detect new patches (detection radius) relative to the mean distance between patches; and i , rate of immigration into the area. During a particular simulation, the value of each parameter is actually the mean of a random variable. The actual values used in the simulation vary stochastically about the means, among the patches and over the time steps. The simulation does not follow the fate of each organism; instead, calculations are based on the total population sizes in each patch.

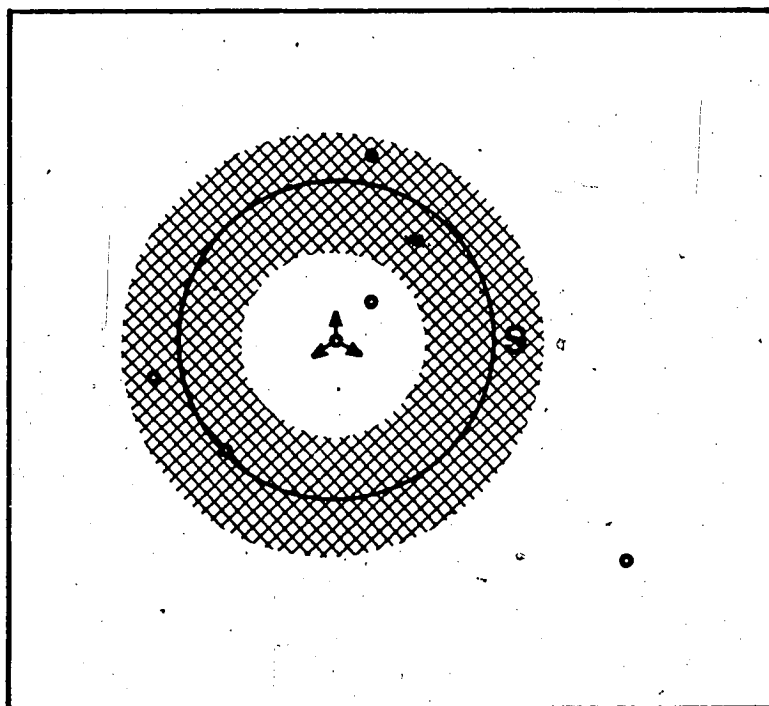
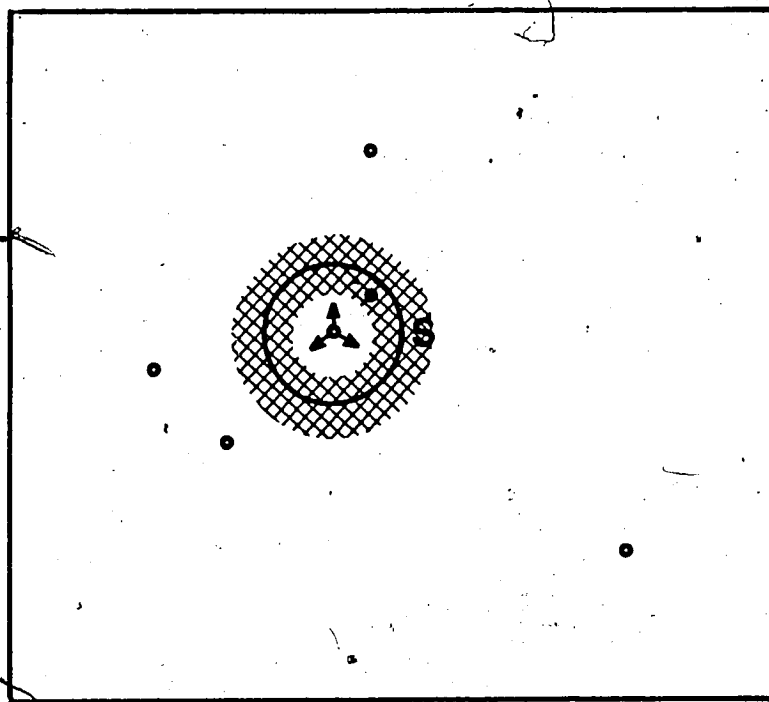
Dispersal from each patch is assumed to be, on average, equally likely in all directions, except when one patch is within detection range of another. The mean dispersal distance (s) is expressed as a fraction of the average distance among patches. This is necessary because the absolute dispersal distance is meaningful only in the context of a particular organism and habitat. I do not assume that all dispersers move exactly the mean dispersal distance, but rather that they are spread out over space. The mean dispersal distance is taken as the mean of a normal distribution, the standard deviation of which is arbitrarily chosen as 40% of the mean. This means that, for large dispersal distances, dispersers are spread over a much larger

area than for small dispersal distances (see Figure 46).

Patches are assumed to "attract" all those dispersers which, by chance, fall within the "detection zone" of the patch, the size of which is determined by the detection radius (d). Note that there is a possibility that the detection zones of two patches, say p_1 and p_2 , overlap. In this case, those organisms dispersing from a third patch that "land" in the overlap area are divided between p_1 and p_2 . It is also possible that the detection zone of a recipient patch, say p_3 , overlaps with a patch, say p_4 from which organisms are dispersing. This means that organisms in p_4 are able to detect p_3 from within p_4 . In this case, it is assumed that for those organisms dispersing from p_4 to distances within the detection zone of p_3 , dispersal directionality is not random, but is directed towards the overlapping patch (p_3).

The main difference between the model as used in this set of simulations and that used in the preliminary set in Chapter 5, is that here I include a "dispersal pool". Those dispersing organisms which do not successfully find a new patch in a particular time step may die, emigrate from the area, or successfully detect a new patch at some future time step. Those which remain in the area until the next time period are assumed to join a dispersal pool, from which a fraction of organisms enter each patch in each time period. Organisms which immigrate into the area from outside it (immigration rate = i) are assumed to enter the dispersal pool before immigrating into the actual patches. It is assumed that dispersers which successfully find a patch, enter it only if the resident population level is below the carrying capacity of the patch. Likewise, it is assumed that dispersers enter patches from the dispersal pool only if the population in the patch is below the patch carrying capacity. By calculating the number of organisms which directly disperse between patches in each time period, the effects of the exact spatial locations of the patches are preserved. The inclusion of the dispersal pool means that it is not necessary to keep track of the exact spatial location of organisms in the non-patch matrix area in each time step.

Figure 16. Illustration of the effect of dispersal distance. Small circles: patches, S : mean dispersal distance as a fraction of mean inter-patch distance. Above: $S = .25$. Below: $S = .60$. Shaded areas indicate one standard deviation from S (i.e., 40% of S). Notice that, if dispersal rates (i.e., fraction of organisms dispersing from patches) are equal, then higher dispersal distances result in successful dispersal to more patches, but much lower numbers of dispersers reaching them.



In general this model is highly flexible; adjustment of parameter values can result in a "dispersal pool model" or a "dispersal corridor model" (see Chapter 5), and a wide range of possibilities in-between. However, it is important to note that the model in its present form does not include the large number of species for which dispersal occurs in one predominant direction, such as with a wind or water current, downhill, uphill, or in a particular compass direction. Once general relationships are developed from the present model, it will be appropriate to add this type of overall dispersal directionality to the model, to see if it influences the results.

Although the model includes stochastic variation in parameter values among patches and over time, there is no correlation over time among the deviations from the means in the parameter values chosen for a particular patch. This means that persistent differences among patches are not included. This assumption is often unrealistic. For example, patches in nature are different shapes (e.g., proportion of patch edge to patch area). This may affect parameters in the model such as carrying capacity or dispersal rate. Such consistent differences among patches in parameter values adds a level of complexity to the simulations which is best addressed after the more simple situation is studied.

Simulation Experiments

Two thousand runs of the model were conducted. In each run there were 10 patches, and 150 time steps. A different spatial arrangement of the 10 patches was used for each run. The x and y-co-ordinates of each patch were chosen using a random number generator, and the distances between all pairs of patches were then calculated. The initial population size in all patches and for all runs was 100 organisms. The mean values of the six parameters r, k, p, s, d, i were chosen at random from a uniform distribution at the beginning of each run. The ranges of these parameters are given in Table 7. Stochastic variation in the parameters was included, so that their actual values fluctuated randomly among the 10 patches (except i) and between the time periods. The value used for a parameter in a particular step in the simulation was drawn from a normal distribution, centered on the mean value of the

Table 7. Upper Limits of Parameter Values Used in the Simulation Experiments.

Note: lower limit in all cases is 0, standard deviation/mean is 0.1.

Parameter	Upper Limit of Mean Value
r (growth rate)	0.1
k (carrying capacity)	10000
p (dispersal rate)	1.0
s (dispersal distance/mean inter-patch distance)	2.0
d (detection radius/mean inter-patch distance)	0.3
i (immigration rate)	1000

parameter, and having standard deviation arbitrarily set at 10% of the mean.

The population size in each of the patches was calculated for the 150 time steps. The temporal average population size in each patch over the final 100 time steps was then calculated. The initial 50 time steps were not included, to allow for a "settling down" period in the dynamics. The length of this period was chosen by plotting several trial runs; the initial increase or decrease phase was completed by 20 time steps in each trial. The spatial average of the 10 mean population sizes was then calculated. If the spatial location of patches has a large impact on local population sizes, then one would expect to find large differences among similar patches, due to their individual spatial relationships with the remaining patches. For example, in a group of patches, one might expect the population sizes in central patches to be higher than in peripheral patches, if patch spatial arrangement is important. Therefore, the type of variable which would be appropriate for measuring the effect of spatial arrangement would be one which measures the degree to which the populations in a group of similar patches differ. However, the degree of variability between patches is likely to be significantly correlated with the degree of variability within patches over time. Therefore, a variable which truly reflects effects of spatial arrangement should measure the variability between patches, corrected for the variability within patches over time. For each run, I calculated the coefficient of variation (C.V.) over the 100 time units for each patch, and then took the mean of these C.V.'s as a measure of within-patch variability over time for that run; this variable was named *tempvar* (i.e., temporal variability). The coefficient of variation (C.V.) among the 10 mean patch population sizes was also calculated for each run, and was labelled *patvar* (i.e., variability between patches). A significant linear relationship was found between $\ln(\text{tempvar})$ and $\ln(\text{patvar})$. The residuals from the regression of $\ln(\text{patvar})$ on $\ln(\text{tempvar})$ are a measure of the variability between patches, corrected for the variability within patches. They are therefore a measure of the importance of patch spatial arrangement on local population size. The residuals were labelled *spatvar* (i.e., pure spatial variability). The analysis of variance for the regression is shown in Table 8.

Table 8. Regression Analysis of *patvar* (Variability Among Patches)
on *tempvar* (Variability Within Patches Over Time) for 2000 Simulations

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>tempvar</i>	1	32.32	1173.8	0.0001
Error	1998	54.87		
Total	1999	87.10		

$R^2=0.37$

Results

The data resulting from each simulation experiment consisted of 6 independent variables: mean intrinsic growth rate (r), mean carrying capacity (k), mean dispersal rate (p), mean dispersal distance (s), mean detection radius (d), mean immigration rate (i). There were also two response variables: the mean of the 10 patch populations ($mnpop$), and the spatial variation among the 10 patches due to spatial arrangement ($spatvar$). Natural logarithms of $mnpop$ were taken, to normalise the data.

Although the proportion of dispersers detecting patches was not explicitly included as an input variable in the model, the fraction of dispersers from any particular patch which successfully detected any other patch was calculated as part of the simulations. As stated in the methods section, this calculation was complex because of the possible effects of overlap among patch detection zones. As well, it depended on the distance of the recipient patch from the donor patch, relative to the mean distance of dispersing organisms. For any particular run, the average probability of organisms detecting patches therefore depended, in a complex manner, on the dispersal distance, the detection radius, and the particular spatial arrangement chosen for the run. I felt the results of the simulations might be more easily interpreted if the average detection probability (dp) were included as a further independent variable in the analyses. dp was therefore calculated for each run.

To gain a general understanding of the way in which the detection probability depends on the detection radius and the dispersal distance, I conducted multiple regression analyses using detection probability as the dependent variable, and mean detection radius (d), mean dispersal distance (s), d^2, d^3, s^2, s^3 , and all other second, third and fourth order interactions as independent variables. The resulting regression equations are shown in Figures 17a and 17b. Notice that patch detection probability is highest for intermediate dispersal distances (Figure 17a). This is reasonable because for very small dispersal distances, the majority of dispersers do not move far enough to find another patch. At high dispersal distances, two factors result in the decrease in patch detection probability. First, dispersers may overshoot the other

Figure 17a. Relationship between patch detection probability and dispersal distance, for three levels of patch detection radius (D).

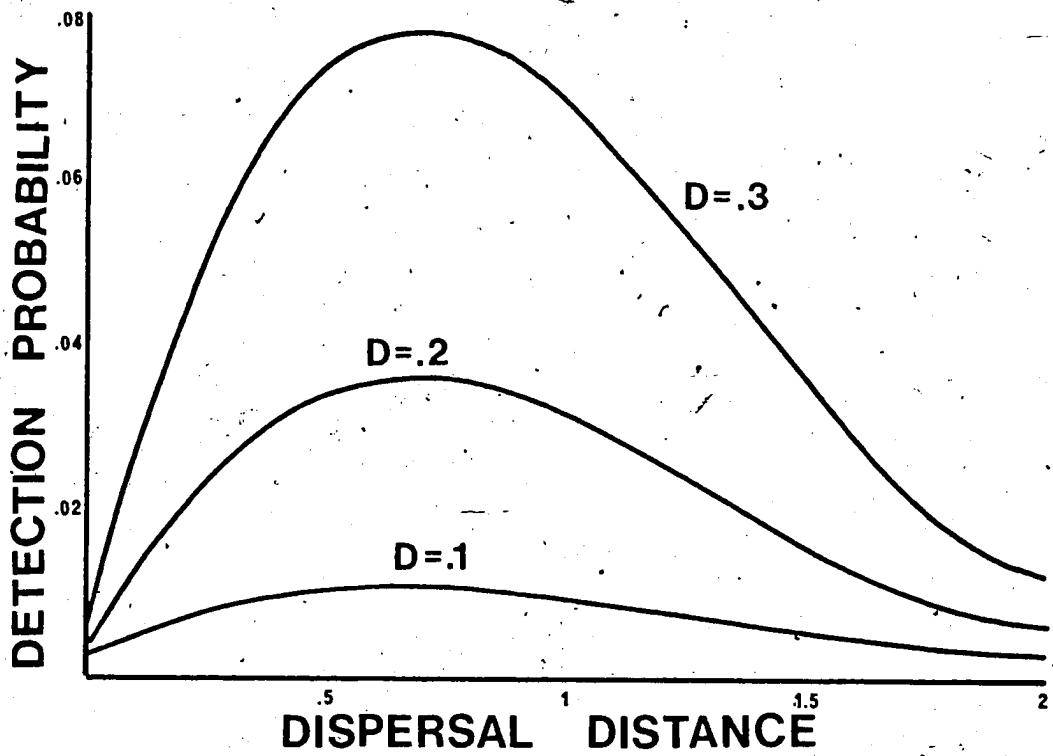
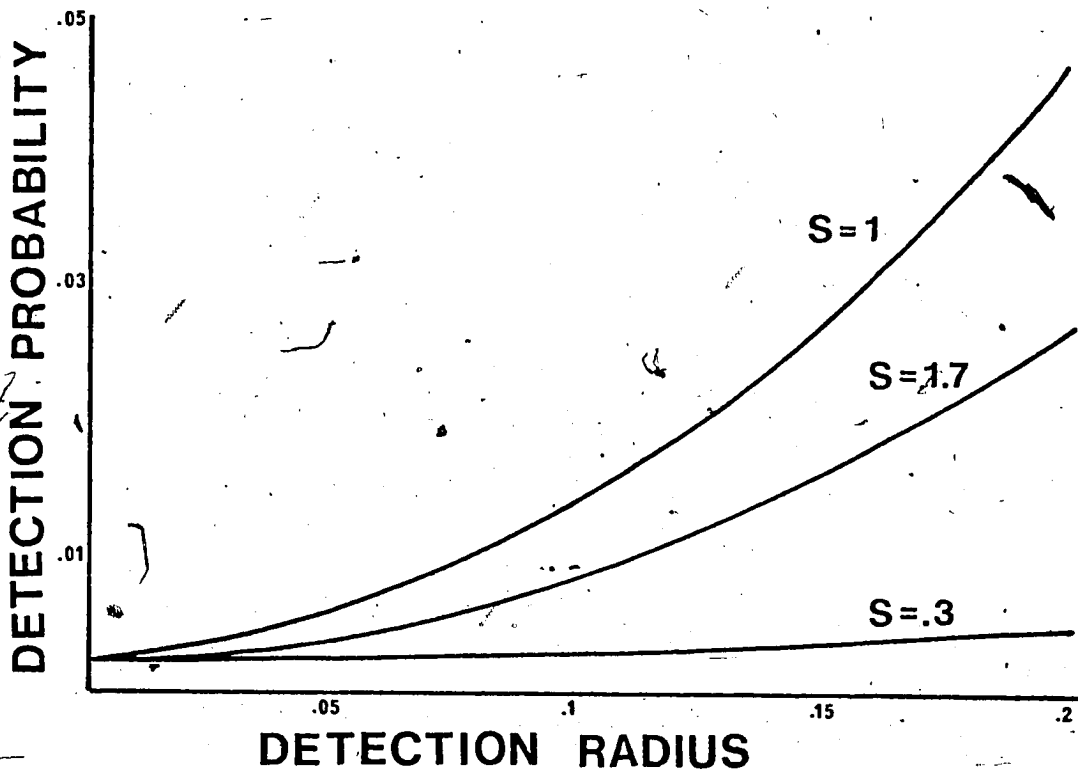


Figure 17b. Relationship between patch detection probability and patch detection radius, for three levels of dispersal distance (S).



patches in the area. Second, at high dispersal distances dispersers are spread over much larger areas than at smaller distances, because the standard deviation in dispersal distance is proportional to the mean (see Figure 16). Notice also that patch detection probability increases with increasing detection radius (Figure 17b). This relationship is most pronounced for intermediate dispersal distances, which, as stated above, are the distances at which detection probability is highest. Detection probability (dp) was used as an additional independent variable in the remainder of the analyses.

The purpose of analysing the simulation results was to determine which types of organisms (i.e., species characterised by which combinations of independent variables) are expected to have low or high patch population sizes (i.e., low or high values of $\ln(mnpop)$), and a low or high effect of patch spatial arrangement on population abundance (i.e., low or high values of $\ln(spatvar)$). A standard statistical approach to problems in which relationships between several independent variables and one dependent variables are sought, is to use the least squares method to build the best polynomial model relating the independent variables to the dependent variable (Box and Draper 1987). Although this method results in an adequate empirical model, in this case it does not clarify our understanding of the qualitative relationships between the independent and dependent variables. In particular, it does not give me an estimate of the relative importance of each independent variable in explaining variation in the dependent variable. I therefore used the following method for analysing the simulation results. First, polynomial regression equations were calculated for each of the dependent variables (i.e., $\ln(mnpop)$ and $spatvar$) on each of the independent variables (i.e., r , k , p , s , d , i , and dp). This provided me with estimates of the forms of the underlying relationships. To determine the relative importance of the independent variables, the polynomial regression equations were then used as polynomial variables in stepwise regressions of $\ln(mnpop)$ and $spatvar$.

The polynomial regression equations giving the forms of the underlying relationships between the independent variables and the dependent variables are given in Table 9. Although there was a significant polynomial regression for almost all of the variables, there

Table 9. Polynomial Regression Equations

a. Regressions of $\ln(mnpop)$, population abundance averaged over patches.		
Regression Equation (i.e. $\ln(mnpop) = \dots$)	R^2	Name of Polynomial Variable
Growth Rate: $2.21 + 7.214(r)$	.0093	$r(mn)$
Carrying Capacity: $1.92 + 0.000524(k) - 1.09 \times 10^{-7}(kk^2) + 6.63 \times 10^{-12}(kk^3)$	.0067	$k(mn)$
Dispersal Rate: $7.01 - 35.3(p) + 94.6(p^2) - 107.0(p^3) + 42.3(p^4)$	.2982	$p(mn)$
Dispersal Distance: $1.36 + 11.5(s) - 19.2(s^2) + 11.5(s^3) - 2.40(s^4)$	.1269	$s(mn)$
Detection Radius: $0.535 + 13.6(d)$	.3080	$d(mn)$
Immigration Rate: $1.53 + 3.36 \times 10^{-3}(i) - 1.93 \times 10^{-6}(i^2)$	.0421	$i(mn)$
Detection Probability: $1.04 + 137.0(dp) - 1.78 \times 10^3(dp^2) + 2.4010^6(dp^3)$	.3890	$dp(mn)$
b. Regressions of $spatvar$, variation among patch abundances due to spatial arrangement.		
Regression Equation (i.e. $spatvar = \dots$)	R^2	Name of Polynomial Variable
Growth Rate: no significant regression		
Carrying Capacity: no significant regression		
Dispersal Rate: no significant regression		
Dispersal Distance: $0.143 - 0.198(s) + 0.0273(s^3)$	.1395	$s(sv)$
Detection Radius: $-0.069 + 3.82(d^2) - 28.1(d^4)$	.0819	$d(sv)$
Immigration Rate: $0.0267 - 5.27 \times 10^{-5}(i)$	.0084	$i(sv)$
Detection Probability: $0.131 + 6.41 - 93.7(dp^2) + 481(dp^3)(dp)$	.0657	$dp(sv)$

were large differences in the degree to which each of them accounted for the observed variation in the response variables (see R^2 values in Table 9).

The results of the stepwise regressions of the dependent variables (i.e., $\ln(mnpop)$ and $spatvar$) on the polynomial variables (Table 9) are shown in Table 10. The effects of the first order interactions among the polynomial variables were also considered, but they added only slightly to the proportion of the variance explained by the polynomial variables.

The polynomial variables for mean patch detection probability (dp) and mean dispersal rate (p) were the most important factors determining average local population size, with partial R^2 values of .3890 and .2923 respectively. The polynomial regression equations for dp and p are plotted in Figures 18a and 18b.

The polynomial variables for mean dispersal distance (s) and mean detection radius (d) were the most important factors determining the spatial variation among local populations, with partial R^2 values of .1395 and .0825 respectively. The equations for these variables are shown in Figures 19a and 19b.

The results suggest the following hypotheses for populations distributed in patchy habitats. If a species' patch detection probability is high, and its dispersal rate is low, then local population abundance is expected to be high. Conversely, for high dispersal rates and low patch detection probabilities, the average patch population size is expected to be low. If a species' dispersal distance is low, and its detection radius high, then the exact spatial location of habitat patches is expected to have a strong influence on local population dynamics (i.e., high value of $spatvar$). Conversely, if the dispersal distance is high and the detection radius is low, exact spatial relationships among habitat patches are not expected to significantly affect local population abundances (i.e., low value of $spatvar$).

The results indicate that these hypotheses should hold, virtually irrespective of other major aspects of population dynamics such as intrinsic growth rate (r), patch carrying capacity (k), or the rate of immigration from outside the region (i). The implications and limita-

Table 10. Stepwise Multiple Regressions of Polynomial Variables on Response Variables

Note: for definitions of polynomial variables see Table 9.

(a) Regression of $\ln(\text{average patch population sizes})$, i.e. $\ln(\text{rhnpop})$ on polynomial variables.

Polynomial Variable	Partial R^2	F-statistic	Probability
$dp(mn)$	0.3890	1272.00	<0.0001
$p(mn)$	0.2923	1831.19	<0.0001
$i(mn)$	0.0432	312.65	<0.0001
$s(mn)$	0.0297	269.57	<0.0001
$r(mn)$	0.0145	110.81	<0.0001
$d(mn)$	0.0122	97.78	<0.0001
$k(mn)$	0.0022	8.00	<0.0001

(b) Regression of spatial variation among patches due to spatial arrangement, i.e. $spatvar$, on polynomial variables.

Polynomial Variable	Partial R^2	F-statistic	Probability
$s(sv)$	0.1395	323.81	<0.0001
$d(sv)$	0.0825	211.82	<0.0001
$i(sv)$	0.0063	16.34	<0.0001
$dp(sv)$	0.0059	15.44	<0.0002

Figure 18a. Relationship between patch detection probability and log-transformed values of average patch population abundance (averaged over 10 patches).

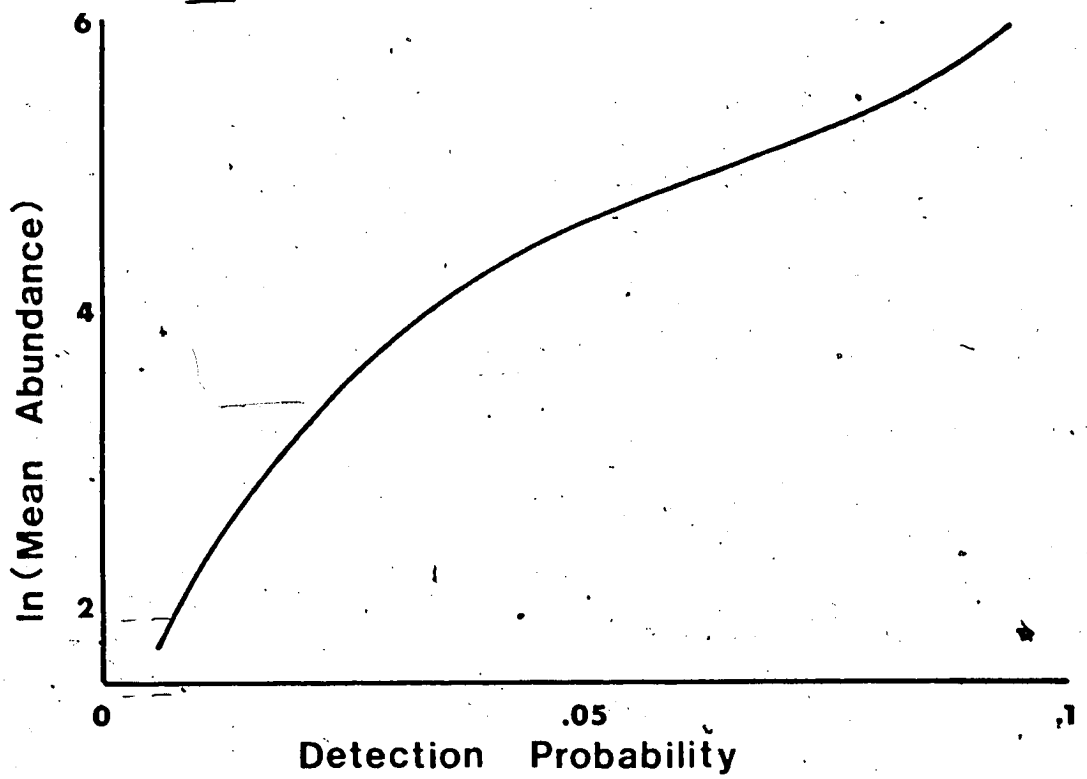


Figure 18b. Relationship* between dispersal rate of organisms from patches and log-transformed values of average patch population abundance (averaged over 10 patches).

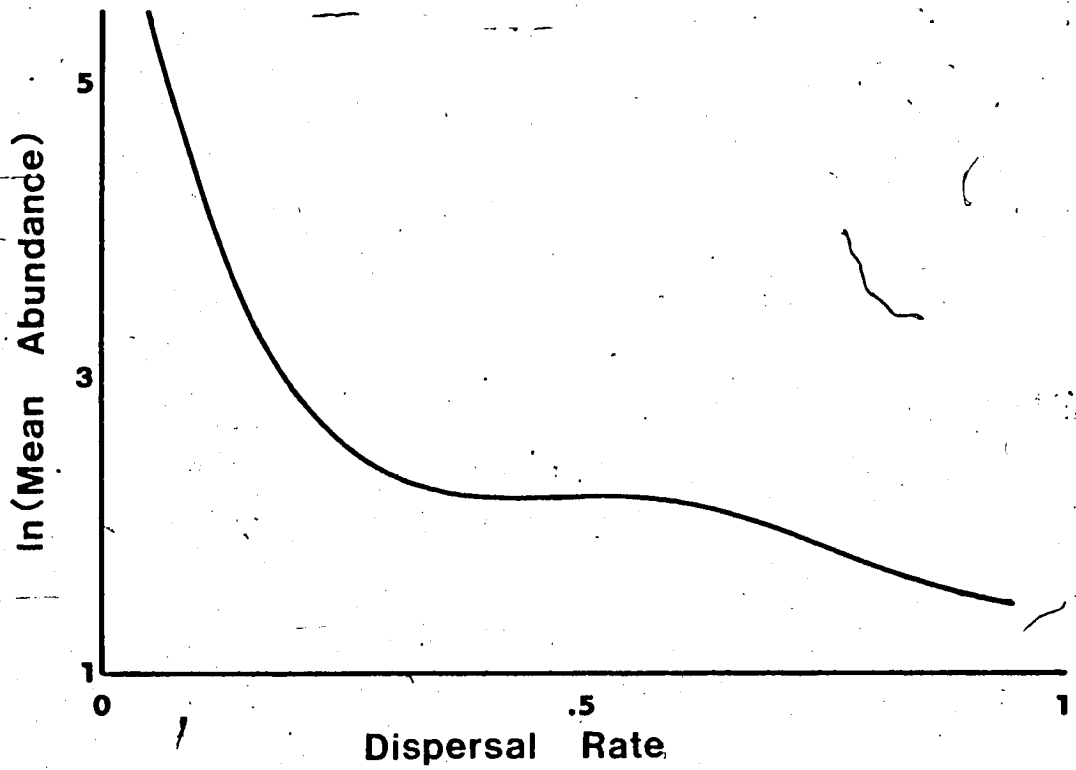


Figure 19a. Relationship between dispersal distance and spatial variation among 10 patch population means due to patch spatial arrangement; for definition see Methods section.

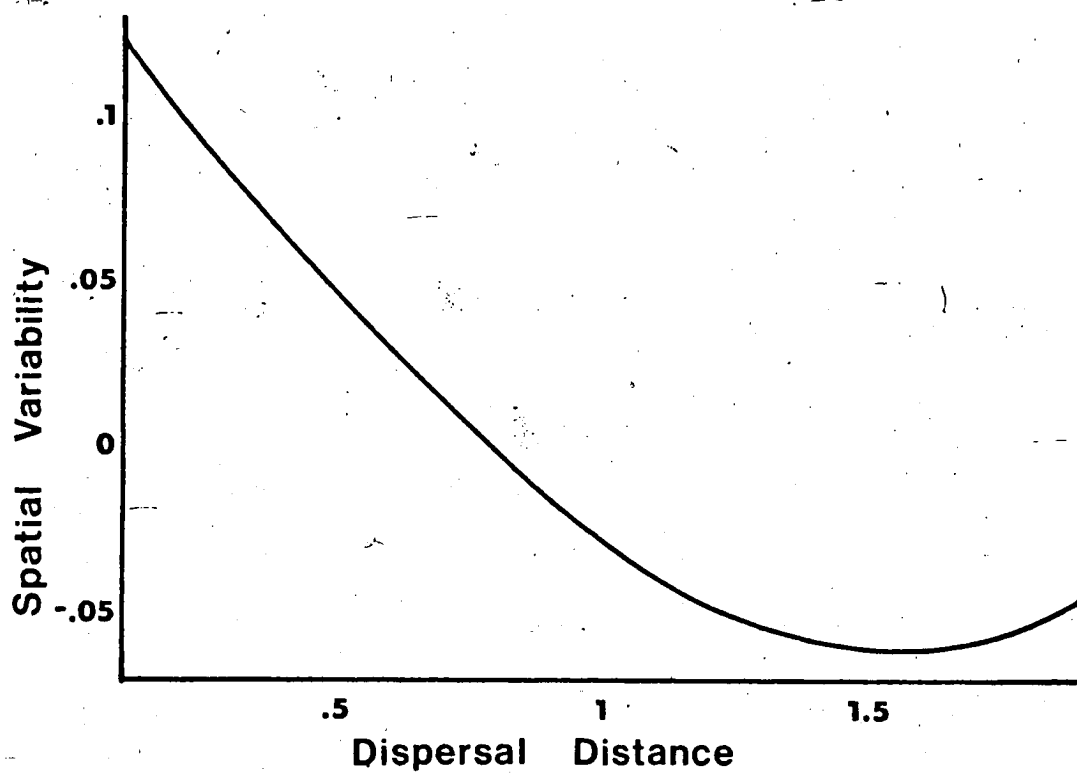
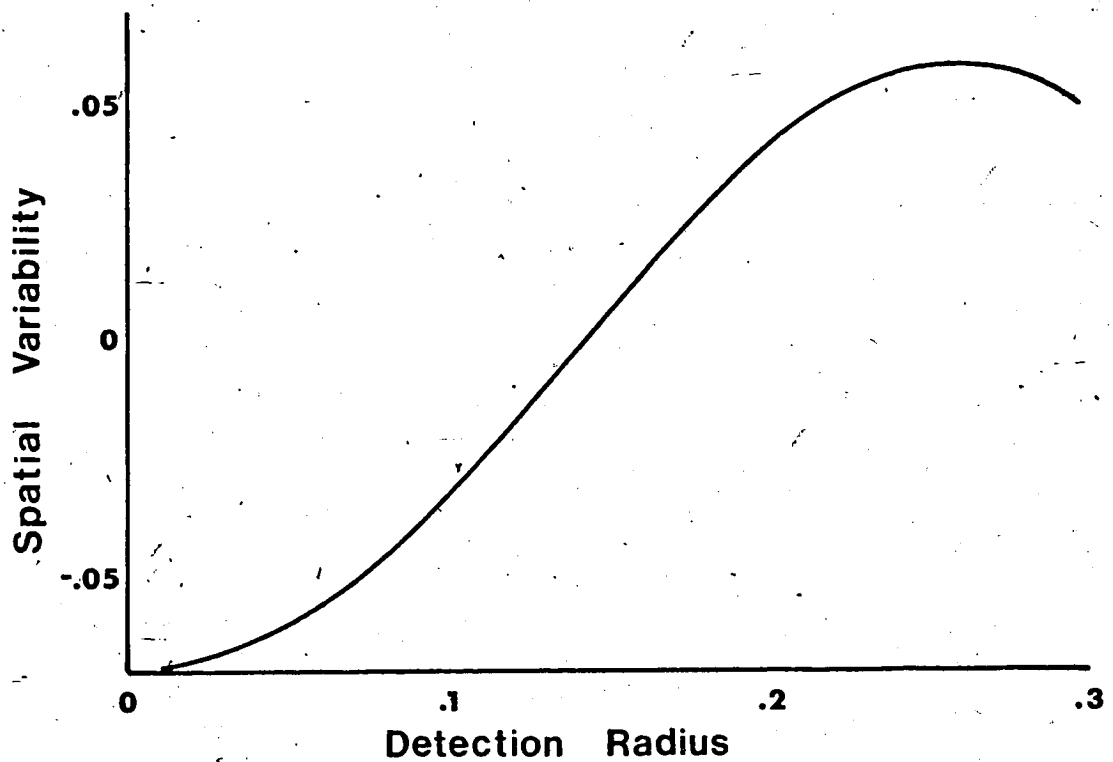


Figure 19b. Relationship between detection radius and spatial variation among 10 patch population means due to patch spatial arrangement; for definition see Methods section.



tions of the hypotheses are discussed in the general discussion (Chapter 9).

The results of this study have interesting implications for *P. rapae*. In the introduction to this chapter, I argued that the work to that point supported the argument that the spatial arrangement of habitat patches has little impact on local population size, because of the low host detection radius for this species. However, the results of this chapter imply an alternate hypothesis. The dispersal distance of *P. rapae* is quite high relative to the distances among host plant patches (Jones et al. 1980). According to the results of this chapter, this high dispersal distance may be more important in reducing the effect of patch spatial arrangement on local *P. rapae* population size than its low detection radius.

8. Local Extinction and Global Survival

It is widely believed that dispersal among local populations increases the global survival probability of patchy populations (DeAngelis et al. 1979, Lomnicki 1980, den Boer 1981, Hastings 1982, Fahrig and Merriam 1985). This is because dispersal allows for re-establishment of local populations which become extinct due to stochastic factors. However, it is also understood that dispersal from local populations has the effect of lowering the average expected population size (see chapter 7, and Myers 1976, Lomnicki 1980). It is clear, therefore, that the longterm average population size, and probability of global extinction of a patchy population, will depend on the relative magnitudes of the dispersal rate among patches, and the probability of local extinctions. The purpose of the work in this chapter was to examine this relationship, using the general simulation model discussed in chapters 5 and 7.

Previous Studies

Analytical studies have dealt with the effects of stochastic variation in parameter values, on system stability. May (1973) studied the logistic equation

$$\frac{dN(t)}{dt} = N(t)[k - N(t)]$$

with

$$k = k_0 + \gamma(t),$$

where N is the population size, t is time, and k is the carrying capacity of the environment. k fluctuates randomly about the mean value k_0 , according to a Gaussian "white noise" (i.e. uncorrelated fluctuations) process, $\gamma(t)$, which has mean zero and variance σ^2 . May found that in this case, there is no equilibrium probability distribution for N unless $k > \frac{1}{2}\sigma^2$. Survival of the population is virtually ensured if $k > \sigma^2$. The expected population size in this stochastic environment is $k_0[1 - (\frac{\sigma^2}{2k_0})]$. Since in the deterministic case the expected population size would be equal to k_0 , this implies that the average expected population size in the stochastic

environment is lower than that in the deterministic environment.

May (1974) also studied the effect of stochastic variation in population growth rate, λ . For the case of a spatially homogeneous population (i.e. a single patch), he found an analogous result to that above, namely that population survival is virtually assured if $\lambda > \sigma^2$, where σ^2 is now the variance associated with the random fluctuations in λ . However, he also studied the spatially heterogeneous case in which the population was assumed to be distributed among several patches. He described the dispersal process as

$$N_{\alpha}(t+1; \text{after dispersal}) = \frac{1}{p} \sum_{\beta=1}^p N_{\beta}(t; \text{before dispersal}),$$

where α and β denote patches, and p is the number of neighbouring patches. May showed that the criterion for a particular population to persist is now $\lambda > \frac{\sigma^2}{p}$, rather than $\lambda > \sigma^2$ as above. The exchange of organisms among patches is therefore expected to average out local fluctuations over space, and enhance local population survival.

Although the results of May seem to be intuitively reasonable, it has been shown that in the ecological context there are two possible methods for interpreting the solution of the stochastic differential logistic equation (Feldman and Roughgarden 1975, Turelli 1977). The purpose of assuming Gaussian white noise as the form of the stochastic fluctuations in the model is so that the stochastic output will be a reaction-diffusion equation, and therefore amenable to standard analytical techniques (Turelli 1977). However, there are two main possible methods of integration which can be used to solve the stochastic differential logistic equation for the reaction-diffusion solution. The methods, known as the Ito calculus and the Stratanovich calculus, differ in their interpretations of the appropriate form for the "reaction" portion of the solution (Feldman and Roughgarden 1975, Turelli 1977). The results of May (1973, 1974) described above were obtained using the Ito method. Feldman and Roughgarden (1974) have shown that the effects of variability in k_0 on population survival are very different if the Stratanovich calculus is assumed. In particular they show that (i) a stable population solution exists in all cases, and does not depend on the ratio between the mean and the

variance of k_0 , as in the Ito case, and (ii) the expected mean population size is equal to k_0 , and not less than k_0 , as in the Ito case.

Turelli (1977) undertook a detailed analysis of the Ito versus Stratanovich problem. He compared the behaviour of the two solutions to behaviour of more realistic (though more cumbersome) models. For example, he found that the Ito solution of the stochastic differential model behaves more closely to a difference model (assumed to be biologically more realistic than differential models), than the Stratanovich does. If the variability in the model is assumed to be autocorrelated instead of Gaussian white noise, then the Stratanovich model is a better approximation in some cases. However, in other cases neither the Ito nor the Stratanovich method provide reasonable solutions.

Vance (1980, 1984) studied a more complicated stochastic logistic model. In his model the per capita death rate in each patch was

$$d + \sigma_d e_i(t) + d_1 N_1$$

Here, d is the mean per capita death rate, $\sigma_d e_i$ is stochastic variability in the death rate in patch i in time t , and $d_1 N_1$ is the effect of juvenile population size (N_1) on juvenile death rate (d_1). This final term represents the "logistic" portion of the model. Vance found that if only one patch is considered, the population variance is

$$\frac{N^2 \sigma_d^2}{2(b-d)}$$

If many patches are included, and assuming that dispersers from one patch are evenly distributed among all other patches ("dispersal pool" assumption; see chapter 5), then the population variance is

$$\left[1 - \left(\frac{n-1}{n} \right) \left(\frac{b}{2b-d} \right) \right] \frac{N_i^2 \sigma_d^2}{2(b-d)}$$

where n is the number of patches. This is clearly lower than the variability in the single-patch case, which qualitatively confirms the results of May (1974). However, Vance also found

cases in which dispersal among patches can increase the probability of extinction by amplifying local instability. For example, if large stochastic variability is included in the per capita birth rates, then dispersal among patches can make the system less stable. He found that this was more common in discrete than in continuous models (Vance 1980).

The results of the analytical studies are therefore somewhat ambiguous. More detailed predictions can be made from computer simulations. Reddingius and den Boer (1970) and Roff (1974a, b) studied simulations of populations in evenly distributed patches. Their studies tend to confirm the result of May (1974), that dispersal among patches increases the survival probability of local and regional populations. Roff (1974a, b) also found that (i) the mean population size was a decreasing linear function of the variance in local carrying capacity (confirms the result of May (1973, 1974)), and (ii) the mean population size was a decreasing linear function of the mean number of catastrophes (local extinctions) per time unit.

The purpose of this chapter was to use the simulation model described in chapters 5 and 7 to simultaneously observe the effects of dispersal rate and local extinction rate on the survival time of patchy populations. Since local extinctions are the logical outcome of large stochastic fluctuations in parameters such as carrying capacity, growth rate, birth rate, or death rate, these simulations clarify the rather varied and diffuse results found in the literature. In this chapter I also examine the effect of detection radius (d , distance from which dispersers detect patches) on global population survival. Finally, I study the effects of small stochastic fluctuations in parameter values over time, on population survival.

Methods

The simulation model described in chapters 5 and 7 was used for the simulation experiments. However, the immigration term (i) was not included; the system of patches was therefore assumed to be closed to the outside area. In addition I included a term, x , the probability of local extinction (i.e., death of all organisms in a patch) in each time step.

The main purpose of the experiments reported in this chapter was to study the following questions: (i) does dispersal allow global populations to survive for longer time periods than otherwise; (ii) if so, for what level(s) of dispersal is this effect greatest; (iii) does patch detection radius (d) affect global survival and (iv) does stochastic variability in population parameters affect global survival?

I conducted 500 simulations in each of four categories. In each simulation a random value between 0.0 and 1.0 was chosen for the local extinction probability (x) and the dispersal rate (p). The four categories were: (i) no stochastic variation in parameter values, detection radius (d) = 0.1, (ii) no stochastic variation in parameter values, d = 0.3, (iii) stochastic variation in parameter values, d = 0.1, (iv) stochastic variation in parameter values, d = 0.3. In cases (iii) and (iv), each of the parameter values, r , k , p , d , s (see chapter 7) and x (see above) were assumed to be normal variates. The mean values are shown in Table 11. In each case the standard deviation was 10% of the mean.

Each simulation ran for a maximum of 500 time steps. If the population became globally extinct (i.e., all patches simultaneously extinct) before completion of the 500 steps, the simulation was terminated, and the time of global extinction was recorded.

For each of the sets of 500 simulations, stepwise multiple regressions of the $\ln(\text{survival time} + 1)$ on all first, second, and third order polynomial terms of dispersal rate (p) and local extinction probability (x) (i.e., p , x , p^2 , x^2 , px , p^3 , x^3 , d^2x , dx^2) were conducted.

Results

The results are summarised in figures 20, 21 and 22.

Figure 20 indicates that dispersal increases global survival time. For a dispersal rate of 0.5, the survival time is on the order of 4 times greater with dispersal than without dispersal.

Figures 21 and 22(A) indicate that dispersal may decrease survival for very low levels of local extinction probability. This is reasonable in light of the results of chapter 7. Here it was

Table 11. Mean values of parameters used in the simulations.

Parameter	Mean
Growth Rate (r)	0.2
Carrying Capacity (k)	10000
Dispersal Distance (s)	1.0
(fraction of mean inter-patch distance)	
Detection Radius (d)	0.1, 0.3
(fraction of mean inter-patch distance)	
Dispersal Rate (p)	0.0 - 1.0
	(uniform random number)
Local Extinction Probability (x)	0.0 - 1.0
	(uniform random number)

Figure 20. Relationships between $\ln(\text{global population survival time})$ and local extinction probability under four sets of conditions. 1: baseline curve of survival time with no dispersal between patches; 2-5: dispersal rate from patches is 0.5 per time period; 2: no stochastic variation in parameter values, detection radius (d)=0.1; 4: no stochastic variation in parameter values, $d=0.3$; 3: stochastic variation in parameter values (s.d./mean=0.1 for all parameters), $d=0.1$; 5: stochastic variation in parameter values (s.d./mean=0.1 for all parameters), $d=0.3$.

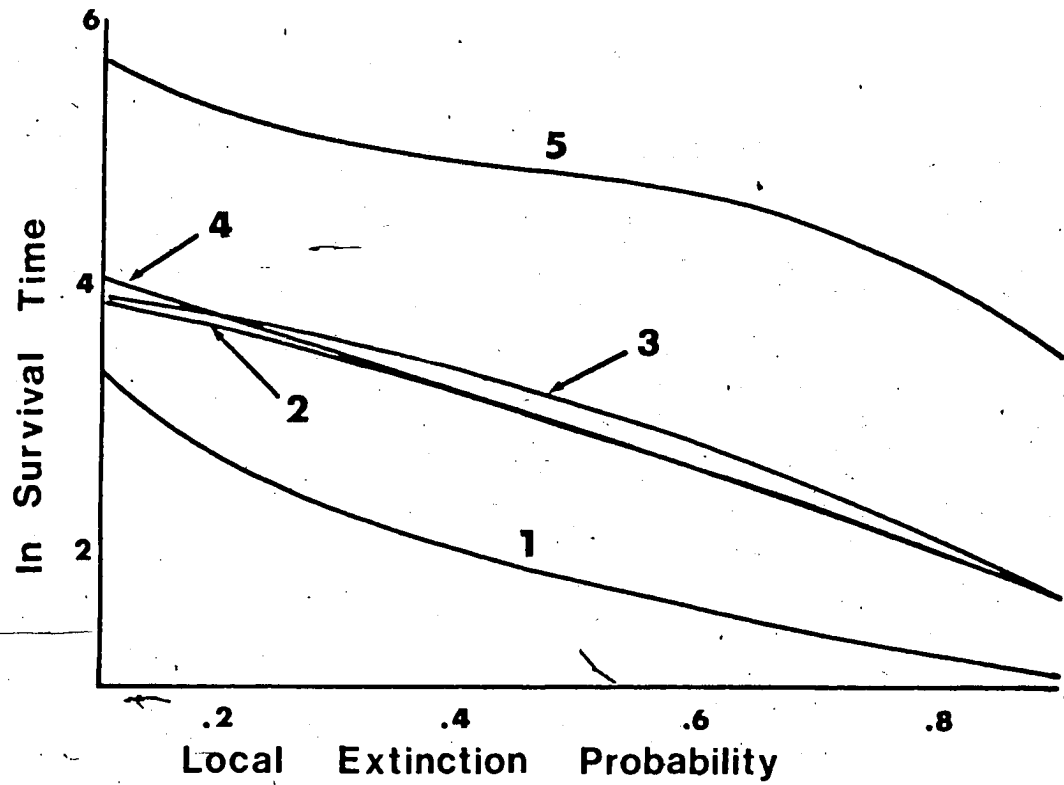


Figure 21. Relationship between $\ln(\text{survival time} + 1)$ and local extinction probability (ex) and dispersal rate (di) for simulations with no stochastic variation in parameter values. A: detection radius=0.1. B: detection radius=0.3.

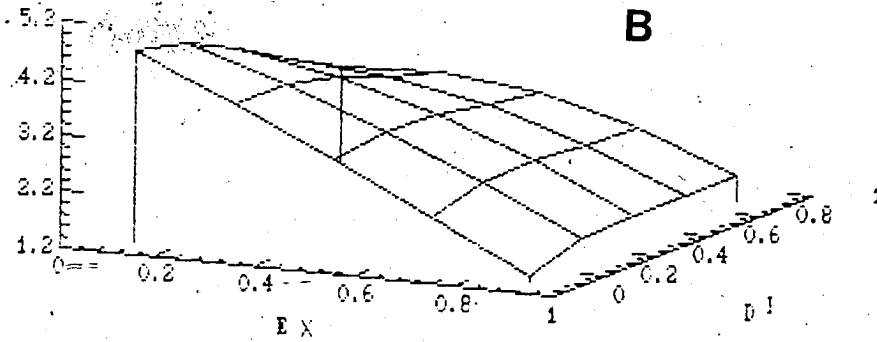
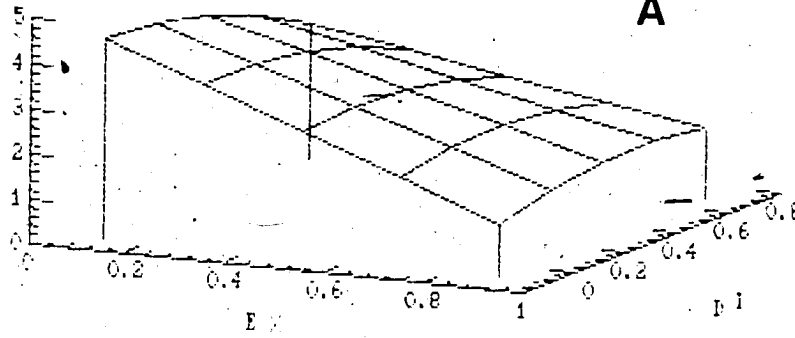
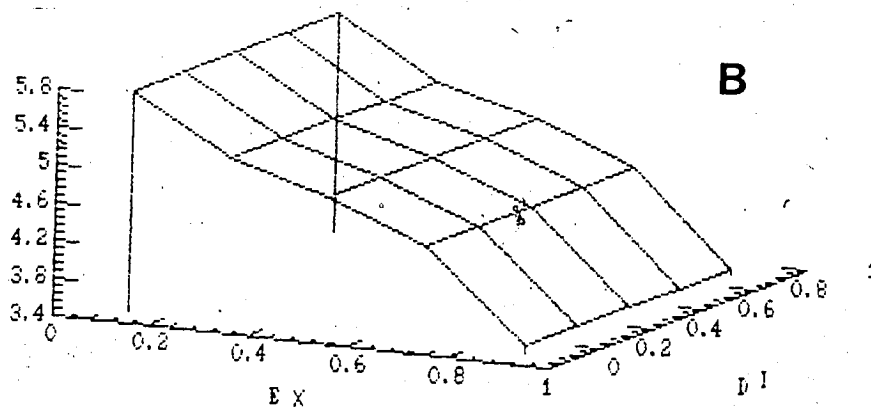
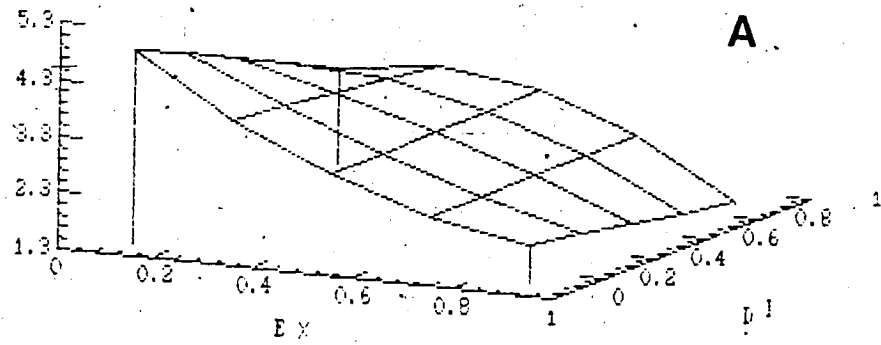


Figure 22. Relationship between $\ln(\text{survival time} + 1)$ and local extinction probability (ex) and dispersal rate (di) for simulations with stochastic variation in parameter values (s.d./mean=0.1 for all parameters). A: detection radius=0.1. B: detection radius=0.3.



shown that there is generally a negative relationship between dispersal rate and population size (Figure 18b). If the probability of local extinction is very low, then the reduction in population size due to high dispersal rates increases the probability of global extinction.

However, the negative effect of dispersal rate only holds for very low extinction probabilities. Figures 21 and 22(A) show that for higher local extinction probabilities, there is a positive relationship between dispersal rate and survival time. In this case, locally extinct patches are recolonised by the dispersers which increases global survival time.

Figure 20 indicates that the combination of stochastic variability in parameter values and a high patch detection radius (0.3) results in a marked increase in survival time (curve 5). In this case the survival time is over 7 times greater than that of the other three cases (curves 2, 3, and 4). This can be explained as follows. Depending on the initial conditions of a simulation, a global population will usually either decrease until it becomes regionally extinct, or increase to the carrying capacity, thus virtually ensuring survival. Two factors which will tend to increase the probability that a particular simulation will take the second course (population increase) are stochastic variation and increased detection probability.

Finally, Figure 22(B) indicates that under conditions of stochastic variation in parameter values and high detection radius (0.3), the actual level of dispersal has no detectable effect on population survival. This implies that (i) only a small dispersal rate is required to ensure global survival under these conditions and (ii) for low local extinction probabilities even high dispersal rates cannot depress the population level sufficiently to decrease global survival rate under these conditions.

9. General Discussion

Cabbage Butterfly Dispersal and Host Detection

The finding that *P. rapae* females do not orient towards their larval host plants from a distance (see Chapters 3 and 4) is consistent with current knowledge of butterfly host-finding behaviour. 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 recognise colours or shapes of host plants from short distances (less than 1 m) (Rausher 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.

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 would explain the large variability in the data on egg-laying rate and patch size (Figure 3).

Commonly, plants at the edge of a patch have higher *P. rapae* egg densities than those in the centre (Harcourt 1961, Kobayashi 1965, Jones 1977); this is known as the "edge effect". It is consistent with the scenario for dispersal and egg-laying described in Chapter 3. 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 uncorrelated with patch size (Figure 3). 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). This is apparently accomplished through short-term visual memory. 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, I 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 250-700 m per day (Jones et al. 1980)), the ability to detect a new patch appears to be low (Chapters 3 and 4). 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 which 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 its host plant distribution before man's influence on the habitat than to its current distribution. 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. virginiensis* 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 which 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.

Effect of Patch Spatial Arrangement on Cabbage Butterfly Populations

The simulation model described in Chapter 6 is a useful tool for examining the possible effects of patch spatial arrangement on local *P. rapae* abundance. However, the values used for the development rates of the eggs, larvae and pupae were based on mean weather conditions in the Elora, Ontario area. Since these development rates are very sensitive to temperature, the model in its present form can not be expected to predict the population dynamics for a particular season with high accuracy. One would need to include the effects of the specific weather conditions for that season. This is the most likely explanation for two discrepancies in timing which occurred between the model and field data. First, the model predicted an earlier onset of population growth than occurred in the field data. This was probably a result of a colder spring than average, in the Elora area in 1986. Second, the field data indicate two separate population peaks, one in early July and the second in August. Because of the variability in the field data, the polynomial regression equation did not track these two peaks, but inspection of the graph (Figure 15) shows a dip in population density in late July. This dip appears to be smaller in the simulation; the onset of the second population increase occurs almost at the peak of the first.

Another limitation of the model is that the dispersal rate from cabbage patches was based on the work in Chapter 3, in which the dispersal rate of females from a cabbage patch containing 450 plants was determined. It is not known how this rate might change for much smaller or much larger patches. Extensions of the model to such situations would be premature, until the necessary data on dispersal rates are available.

The results of the field study in Chapter 6 support the main predictions of the simulations. *P. rapae* egg densities in the three categories of field occurred in the same order for both simulation and field data (i.e. $M > C > I$). However, the effect of spatial arrangement as predicted by the model (Figure 14) appears to be smaller than the effect observed in the field (Figure 15). There are several possible explanations for this. First, in the field data, the egg density in M was significantly higher than I, but C was not significantly different from M or I

(see Figure 15). This implies that the actual differences may not be as great as they appear in Figure 15. Second, the variability in the field data meant that, as stated above, the polynomial regression did not track the two-peaked population curve. By using a third order polynomial to approximate a curve of higher order, the differences in eggs densities are exaggerated at high densities. Third, 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 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 simulation model, the predicted effect of patch spatial arrangement would be greater. This is particularly likely for this model because it is non-linear; 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 non-linear stochastic process by a deterministic model. I did not have estimates of real variability for the parameters in this model, so a deterministic approach was chosen.

A difficulty with this study is that, because the effect of spatial arrangement was expected to be small, it was not possible to design a completely rigorous field test of the model predictions. For example, if there had been no effect of cabbage patch spatial arrangement on population density, then no matter what the ordering of the densities by field type, I would not have been able to reject the predictions of the simulations. However, if the field study had shown that either of C or I was significantly greater than M, then the field results would have been deemed inconsistent with the predictions of the simulations. Therefore, although both the observed and predicted differences were small, the results are consistent with the predictions.

As mentioned above, two assumptions in the model are that mating success is perfect, and females complete at least one egg-laying bout on the host patch on which they fed as larvae. For the current set of simulations, these assumptions are expected to have a quantitative, but not a qualitative effect on the predictions. However, it is interesting to note that, over the long term, both of these assumptions may be critical to the predicted survival rate of the regional population. The most critical period in terms of the long-term survival of *P. rapae* populations is probably the early spring. At this time, population levels are at their lowest level for the year, and survival of the population will depend on efficient mate-finding and egg-laying in this first generation of adults.

Combined Importance of Dispersal Characteristics on Local Population Size

The results in Chapter 7 of the analyses on average patch population size indicate the importance of dispersal on local population size. The most important factor determining size is the probability that dispersers successfully detect new patches; the higher this probability, the higher the average patch population size. This result is analogous to that of Levin et al. (1984) who found that, at the level of individual fitness, the optimal level of dispersal increases with an increase in the probability of a dispersing propagule successfully attaining a new site. The relative unimportance of dispersal distance (s) and detection radius (d) (Table 10a) result from the fact that the effects of these two parameters are largely encompassed by the effect of detection probability (dp).

The importance of the dispersal rate (fraction of local population dispersing) reflects the high risk associated with dispersal; high dispersal rates generally result in lower mean patch population sizes, unless the probability of dispersers detecting new patches is very high. A negative relationship between dispersal rate and population size has also been found in theoretical studies in which all patches are assumed to be equally accessible to all other patches (Lomnicki 1980), or in which patches are assumed to be evenly distributed in space (Roff 1974a,b):

An interesting aspect of the results is that the intrinsic growth rates and carrying capacities have little effect on average population sizes in a patchy environment. Although their effects are significant and positive (see Table 9a), each of them explains less than 1% of the explained variation in $\ln(mnpop)$ (see Table 10a). Their effects were almost completely swamped by the dynamics of inter-patch dispersal. I do not feel that this result is an artifact of the range of values chosen for the parameters (see Table 7). The result is important because it suggests that between-patch processes (i.e., dispersal) will often be more important than within-patch processes (i.e., births and deaths) in determining local population size within a habitat patch.

As described in the methods section of Chapter 7, the residual spatial variation among patch population sizes, after accounting for within-patch variability (*spatvar*), can be taken as a measure of the degree to which the particular spatial relationships between a patch and other patches in the region affects the population size within the first patch. Once again, the results indicate that the dynamics of dispersal among patches are most important in determining the level of this effect (Table 10b). The most important factor in this case is the dispersal distance. The greater the dispersal distance, the less important is the spatial arrangement of patches in causing differences among local population sizes (lower values of *spatvar*). This is reasonable since, for larger distances, the same number of dispersing organisms are spread over a much larger area (Figure 16). The result is that dispersal from a particular patch has a more general influence (i.e., affects more patches) for large dispersal distances than for small ones. Conversely, if the dispersal distance is small, then those patches which have neighbours at close distances will receive many more dispersers than those which do not. In this case, the spatial relationships among patches will be an important determinant of the local population size, and the spatial variation among patch sizes will be high.

The detection radius is also important in determining the influence of patch spatial arrangement; patch spatial arrangement is more important (i.e., *spatvar* is higher) when the detection radius is high. This also makes sense because, for higher detection radii, dispersers

are more likely to detect other patches; this means the spatial relationships among patches are more important.

Once again, the within-patch population dynamics (r and k) are not important determinants of the effect of patch spatial arrangement on local population size. This is readily understandable since between-patch dynamics (i.e., inter-patch dispersal) are more likely to be related to the level of importance of patch spatial arrangement.

The reasons for the lack of importance of the rate of immigration from outside the study region are less obvious. One would expect that for high rates of immigration, the effects of inter-patch dispersal would be swamped, and in this case the patch spatial arrangement would have less effect on local population size. The general shape of the relationship between immigration rate and *spatvar* confirms this general expectation (see Table 9b); *spatvar* decreases with increasing immigration rate. However, this relationship explains only a small fraction of the overall variability in *spatvar* (*partial* $R^2=0.0063$; see Table 10b). The effects of dispersal distance and dispersal rate far outweigh the effect of immigration rate. It is possible that for much higher immigration rates this swamping effect of immigration would be more pronounced. In this study, the upper limit to immigration rate was 1000 individuals per time unit. Relative to the ranges of the other parameters in the model (see Table 7), I feel this represents a large immigration rate. The results indicate therefore, that immigration from outside the study area is not expected to significantly swamp the effects of inter-patch dispersal, except for at extremely high immigration rates.

As mentioned in Chapter 7, the results of these general simulations lead to a more comprehensive explanation for the small effect of cabbage patch spatial arrangement on *P. rapae* local population size. This 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. Also, since dispersing

females can not detect new patches from a distance, direct population exchange among any pair of patches is limited. The contribution of dispersers directly from other patches is therefore low relative to the contributions from butterflies which are "milling about" in the inter-patch area. This results in similar immigration rates in all patches, and reduces the effect of spatial arrangement on population abundances.

In general, the results of this study indicate that it is important to have a good understanding of the dispersal behaviour 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, Leskovitch and Fahrig 1985). However, if the organisms disperse large distances in random directions from patches, and do not detect patches from a distance, as in this study, then the spatial arrangement of habitat will have less effect on population dynamics.

The results are also of considerable importance for predictions concerning the effects of spatial arrangement of habitat on population dynamics, particularly of those species which disperse large distances, and are unable to detect new habitat patches from a distance. This appears to be the case for many insect species (Kennedy and Stroyan 1959, Van Emden et al. 1969, Aikman and Hewitt 1972, Finch and Skinner 1982). If this is true for an insect pest, then the hope that the pest can be controlled by manipulating the spatial arrangement of breeding habitat will likely be disappointed.

However, this may not be the case if one were to include possible interactions among species, such as predator-prey interactions. For example, for a prey species which is a pest, it may be possible to manipulate the spatial arrangement of habitat to maximise the effect of the predator on the prey, even if the prey population alone would not be affected by habitat spatial arrangement.

In interpreting the results of this work, it is important to note that the habitat of any organism may be composed of several different types of habitat patches including breeding habitat, feeding habitat, and mating habitat. Also, different life history stages of the same species may use different types of habitat. The spatial distributions of the various types of habitat patches may overlap completely, partially, or not at all. Predictions concerning the potential effects of the spatial arrangement of habitat patches may be different depending on which type of habitat is considered to be most important. In the case of *P. rapae*, I considered the adult breeding, egg-laying, and larval feeding habitat (i.e. host plant patches) to be most important. However, this does not include the adult feeding habitat, which consists of patches of flowers such as dandelions and clovers. It may be possible that manipulation of the spatial arrangement of such patches may influence population levels.

Although the model I used for this simulation study was quite general, it was also quite simple, to allow me to obtain general hypotheses. The hypotheses developed here are therefore limited to the extent that the modelling is limited.

One simplification in the model is the fact that the detection radius and the carrying capacity are not correlated. If larger patches are more likely to be detected from greater distances, and if larger patches have higher carrying capacities, then these two parameters would be expected to be correlated, since they are both related to patch size. However, the exact nature of these relationships, and therefore the functional form of the relationship between detection radius and carrying capacity will depend on the species under consideration. I therefore felt that, for the general simulations conducted here, it was preferable to assume independence of these two parameters, and to test for their effects separately.

Perhaps the most important aspect of dispersal which is not included in the model is that for many organisms, dispersal from patches is not equally likely in all directions, but instead the whole population is "pushed" in one general direction by forces such as wind or water currents, light or temperature gradients, or gravity. It is not clear to me that such forces would have a consistent impact on the general results I have found in these simulations.

Further study is necessary, however, to determine if this is true.

Finally, this model is a consideration of populations of single species. Consideration of effects of patch spatial arrangement on two or more interacting species will almost certainly result in more complex hypotheses.

Global Survival

The results of Chapter 8 imply that dispersal in patchy habitats does not necessarily always have the effect of increasing population survival time. In general, if the probability of local population extinction is relatively high, dispersal does increase global survival time. However, for very low levels of local extinction probability dispersal can have the opposite effect.

Chapter 8 also demonstrates that the effects of stochastic variation in parameter values can be quite complex. Stochastic variation can interact with mean values of parameters (here detection radius) to produce markedly different outcomes than when no stochastic variability is included. It is known that for nonlinear models mean predictions of stochastic runs are not expected to be equal to predictions of deterministic runs (Chesson 1981, Morrison 1986). This implies that one must be cautious when using deterministic models to form predictions about ecological systems, in which many relationships are known to be nonlinear, and most (all?) variables have significant stochastic fluctuations.

10. Summary

Chapters 3, 4, and 5 can be summarised as follows: I first found that cabbage butterflies do not detect their host plants from a distance (Chapter 3); this was corroborated by the modelling results in Chapter 4; general simulations then led to the prediction that, for organisms which do not detect host patches from a distance, the spatial arrangement of patches should have little effect on local population size (Chapter 5); finally, this prediction was confirmed for *P. rapae* through simulations and corresponding field study (Chapter 6). At the end of Chapter 6, therefore, a reasonable explanation for the limited effect of patch spatial arrangement on local population size in *P. rapae* was the inability of dispersers to detect new host patches from a distance. However, the results of a more complete set of general simulations (Chapter 7) cast doubt on this conclusion, by producing the hypothesis that an organism's dispersal distance is more important than its patch detection radius, in determining the degree to which patch spatial arrangement affects local population size. To test this hypothesis would of course require much more field work and theoretical investigations, probably on several different species. The implication of this result for *P. rapae* is that the high dispersal distance of *P. rapae* is the most likely explanation for the low effect of host patch spatial arrangement on local population size.

2

Résumé

Des observations sur le terrain (3ième chapitre) et les résultats d'un modèle prédictif (4ième chapitre) ont démontré que les femelles de la Piéride du chou, *Pieris rapae*, ne s'orientent pas de loin vers les plantes hôtes. Des simulations générales sur ordinateur (5ième chapitre) ont suggéré que, si une espèce ne s'oriente pas vers les groupes d'hôtes, l'arrangement spatial de ces groupes n'a qu'un effet minimal sur la densité de la population locale. Cette prédiction a été confirmée (6ième chapitre) dans le cas de *P. rapae* par des simulations et des observations complémentaires sur le terrain. Donc, on pourrait conclure que l'effet minimal de l'arrangement des groupes de choux sur la densité locale de *P. rapae* résulte du manque relatif d'orientation des femelles vers les plantes hôtes. Cependant, les résultats de simulations plus complètes (7ième chapitre) ne sont pas en accord avec cette conclusion. Ces résultats suggèrent que la distance de dispersion est plus importante que la limite de détection des groupes d'hôtes, pour déterminer à quel point l'arrangement des groupes d'hôtes peut affecter la densité locale. Pour tester cette hypothèse, on aurait besoin de beaucoup plus d'observations sur le terrain, probablement avec plusieurs espèces différentes. Ce résultat suggère que, pour *P. rapae*, l'effet minimal de l'arrangement des groupes d'hôtes sur la densité locale est dû au fait que les femelles volent sur de grandes distances lors de la dispersion.

References

- Atkinson, W.D. and B. Shorrocks. 1981. Competition on a divided and ephemeral resource: a simulation model. *Journal of Animal Ecology* 50: 461-471.
- Baker, R.R. 1970. Bird predation as a selective pressure on the immature stages of the cabbage butterflies, *Pieris rapae* and *P. brassicae*. *Journal of Zoology* 162: 43-59.
- Bateman, M.A. 1972. The ecology of fruit flies. *Annual Review of Entomology* 17: 493-518.
- Batschelet, E. 1981. Circular statistics in biology. Academic, Toronto.
- Box, G.E.P. and N.R. Draper. 1987. Empirical model-building and response surfaces. John Wiley and Sons, Toronto.
- Burnham, K.P., D.R. Anderson, and J.L. Laake. 1980. Estimation of density from line transect sampling of biological populations. *Wildlife Monographs* No. 72.
- Cappuccino, N. and P. Kareiva. 1985. Coping with a capricious environment: a population study of a rare pierid butterfly. *Ecology* 66: 152-161.
- Chesson, P.L. 1981. Models for spatially distributed populations: the effect of within-patch variability. *Theoretical Population Biology* 19: 288-325.
- Chesson, P.L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology* 28: 263-287.
- Chesson, P.L. and W.W. Murdoch. 1986. Aggregation of risk: relationships among host-parasitoid models. *American Naturalist* 127: 696-715.
- Chew, F.S. 1981. Coexistence and local extinction in two pierid butterflies. *American Naturalist* 118: 665-672.
- Comins, H.N., W.D. Hamilton and R.M. May. 1980. Evolutionarily stable dispersal strategies. *Journal of Theoretical Biology* 82: 205-230.

- Comins, H.N. and I.R. Noble. 1985. Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *American Naturalist* 126: 706-723.
- Courtney, S.P. and A.E. Duggan. 1983. The population biology of the Orange Tip butterfly *Anthocharis cardamines* in Britain. *Ecological Entomology* 8: 271-281.
- Cromartie, W.J. Jr. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology* 12: 517-533.
- Cross, W.H. 1973. Biology, control, and eradication of the boll weevil. *Annual Review of Entomology* 18: 17-46.
- Davis, B.N.K. and P.E. Jones. 1986. Insects on isolated colonies of common rock-rose *Helianthemum chamaecistus*. *Ecological Entomology* 11: 267-281.
- DeAngelis, D.L., C.C. Travis and W.M. Post. 1979. Persistence and stability of seed-dispersed species in a patchy environment. *Theoretical Population Biology* 16: 107-125.
- Dempster, J. 1967. The control of *Pieris rapae* with D.D.T. I. The natural mortality of the youngest stages of *Pieris*. *Journal of Applied Ecology* 4: 485-500.
- den Boer, P.J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheoretica* 18: 165-194.
- den Boer, P.J. 1981. The survival of populations in a heterogeneous and variable environment. *Oecologia* 50: 39-53.
- Dindonis, L.L. and J.R. Miller. 1980. Host-finding behavior of onion flies, *Hylema antiqua*. *Environmental Entomology* 9: 769-772.
- Fahrig, L., L.P. Lefkovitch and H.G. Merriam. 1983. Population stability in a patchy environment. In: W.K. Lauenroth, G.V. Skogerboe and M. Flug (eds.). *Analysis of ecological systems: state-of-the-art in ecological modelling*. Elsevier, New York. pp. 61-67.

- Fahrig, L. and H.G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* 66: 1762-1768.
- Feeny, P., L. Rosenberry and M. Carter. 1983. Chemical aspects of oviposition behaviour in butterflies. In: S. Ahmad (ed.). *Herbivorous insects: host seeking behavior and mechanisms*, ch. 2. Academic Press, Toronto.
- Feldman, M.W. and J. Roughgarden. 1975. A population's stationary distribution and chance of extinction in a stochastic environment with remarks on the theory of species packing. *Theoretical Population Biology* 7: 197-207.
- Finch, S. and G. Skinner. 1982. Upwind flight by the cabbage root fly, *Delia radicum*. *Physiological Entomology* 7: 387-399.
- Gossard, T. and R.E. Jones. 1977. The effects of age and weather on egg laying in *Pieris rapae*. *Journal of Applied Ecology* 14: 65-71.
- Gurney, W.S.C. and R.M. Nisbet. 1978. Single-species population fluctuations in patchy environments. *American Naturalist* 112: 1075-1090.
- Hamilton, W.D. and R.M. May. 1977. Dispersal in stable habitats. *Nature* 269: 578-581.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38: 210-221.
- Hanski, I. 1983. Coexistence of competitors in a patchy environment. *Ecology* 64: 493-500.
- Hanski, I. 1985. Single-species spatial dynamics may contribute to long-term rarity and commonness. *Ecology* 66: 335-343.
- Harcourt, D.G. 1961. Spatial patterns of the imported cabbageworm, *Pieris rapae* (L.) on cultivated cruciferae. *Canadian Entomologist* 93: 945-952.
- Harcourt, D.G. 1963. Biology of cabbage caterpillars in eastern Ontario. *Proc. Ent. Soc. Can.* 32: 55-66.

- Harcourt, D.G. 1966. Major factors in survival of the immature stages of *Pieris rapae* (L.). Canadian Entomologist 98: 653-662.
- Hassell, M.P. 1985. Insect natural enemies as regulating factors. Journal of Animal Ecology 54: 323-334.
- Hassell, M.P. and R.M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. Journal of Animal Ecology 43: 567-587.
- Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. Theoretical Population Biology 12: 37-48.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18: 363-373.
- Hastings, A. 1982. Dynamics of a single species in a spatially varying environment: the stabilising role of high dispersal rates. Journal of Mathematical Biology 16: 49-55.
- Hastings, A. 1983. Can spatial variation alone lead to selection for dispersal? Theoretical Population Biology 24: 244-251.
- Hilborn, R. 1975. The effect of spatial heterogeneity on the persistence of predator-prey interactions. Theoretical Population Biology 8: 346-355.
- Hodgson, C.J. and I.B. Elbakheit. 1985. Effect of colour and shape of 'target' hosts on orientation of emigrating adult apterous *Myzus persicae* in the laboratory. Entomologica Experimentalis et Applicata 38: 49-56.
- Holt, R.D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28: 181-208.
- Horvitz, C.C. and D.W. Schemske. 1986. Seed dispersal and environmental heterogeneity in a neotropical herb: a model of population and patch dynamics. In: Estrada, A. and T.H. Fleming (eds.). Frugivores and Seed Dispersal. Dr. W. Junk Publishers, Dordrecht.

- Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27: 343-383.
- Hughes, R.D. and N. Gilbert. 1968. A model of an aphid population - a general statement. *Journal of Animal Ecology* 37: 553-563.
- Ives, P.M. 1978. How discriminating are cabbage butterflies ? *Australian Journal of Ecology* 3: 261-276.
- Jander, R. 1963. Insect orientation. *Annual Review of Entomology* xxx: 95-114.
- Jones, R. 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* 46: 195-212.
- Jones, R., N. Gilbert, M. Guppy and V. Neals. 1980. Long-distance movement of *Pieris rapae*. *Journal of Animal Ecology* 49: 629-642.
- Jones, R.E. and P.M. Ives. 1979. The adaptiveness of searching and host selection behaviour in *Pieris rapae* (L.). *Australian Journal of Ecology* 4: 75-86.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 5: 261-282.
- Kennedy, J.S. and H.L.G. Stroyan. 1959. Biology of aphids. *Annual Review of Entomology* 4: 139-160.
- Kishi, M. and S. Ikada. 1986. Population dynamics of 'red tide' organisms in eutrophicated coastal waters - numerical experiments of phytoplankton bloom in the East Seto Inland Sea, Japan. *Ecological Modelling* 31: 145-174.
- Kitching, R. 1971. A simple simulation model of dispersal of animals among units of discrete habitat. *Oecologia* 7: 95-116.

- Kobayashi, S. 1960. Studies on the distribution pattern of the eggs of the common cabbage butterfly, *Pieris rapae crucivora* in a cabbage farm and the factors affecting its concentrating trend. Japanese Journal of Ecology 10: 154-160.
- Kobayashi, S. 1965. Influence of adult density upon the oviposition site in the cabbage butterfly, *Pieris rapae-crucivora*. Japanese Journal of Ecology 15: 35-38.
- Leather, S.R. 1986. Host monitoring by aphid migrants: do gynoparae maximise offspring fitness? Oecologia 68: 367-369.
- Lecomte, C. and J. Pouzat. 1986. Etude electroantennographique de la reception de stimulus odorants d'origine vegetale chez *Acrolepiopsis assectella*. Entomologica Experimentalis et Applicata 40: 13-24.
- Lefkovich, L.P. and L. Fahrig. 1985. Spatial characteristics of habitat patches and population survival. Ecological Modelling 30: 297-308.
- Levin, S.A. 1974. Dispersion and population interactions. American Naturalist 108: 207-228.
- Levin, S.A., D. Cohen and A. Hastings. 1984. Dispersal strategies in patchy environments. Theoretical Population Biology 26: 165-191.
- Lomnicki, A. 1980. Regulation of population density due to individual differences and patchy environment. Oikos 35: 185-193.
- Mackay, D.A. 1985. Prealighting search behavior and host plant selection by ovipositing *Euphydryas editha* butterflies. Ecology 66: 142-151.
- Maguire, L.A. 1983. Influence of collard patch size on population densities of Lepidopteran pests (Lepidoptera: Pieridae, Plutellidae). Environmental Entomology 12: 1415-1419.
- May, R.M. 1973. Stability and complexity in model ecosystems. Monographs in population biology no. 6. Princeton University Press, Princeton.
- May, R.M. 1974. Ecosystem pattern in randomly fluctuating environments. In: R. Rosen and R. M. Snell (eds.). Progress in theoretical biology, Volume 3. Academic Press, Toronto.

- McMullen, L.H. and M.D. Atkins. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae). Canadian Entomologist 94: 1309-1325.
- Michaelowicz, W.J. 1980. An ecological investigation of *Pieris rapae* (L.) (Lepidoptera: Pieridae) and its natural enemies in southern Ontario. MSc. thesis, University of Guelph.
- Moericke, V., R.J. Prokopy, S. Berlocher and G.L. Bush. 1975. Visual stimuli eliciting attraction of *Rhagoletis pomonella* (Diptera: Tephritidae) flies to trees. Entomologica Experimentalis et Applicata 18: 497-507.
- Morrison, G. 1986. Stochastic aggregative response and spatial host-parasitoid interactions. Oecologia 68: 298-303.
- Morrison, G. and P. Barbosa. Spatial heterogeneity, population "regulation" and local extinction in simulated host-parasitoid interactions. In preparation.
- Motro, U. 1982. Optimal rates of dispersal I. haploid populations. Theoretical Population Biology 21: 394-411.
- Muggeridge, J. 1943. The white butterfly (*Pieris rapae* L.) II. Parasites of the butterfly. New Zealand Journal of Science and Technology 25: 1-18.
- Muggeridge, J. 1943. The white butterfly (*Pieris rapae* L.) III. Introduction of parasites, method and technique. New Zealand Journal of Science and Technology 25: 18-30.
- Myers, J.H. 1976. Distribution and dispersal in populations capable of resource depletion. Oecologia 23: 255-269.
- Myers, J.H. 1985. Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, *Pieris rapae*. Journal of Animal Ecology 54: 193-204.
- Pajunen, V.I. 1986. Distributional dynamics of *Daphnia* species in a rock-pool environment. Annales Zoologici Fennici 23: 131-1140.

- Papaj, D.R. and M.D. Rausher. 1983. Individual variation in host location by phytophagous insects. In: S. Ahmad (ed.). *Herbivorous insects: host-seeking behavior and mechanisms*, ch. 3. Academic Press, Toronto.
- Parker, F.D. 1970. Seasonal mortality and survival of *Pieris rapae* (Lepidoptera: Pieridae) in Missouri and the effect of introducing an egg parasite, *Trichogramma evanescens*. *Annals of the Entomological Society of America* 63: 985-994.
- Pimentel, 1961. Natural control of caterpillar populations on cole crops. *Journal of Economic Entomology* 54: 889-892.
- Prokopy, R.J., R.H. Collier and S. Finch. 1983. Visual detection of host plants by cabbage root flies. *Entomologica Experimentalis et Applicata* 34: 85-89.
- Rausher, M. 1978. Search image for leaf shape in a butterfly. *Science* 200: 1071.
- Reddingius, J. and P.J. den Boer. 1970. Simulation experiments illustrating stabilisation of animal numbers by spreading of risk. *Oecologia* 5: 240-284.
- Renwick, J.A.A. and C.D. Radke. 1983. Chemical recognition of host plants for oviposition by the cabbage butterfly, *Pieris rapae* (Lepidoptera: Pieridae). *Environmental Entomology* 12: 446-450.
- Richards, O.W. 1940. The biology of the small white butterfly (*Pieris rapae*) with special reference to the factors controlling its abundance. *Journal of Animal Ecology* 9: 243-288.
- Roff, D.A. 1974a. Spatial heterogeneity and the persistence of populations. *Oecologia* 15: 245-258.
- Roff, D.A. 1974b. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. *Oecologia* 15: 259-275.
- Root, R.B. and P.M. Kareiva. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequence and adaptive significance of Markovian movements in a

- patchy environment. *Ecology* 65: 147-165.
- Root, R.B. and P. Kareiva. 1986. Is risk-spreading so unrealistic? *Oikos* 47: 114-116.
- Roughgarden, J. and Y. Iwasa. 1986. Dynamics of a metapopulation with space-limited subpopulations. *Theoretical Population Biology* 29: 235-261.
- Sawyer, A.J. and D.L. Haynes. 1985. Simulating the spatiotemporal dynamics of the cereal leaf beetle in a regional crop system. *Ecological Modelling* 30: 83-104.
- Saxena, K.N. and S. Goyal. 1978. Host-plant relations of the citrus butterfly *Papilio demoleus* L.: orientational and ovipositional responses. *Entomologica Experimentalis et Applicata* 24: 1-10.
- Shmida, A. and S. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58: 29-55.
- Silberglied, R.E. 1984. Visual communication and sexual selection among butterflies. In: R.I. Vane-Wright and P.R. Ackery (eds.). *The biology of butterflies*, ch. 20. Academic Press, Toronto.
- Slatkin, M. 1974. Competition and regional coexistence. *Ecology* 55: 128-134.
- Sogawa, K. 1982. The rice brown planthopper: feeding physiology and host plant interactions. *Annual Review of Entomology* 27: 49-73.
- Stanton, M.L. 1983. Spatial patterns in the plant community and their effect upon insect search. In: S. Ahmad (ed.). *Herbivorous insects: host-seeking behavior and mechanisms*, ch. 4. Academic Press, Toronto.
- Stanton, M.L. 1984. Short-term learning and the searching accuracy of egg-laying butterflies. *Animal Behavior* 32: 33-40.
- Stanton, M.L. and R.E. Cook. 1984. Sources of intraspecific variation in the hostplant seeking behavior of *Colias* butterflies. *Oecologia* 61: 265-270.

- Taylor, L.R. and R.A.J. Taylor. 1977. Aggregation, migration and population mechanics. *Nature* 265: 415-421.
- Thorsteinsen, A.J. 1960. Host selection in phytophagous insects. *Annual Review of Entomology* 5: 193-218.
- Traynier, R.M.M. 1979. Long-term changes in the oviposition behaviour of the cabbage butterfly, *Pieris rapae*, induced by contact with plants. *Physiological Entomology* 4: 87-96.
- Traynier, R.M.M. 1984. Associative learning in the ovipositional behaviour of the cabbage butterfly, *Pieris rapae*. *Physiological Entomology* 9: 465-472.
- Traynier, R.M.M. 1986. Visual learning in assays of sinigrin solution as an oviposition releaser for the cabbage butterfly, *Pieris rapae*. *Entomologica Experimentalis et Applicata* 40: 25-33.
- Turelli, M. 1977. Random environments and stochastic calculus. *Theoretical Population Biology* 12: 140-178.
- Twinn, C.R. 1924. Studies in the life-history, bionomics, and control of the cabbage worm in Ontario. *Annual Report of the Entomological Society of Ontario* pp. 82-86.
- Twinn, C.R. 1925. Observations of the host-selection habits of *Pieris rapae* L. *Annual Report of the Entomological Society of Ontario* pp. 75-80.
- Urban, D.L. and H.H. Shugart Jr. 1986. Avian demography in mosaic landscapes: modeling paradigm and preliminary results. In: Verner, J., M.L. Morrison and C.J. Ralph. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. The University of Wisconsin Press, Madison.
- Vance, R.R. 1980. The effect of dispersal on population size in a temporally varying environment. *Theoretical Population Biology* 18: 343-362.
- Vance, R.R. 1984. The effect of dispersal on population stability in one-species, discrete-space population growth models. *American Naturalist* 123: 230-254.

- Vandermeer, J.H. 1973. On the regional stabilization of locally unstable predator-prey relationships. *Journal of Theoretical Biology* 41: 161-170.
- Visser, J.H. and J.K. Nielson. 1977. Specificity in the olfactory orientation of the Colorado beetle, *Leptinotarsa decemlineata*. *Entomologica Experimentalis et Applicata* 21: 14-22.
- Wallace, G.K. 1958. Some experiments on form perception in the nymphs of the desert locust, *Schistocerca gregaria* Forskal. *Journal of Experimental Biology* 35: 765-775.
- Warkowska-Dratnal, H. and N.C. Stenseth. 1985. Dispersal and the microtine cycle: comparison of two hypotheses. *Oecologia* 65: 468-477.
- Wiklund, C. 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. *Oecologia* 63: 23-29.
- Wiklund, C. and C. Ahrberg. 1978. Host plants, nectar source plants, and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). *Oikos* 31: 169-183.
- Yamamoto, M. 1981. Comparison of population dynamics of two Pierid butterflies, *Pieris rapae crucivora* and *P. napi nesis*, living in the same area and feeding on the same plant in Sapporo, northern Japan. *Journal of the Faculty of Science at Hokkaido University, Series VI, Zool.* 22(3).

Appendix 1. Two-way Contingency Tables of Female Cabbage Butterfly

Flight Direction

Flight Direction	Collection Site		
	Rapeseed	Cabbage Patch Other than Release Site	Same Cabbage Patch as Release Site
Flight Toward Cabbage	142	109	80
Flight Away From Cabbage	156	92	69

$\chi^2=2.6$; prob.=0.2717

Flight Direction	Release Site		
	Small Cabbage Patch	Medium Cabbage Patch	Large Cabbage Patch
Toward Cabbage	98	96	137
Away From Cabbage	102	102	113

$\chi^2=2.264$; prob.=0.3223

Distance of Release from Cabbage Patch (m)

Flight Direction	1	5	10	20
Toward Cabbage	96	82	81	72
Away From Cabbage	77	73	97	70

$\chi^2=3.775$; prob.=0.2868

Cabbage Age in Days Since Transplanting

Flight Direction	<28	28-52	>52
Toward Cabbage	99	127	105
Away From Cabbage	112	125	80

$\chi^2=3.895$; prob.=0.1427

Cabbage Size in cm^2

Flight Direction	<560	560-880	881-1300	1301-1520	>1520
Toward Cabbage	117	39	103	21	51
Away From Cabbage	122	45	107	8	35

$\chi^2=9.115$; prob.=0.0531

Number of Holes per dm Leaf Area

Flight Direction	<1.8	1.8-8.8	>8.8
Toward Cabbage	95	172	64
Away From Cabbage	93	171	53

$\chi^2=0.756$; prob.=0.6851

Condition of Cabbage Plants (see text for explanation)

Flight Direction	<2.1	2.1-3.4	>3.4
Toward Cabbage	19	133	179
Away From Cabbage	28	103	186

$\chi^2=5.371$; prob.=0.0682

Number of Eggs per Plant

Flight Direction	<4.5	4.5-13.5	>13.5
Toward Cabbage	217	98	16
Away From Cabbage	215	84	18

$\chi^2=0.902$; prob.=0.6371

Number of Young Larvae (Instars I and II) per Plant

Flight Direction	<1.2	1.2-4.0	>4.0
Toward Cabbage	211	95	25
Away From Cabbage	194	88	35

$\chi^2=2.347$; prob.=0.3093

Number of Old Larvae (Instars III, IV and V) per Plant

Flight Direction	<1.5	1.5-6.5	>6.5
Toward Cabbage	255	57	19
Away From Cabbage	234	55	28

$\chi^2=2.360$; prob.=0.3073

Appendix 2. Data of Immigration onto Host and Non-host Areas

NOTE: DAY: NUMBER OF DAYS SINCE APRIL 24 1986.

C: CABBAGE PATCH.

N: NON-HOST PLANT AREA.

TIME: TOTAL OBSERVATION TIME IN MINUTES.

TOTF: TOTAL NUMBER OF FEMALE IMMIGRANTS.

TOTM: TOTAL NUMBER OF MALE IMMIGRANTS.

TOT?: TOTAL NUMBER OF IMMIGRANTS OF UNKNOWN SEX.

1HRF: NUMBER OF FEMALES IN FIRST HOUR OF OBSERVATION.

1HRM: NUMBER OF MALES IN FIRST HOUR OF OBSERVATION.

1HR?: NUMBER OF UNKNOWN IN FIRST HOUR OF OBSERVATION.

DAY	C/N	TIME	TOTF	TOTM	TOT?	1HRF	1HRM	1HR?
1	N	150	0	0	0	0	0	0
4	N	120	1	0	0	.	0	0
5	N	285	0	0	0	0	0	0
13	N	180	0	2	0	0	.	0
19	C	285	0	0	0	0	0	0
21	N	155	0	0	0	0	0	0
24	N	225	2	1	0	0	0	0
29	C	185	0	0	0	0	0	0
33	C	210	0	0	0	0	0	0
34	N	225	0	0	0	0	0	0
36	C	180	0	1	0	0	0	0
41	N	150	0	0	0	0	0	0
46	C	140	0	0	0	0	0	0
48	N	165	0	0	0	0	0	0
52	C	240	0	0	0	0	0	0
54	N	120	0	0	0	0	0	0
56	C	120	0	0	0	0	0	0
57	N	210	0	0	0	0	0	0
61	C	180	0	1	0	0	1	0
66	N	150	2	4	2	1	2	0
67	C	240	12	7	3	5	2	0
68	N	240	3	2	7	0	0	1
69	C	240	10	3	6	1	0	2
71	N	215	10	15	8	0	0	0
72	C	150	3	3	7	1	0	3
75	N	155	4	8	21	2	1	7
76	C	90	4	0	1	4	0	0
78	C	125	12	7	14	3	6	6
83	N	155	6	4	23	4	2	6
84	C	115	9	12	12	2	10	7
96	N	65	1	6	23	1	5	23
103	C	40	7	12	14	.	.	.
107	N	15	6	8	19	.	.	.

Appendix 3. Analyses of Variance of Immigration Rates onto Host (Cabbage Patches) and Non-host Areas

Note: in all cases the number of immigrants, n , is transformed to $\ln(\frac{n}{t}+1)$, where t is the observation time in minutes. day is the number of days since April 24 and $field$ is the type of area observed (i.e., cabbage patch or non-host area).

Total Immigrants (Females, Males, and Unknowns)				
Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
day	1	73.48	144.08	0.0001
day^2	1	17.78	34.86	0.0001
day^3	1	1.93	3.78	0.061
$field$	1	0.12	0.23	0.63
Error	28	14.28		
Total	32	107.59		

$$R^2=0.867$$

Female Immigrants				
Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
day	1	32.42	85.33	0.0001
day^2	1	8.30	21.85	0.0001
day^3	1	0.75	1.96	0.17
$field$	1	0.16	0.42	0.52
Error	28	10.64		
Total	32	52.27		

$$R^2=0.796$$

Male Immigrants

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>day</i>	1	34.94	106.80	0.0001
<i>day</i> ²	1	11.48	35.09	0.0001
<i>day</i> ³	1	0.00	0.00	0.99
<i>field</i>	1	0.06	0.20	0.66
Error	28	9.16		
Total	32	55.64		

$R^2=0.835$

Unknown (i.e., Male or Female) Immigrants

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>day</i>	1	58.55	294.47	0.0001
<i>day</i> ²	1	16.72	71.28	0.0001
<i>day</i> ³	1	0.39	1.66	0.21
<i>field</i>	1	0.45	1.90	0.18
Error	28	6.57		
Total	32	82.68		

$R^2=0.921$

87

Total Immigrants in First Hour of Observation

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>day</i>	1	31.61	97.62	0.0001
<i>day</i> ²	1	8.04	36.30	0.0001
<i>day</i> ³	1	0.08	0.36	0.55
<i>field</i>	1	0.64	2.89	0.10
Error	24	5.31		
Total	28	35.68		

$R^2=0.851$

Female Immigrants in First Hour of Observation

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>day</i>	1	4.50	26.49	0.0001
<i>day</i> ²	1	0.92	5.44	0.028
<i>day</i> ³	1	0.26	1.54	0.23
<i>field</i>	1	0.42	2.45	0.13
Error	25	4.24		
Total	29	10.34		

$R^2=0.590$

Male Immigrants in First Hour of Observation

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>day</i>	1	4.91	22.85	0.0001
<i>day</i> ²	1	2.65	12.32	0.0017
<i>day</i> ³	1	0.26	1.22	0.28
<i>field</i>	1	0.22	1.01	0.32
Error	25	5.38		
Total	29	13.43		

$R^2=0.599$

Unknown Immigrants in the First Hour of Observation

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>day</i>	1	10.17	56.43	0.0001
<i>day</i> ²	1	7.18	39.89	0.0001
<i>day</i> ³	1	1.18	6.57	0.017
<i>field</i>	1	0.01	0.03	0.86
Error	26	4.68		
Total	30	23.24		

$R^2=0.798$

Appendix 4. Data of Dispersal from a 450-plant Cabbage Patch

NOTE: DAY IS NUMBER OF DAYS SINCE JULY 16 1980.
NO BUTTERFLIES WERE MARKED ON DAYS 11 AND 16
BECAUSE WEATHER MADE FLIGHT IMPOSSIBLE.
ASTERISK INDICATES PRESENCE OF THE BUTTERFLY;
FIRST ASTERISK INDICATES DATE OF MARKING.
COLOURS ARE B:BLUE, G:GREEN, O:ORANGE, P:RED,
Y:YELLOW, H:BLACK, W:BROWN, F:PURPLE

[illegible]

RRRR
NNNN
GGGG
O
OO
OOO
BBO
BOO
RO
ROO
ROO
NO
NNO
NOO
P
BP
BBP
BPP
RPP
RRP
NP
NNP
W
WW
WWW
BW
BBW
RW
RWW
NW
NNW
OW
OOW
OWW
PW
PPW
PWW
OG
OOG
OGG
PG
PPG
PGG
GW
GGW
GWW
RBO
RBP
OPR
ROW
OWP

BOB
BOW
BOWER
COW
OF C
PSW
BIO
ING
WIG
PRW
REC
IPW
B B
RZF
C C

Appendix 5. Estimation of Parameter Values in Cabbage Butterfly Simulation Model

Early Spring Emergence Rate

Overwintering *P. rapae* pupae emerge in early to mid-April in southern Ontario (Michaewicz 1980, pers. obs.). The males emerge before the females (Richards 1940). The initial spring flux of butterflies is synchronous. My observations indicate that about 0 to 2 females per day arrive at an area of ground equivalent to that of a medium-sized field (450 plants) for about 8 to 10 days during this initial emergence period. Since cabbage-butterfly females do not orient toward their host plants from a distance (Chapter 3), the number of females passing over a given area in a day is the same whether or not the area has host plants on it. Therefore, in the model, I assumed that an average of one female butterfly per day (s.d.=0.1) arrived on the host plant patch for 9 days beginning on 1 April.

Survival Rates

The survival rates for the eight different life history stages were estimated using the combined results of several studies (Richards 1940, Harcourt 1961, 1966, Dempster 1967, Baker 1970, and Jones and Ives 1979). Estimates of the fraction of individuals at the beginning of a stage which survive to the beginning of the next stage, and the number of studies from which the estimate was averaged (in parentheses) are: eggs - 0.686 (6), first instar - 0.641 (5), second instar - 0.711 (5), third instar - 0.696 (5), fourth instar - 0.55 (5), fifth instar - 0.549 (4), and pupa - 0.827 (2). Estimates of fifth instar survival rate in the field are probably underestimates because the fifth instar leaves the host plant to pupate, and the pupae are very difficult to find. No estimates of adult survival rates in the field are available. This is because adults are extremely mobile (Richards 1940, Jones et al. 1980, Yamamoto 1981), making it difficult to separate emigration and death rates.

The daily survival rates for all stages are assumed to be constant during each stage. Daily survival rates were calculated from the stage survival rates and the stage development times: $TS = S^{DT}$, where TS is the total survival rate for the stage, S is the daily survival rate for the stage, and DT is the development time of the stage in days. I do not have different estimates of survival rates for different times during the season. Also, lower temperatures produce longer development times (Jones and Ives 1979). Therefore, the above survival rate formula implies that the daily survival rates decrease through the season. This probably makes sense since natural enemies generally increase in abundance through the season. Only the rates for the first three larval instars were calculated in this way because other factors influence the survival rates of the other stages. These I now describe.

Parasitism accounts for approximately half of the mortality of fourth and fifth instar larvae and pupae (Baker 1970, Harcourt 1966, Pimentel 1961, Richards 1940). The rate of parasitism increases exponentially through the season (Michałowicz 1980, pers. obs.); at the beginning of the season about 0.9 of the individuals in these stages survive to the next, whereas at the end of the season their survival rates fall off to about 0.2. This is accounted for in the model. In southern Ontario, the most common larval parasitoid is *Apanteles glomeratus* (L.). This attacks the first and second instar larvae, and kills the larvae in their fourth or fifth instar (Muggeridge 1943a). The major pupal parasitoids are *Pteromalus puparum* (L.) and *Phryxe vulgaris* (Fallen) (Muggeridge 1943a,b). These attack both the fifth instar larva just prior to pupation and the pupa. The rates at which the fourth and fifth instar and pupal survival rates decrease during the season due to parasitism were calculated as follows: $SB = SE(e^{120r})$, where SB and SE are the daily survival rates of the stage at the beginning and end of the season respectively and r is the rate at which the survival function decreases. The duration of the curve (120 days) corresponds to the four months of simulation of the population. I assume that the survival rate levels off at the end of the season (after Sept. 1) at the final value. The equations for the daily survival rates of the fourth and fifth instars and pupae respectively are: $S(IV) = 1.528 - .585(e^{.00398T})$, $S(V) = 1.686 - .725(e^{.00235T})$ and

$S(P) = 1.803 - .818(e^{.00155T})$, where T is the number of days from the beginning of the period for which the curve is in effect. The curves come into effect not when the initial adults emerge, but when the affected stage in the first generation is expected to be produced.

Jones and Ives (1979) showed that the survival rate of the egg stage depends on the larval density. The effect is apparently linear. I estimated the equation of the line which they present in graphical form. I then modified it to account for the host plant patch size in the simulation (450 plants) and the fact that the model calculates only the female portion of the population. The final equation for the daily survival rate of eggs is:

$$S(E) = .91 - \frac{.0348(N(L_1) + N(L_2) + N(L_3) + N(L_4) + N(L_5))}{225}, \text{ where } N(L_i) \text{ is the abundance of female larvae of instar } i \text{ on the patch.}$$

As has been stated, accurate estimates of adult survival rates under natural conditions are not available. However, the approximate maximum lifespan of a *P. rapae* adult in the wild is 20 days (Gossard and Jones 1977, Harcourt 1963), with about 1 in 20 adults surviving to age 20 days. I used the equation above (ie: $ST = S^{DT}$) with $ST = .01$ and $DT = 20$ to calculate $S = .86$. This is clearly a rough estimate.

Development Rates

Development times of eggs, larvae and pupae are highly dependent on temperature (Richards, 1940, Jones and Ives 1979, Michaelowicz 1980). To obtain accurate estimates of development times, I conducted field studies at the Guelph University agricultural research station near Elora, Ontario in 1985. I built screened enclosures for individual cabbage, *Brassica oleracea* (L.), plants. The area of the base of the enclosures was 0.5 m by 0.5 m, and the height was 1 m. Any *P. rapae* eggs, larvae, or pupae were removed from plants before the enclosures were placed over them. Three to five adult females were placed in each enclosure for one day and then removed, and the eggs on the plants counted. The number of eggs, each larval instar, and pupae were then counted on each enclosed plant each day until all pupae had either emerged, or been killed by parasites. By using this method I ensured that the

development of *P. rapae* on a plant was synchronised; the ages of all individuals in a particular enclosure were the same, to within one day.

The enclosure experiments were spread over the season from 28 June to 30 August; a total of 16 different plants were enclosed. The development times of eggs and larvae for this time period in the model were calculated from the results of this experiment. The early season (April, May, June) development times for eggs and larvae were taken from Jones and Ives (1979), assuming mean southern Ontario temperatures.

None of the pupae successfully emerged, due to 100% pupal parasitism. I feel this is an artifact of the experimental design. Normally fifth instar larvae wander several metres from the host plant to pupate. The pupae in my enclosures were prevented from doing this, and were therefore concentrated within the enclosures. It was probably much easier for parasites to detect them in this condition. Development times for pupae were therefore taken from Michaelowicz (1980).

Table 1 gives the development times of *P. rapae* eggs, larval instars, and pupae for the different time periods during the season.

Egg-laying Rate

Adult male *P. rapae* butterflies are strongly attracted to small white objects resembling females. Mating is therefore very efficient, with virtually all females mated within 24 h of eclosion from the pupal stage (Jones 1977).

Egg-laying rate depends on butterfly age (Gossard and Jones 1977, Michaelowicz 1980), therefore mean daily egg-laying rate was estimated by combining an adult survivorship curve (Gossard and Jones 1977) and a fecundity vs. female age curve (Michaelowicz 1980). By assuming that, at any time during the season, the age distribution of adults is proportional to the survivorship curve, I estimated that the mean daily egg-laying rate is 17.5 eggs per female. This rate is a very crude approximation, since egg-laying rate is also affected by weather, time since previous oviposition (Gossard and Jones 1977), and plant condition (Ives 1978, Jones

and Ives 1979, Myers 1985). Also, the survival curve used (Gossard and Jones 1977) was obtained for caged individuals, and the population age distribution at any particular time is unknown. Since the model simulates only the female portion of the population, the daily egg-laying rate is halved to 8.7 female eggs per female per day.

Dispersal Rate

To estimate the rate of dispersal of females from host plant fields, a cabbage field containing 450 plants was observed each day from 16 July to 1 Aug., 1985. Observation was continuous from before butterfly activity began (about 9:30 A.M.) until 30 min after it ended (about 3:30 P.M.). Every day, each female observed on the field was captured, uniquely marked with coloured markers, and then released in the field; if the butterfly was already marked, the colour combination was recorded. Since virtually all captured butterflies immediately resumed egg-laying upon release, I feel confident that they were not unduly disturbed. A total of 107 butterflies were marked.

The fraction of butterflies which disappeared from one day to the next was 0.74. Although this value is actually a combination of dispersal and mortality, the daily mortality rate is quite low. Therefore, 0.74 was used in the model as the daily rate of dispersal of females.

Rate of Immigration

To estimate the rate of immigration, adult butterfly populations were counted by walking a 500 m "strip transect" line (Burnham et al. 1980) at the Elora research station between 1200 and 1300 h, twice a week for the 1985 season. All butterflies in flight were counted to a distance of 100 m on both sides of the transect. From this I estimated the approximate number of butterflies in flight per m^2 . To convert this number into an estimate of the density of females, I first assumed that the population sex ratio is 50:50. This assumption is valid if the mortality rates for the sexes are approximately equal, since my data indicate that the sex ratio at emergence from the pupal stage is 1:1.

To determine the total density of butterflies from the number in flight, I conducted time budget studies of males and females. Individual butterflies were followed for as long as possible. Observation was terminated when the butterfly was lost from sight, flew out of the research area (30 ha), or had been resting for more than 20 min. A large number of the observations of males were terminated as a result of interaction with another male, making the two indistinguishable. Butterfly activity was classed as flight, nectar feeding, egg-laying, courtship or rest. The data consisted of a list of the times at which the butterfly changed activities, and the activities which were begun at each time. From this I calculated the total time spent in each activity. Initially I was concerned that the fraction of time spent in flight would be underestimated because almost all observations began with a butterfly engaged in flight. However, this bias is compensated for by the fact that most observations also ended during flight.

The data were used to calculate the ratio of nonvisible (resting) to visible (other activities) males and females during the different hours of the day. The noontime ratio for females was 0.596:0.404 and for males was 0.461:0.539. The fraction of visible butterflies that are female is therefore $\frac{.404}{.404 + .539} = .429$. The actual number of female butterflies present during the transect (which was conducted at noon) was then $.429n + (.429n) \left[\frac{.596}{.404} \right]$, where n is the observed number of butterflies. The density of females during the transect is an estimate for one point in time during the day. To convert this to a daily rate of immigration, I had to estimate the rate of turnover of the immigrant population. I know from egg-laying observations that the mean duration of egg-laying on a patch is approximately 15 min. I therefore used this as the turnover time, although I realise this is only a rough approximation. There are about 10 15-minute periods of flying time during an "average" summer day in southern Ontario.

The number of immigrants per day is therefore $10NA$, where N is the number of females per m^2 , and A is the area of the patch. The number of immigrant females per day was found to be a slowly increasing linear function until about 25 June, i.e., $I = .0014t$ where I is the number of female immigrants per day and t is the number of days since 1 April.

Immigration then increased exponentially until about August 24, i.e., $I = .119e^{.001(t-86)}$. After this date the immigration rate levelled off at about 25-30 females per day until the end of August.

Appendix 6. Computer Program of Cabbage Butterfly Population Dynamics and Dispersal (using SAS)

```
// EXEC SAS,OPTIONS='NOGRAPHICS NOINCLUDE'  
//SAS.SYSIN DD *
```

```
* The first two PROC MATRIX sections are used  
to set the input matrices to 0;
```

```
PROC MATRIX;
```

```
* STG - no. of life history stages;
```

```
STG = 8;  
L1 = 10 10 10 10 10 10 10 10;  
L2 = 10 10 10 10 10 10 10 10;  
LD = .6666*(L1+L2);  
PAT = 9;  
AD1 = 0;  
DO I = 1 TO PAT;  
OUTPUT AD1 OUT = ASTRT;  
OUTPUT LD OUT = LDM;  
END;
```

```
* PAT - no. of host plant patches;
```

```
DO I = 1 TO (STG*PAT);  
IN1 = 0;  
OUTPUT IN1 OUT = STRT;  
END;  
PROC MATRIX ;  
PAT = 9;
```

```
* SP - starting period of the simulation;
```

```
SP = 35;
```

```
* DAYS - no. of days in the simulation;
```

```
DAYS = 168+SP;  
FETCH INAD DATA = ASTRT;  
FETCH IN2 DATA = STRT;  
INAT = INAD';  
IN2T = IN2';  
DO K = 1 TO DAYS;  
OUTPUT INAT OUT = ADSTRT;  
OUTPUT IN2T OUT = NSTRT;  
OUTPUT IN2T OUT = SSTRT;  
OUTPUT IN2T OUT = DSTRT;  
OUTPUT IN2T OUT = DTSTRT;  
END;
```

* All the input matrices have now been set to zero.
The following section defines the actual values of
the matrices;

```
PROC MATRIX ;
PAT - 9;
SP - 35;
DAYS - 168+SP;
DIST - 0 0030 0030 0040 0310 0570 0490 0840 1580/
        0030 0 0040 0030 0270 0550 0490 0860 1600/
        0030 0040 0 030 300 540 0450 0810 1540/
        0040 0030 0030 0 260 510 0450 0820 1560/
        0310 0270 0300 0260 0000 0370 0470 0890 1630/
        0570 0550 0540 0510 0370 0000 0280 0620 1320/
        0490 0490 0450 0450 0470 0280 0000 0400 1140/
        0840 0860 0810 0820 0890 0620 0400 0000 0730/
        1580 1600 1540 1560 1630 1320 1140 730 0;
```

```
FETCH LD DATA - LDM;
M = .15*(LD#(1#/DIST));
DO I - 1 TO PAT;
DO J - 1 TO PAT;
IF DIST(I,J) < 250 OR DIST(I,J) > 700 THEN M(I,J) - 0;
END;
END;
* RT - the running time of the simulation;
```

RT - 120;

* CT - the correction time - for time lag;

```
CT - 15;
STG - 8;
X=0;
DO J - 1 TO DAYS;
X - X+1;
OUTPUT X OUT - TIME;
END;
```

* S is the daily survival rate.
D is the daily development rate.
DT is the development time;

```
FETCH AD DATA - ADSTRT;
FETCH S DATA - SSTRT;
FETCH D DATA - DSTRT;
FETCH DT DATA - DTSTRT;
FETCH N DATA - NSTRT;
```

* EGS - no. of eggs laid per female per day;

```
EGS - 8.73;
S1 - .9781 .884 .815 .793 .95 .968 .9896 .870;
S2 - .9663 .866 .815 .775 .943 .961 .9853 .870;
S3 - .9391 .75 .712 .712 .888 .931 .9565 .870;
```

```

D1 = .0606 .1493 .1923 .2174 .1333 .0952 .0292 0;
D2 = .0945 .1639 .2128 .2326 .1538 .1087 .0417 0;
D3 = .136 .223 .307 .305 .256 .177 .061 0;
DT1 = 17 7 5 5 7 11 34 1;
DT2 = 11 6 5 4 6 9 24 1;
DT3 = 6 3 3 3 3 5 8 1;
DO I = 1 TO PAT;
  CPS = I*STG;
  CP1 = CPS-(STG-1);

```

* The following section gives different values of S, D, and DT depending on the time of season;

```

DO L = 1 TO DAYS;
  IF L <= SP+CT+30 THEN DO;
    S(L,CP1:CPS) = S1;
    D(L,CP1:CPS) = D1;
    DT(L,CP1:CPS) = DT1;
  END;
  IF L > SP+CT+30 AND L <= SP+CT+60 THEN DO;
    S(L,CP1:CPS) = S2;
    D(L,CP1:CPS) = D2;
    DT(L,CP1:CPS) = DT2;
  END;
  IF L > SP+CT+60 AND L <= SP+CT+120 THEN DO;
    S(L,CP1:CPS) = S3;
    D(L,CP1:CPS) = D3;
    DT(L,CP1:CPS) = DT3;
  END;
  IF L > SP+CT+120 THEN DO;
    S(L,CP1:CPS) = S3;
    D(L,CP1:CPS) = D2;
    DT(L,CP1:CPS) = DT2;
  END;
END;

```

* The following section adjusts survival rates of 4th and 5th instar larvae and pupae, for the fact that parasitism increases exponentially during the season;

```

DO Q = SP TO DAYS;
  IF Q > SP+DT(1,CP1)+DT(1,CP1+1)+.5#DT(1,CP1+2)
  AND Q <= SP+RT+DT(1,CP1)+DT(1,CP1+1)+.5#DT(1,CP1+2) THEN
    S(Q,CP1+4) = 1.528 - (.585*EXP((.0039788)*
    (Q-SP-DT(1,CP1)-DT(1,CP1+1)-.5#DT(1,CP1+2))));
  IF Q > SP+DT(1,CP1)+DT(1,CP1+1)+DT(1,CP1+2)+.5#DT(1,CP1+3) AND
  Q <= SP+RT+DT(1,CP1)+DT(1,CP1+1)+DT(1,CP1+2)+.5#DT(1,CP1+3) THEN
    S(Q,CP1+5) = 1.686 - (.725*EXP((.00234853)*
    (Q-SP-DT(1,CP1)-DT(1,CP1+1)-DT(1,CP1+2)-.5#DT(1,CP1+3))));
  IF Q > SP+DT(1,CP1)+DT(1,CP1+1)
  +DT(1,CP1+2)+DT(1,CP1+3)+DT(1,CP1+4)+.5#DT(1,CP1+5) AND
  Q <= SP+RT+DT(1,CP1)+DT(1,CP1+1)+DT(1,CP1+2)

```

```

+DT(1,CP1+3)+DT(1,CP1+4)+.5#DT(1,CP1+5) THEN
  S(Q,CP1+6) = 1.8033 - (.818*EXP((.001550690)*
    (Q-SP-DT(1,CP1)-DT(1,CP1+1)-DT(1,CP1+2)
    -DT(1,CP1+3)-DT(1,CP1+4)-.5#DT(1,CP1+5)))));
END;
DO V = SP+RT TO DAYS;
  IF V > SP+RT+DT(1,CP1)+DT(1,CP1+1)+.5#DT(1,CP1+2) THEN
    S(V,CP1+4) = .585;
  IF V > SP+RT+DT(1,CP1)+DT(1,CP1+1)+DT(1,CP1+2)+.5#DT(1,CP1+3) THEN
    S(V,CP1+5) = .725;
  IF V > SP+RT+DT(1,CP1)+DT(1,CP1+1)+DT(1,CP1+2)
  +DT(1,CP1+3)+DT(1,CP1+4)+.5#DT(1,CP1+5) THEN
    S(V,CP1+6) = .818;
END;

```

* Input values for initial early spring emergence
 * of adults;

```

*
N(SP,CPS) = .02;
N(SP+1,CPS) = .10;
N(SP+2,CPS) = 1.0;
N(SP+3,CPS) = 5.0;
N(SP+4,CPS) = 5.0;
N(SP+5,CPS) = 5.0;
N(SP+6,CPS) = 5.0;
N(SP+7,CPS) = 1.0;
N(SP+8,CPS) = .10;
N(SP+9,CPS) = .02;
END;

```

* Simulation;

```

T=SP+9;
DO W = 1 TO (DAYS-SP-9);
  T=T+1;
  DO I = 1 TO PAT;

```

* CP1 = eggs in current patch,
 CPS = adults in current patch;

```

CPS = I*STG;
CP1 = CPS-(STG-1);

```

* Adjustment of egg survival for density-dependent
 effect of larvae;

```

S(T,CP1) = .91 - (.0348*((N(T-1,CP1+1)+N(T-1,CP1+2)+
  N(T-1,CP1+3)+N(T-1,CP1+4)+N(T-1,CP1+5))/100));

```

* Calculation of number of eggs;

```

N(T,CP1) = N(T-1,CP1)*
  S(T-1,CP1)*(1-D(T-1,CP1))
  + EGS*N(T-DT(T,CPS),CPS)

```

```

*(S(T,CPS)**DT(T,CPS));

* Calculation of larvae and pupae;

DO Y = 1 TO (STG-2);
  N(T,CPl+Y) = N(T-1,CPl+Y)*
  S(T-1,CPl+Y)*(1-D(T-1,CPl+Y))
  + N(T-DT(T,CPl+(Y-1)),CPl+(Y-1))*
  (S(T,CPl+(Y-1))*DT(T,CPl+(Y-1)));
END;

* Calculation of adults;

N(T,CPS) = N(T-1,CPS)*S(T-1,CPS);
AD(T,I) = N(T,CPS);
N(T,CPS) = .2637#N(T,CPS)+
  N(T-DT(T,CPl+(STG-2)),CPl+(STG-2))*
  (S(T,CPl+(STG-2))*DT(T,CPl+(STG-2)));

* Addition of immigrant adults;

*IF T > SP AND T <= SP+86 THEN
*N(T,CPS) = N(T,CPS) + .00138*(T-SP);
*IF T > SP+86 AND T <= SP+146 THEN
*N(T,CPS) = N(T,CPS) +
*(.11900*EXP(.0913917*(T-SP-86)));
*IF T > SP+146 THEN
*N(T,CPS) = N(T,CPS) + 28.6420;
*IF T <= 39 THEN
*N(T,CPS) = N(T,CPS);
IF T > 50 AND T <= 160 THEN
N(T,CPS) = N(T,CPS) + .5033 -
  (.5033*(T-39)) + (.015*(T-39)*(T-39));
IF T > 160 THEN
N(T,CPS) = N(T,CPS) + .5033 -
  (.5033*109) + (.015*109*109);
IF T > 50 AND
  N(T,CPS) <= 0 THEN
N(T,CPS) = .001;
END;
AD(T,) = .7353#(AD(T,)*M);
DO I = 1 TO PAT;
CPS = I*STG;
N(T,CPS) = N(T,CPS) + AD(T,I);
END;
END;
NT = INT(N + 0.5);
OUTPUT NT OUT = RSLT(RENAME=(COL1-C1EG COL9-C2EG COL17-C3EG
  COL25-C4EG COL33-M1EG COL41-M2EG COL49-M3EG
  COL57-I1EG COL65-I2EG));

DATA ITER;
SET TIME;
RENAME COL1-DAY;
DROP ROW;

```

```
DATA RESULTS;  
SET RSLT;  
DROP ROW;  
DATA SIMUL;  
MERGE ITER RESULTS;  
PROC PRINT;  
VAR DAY C1EG C2EG C3EG C4EG M1EG M2EG M3EG I1EG I2EG;  
PROC PLOT;  
PLOT C1EG*DAY;  
PLOT C2EG*DAY;  
PLOT C3EG*DAY;  
PLOT C4EG*DAY;  
PLOT M1EG*DAY;  
PLOT M2EG*DAY;  
PLOT M3EG*DAY;  
PLOT I1EG*DAY;  
PLOT I2EG*DAY;  
PROC MEANS;  
VAR C1EG C2EG C3EG C4EG M1EG M2EG M3EG I1EG I2EG;  
//
```

Appendix 7. Field Data: Cabbage Butterfly Population Densities in an Experimental Spatial Arrangement of Cabbage Patches

NOTE: DAY IS NUMBER OF DAYS SINCE MAY 12, 1985.

DAY	FIELD	PLANTING	NO. EGGS PER 20 PLANTS
1	I1	EARLY	2
1	I2	EARLY	1
1	M1	EARLY	10
1	M2	EARLY	6
1	M3	EARLY	2
1	C4	EARLY	9
1	C3	EARLY	2
1	C1	EARLY	1
1	C2	EARLY	7
3	I1	EARLY	0
3	I2	EARLY	1
3	M2	EARLY	2
3	M1	EARLY	7
3	M3	EARLY	4
3	C4	EARLY	7
3	C3	EARLY	4
3	C1	EARLY	4
3	C2	EARLY	2
6	I1	EARLY	0
6	I2	EARLY	1
6	M2	EARLY	3
6	M1	EARLY	2
6	M3	EARLY	2
6	C4	EARLY	5
6	C3	EARLY	3
6	C1	EARLY	3
6	C2	EARLY	3
11	I1	EARLY	0
11	I2	EARLY	0
11	M2	EARLY	0
11	M3	EARLY	0
11	C4	EARLY	0
11	C3	EARLY	1
11	C1	EARLY	2
11	C2	EARLY	0
11	M1	EARLY	1
15	I1	EARLY	0
15	I2	EARLY	0
15	M2	EARLY	0
15	M3	EARLY	1
15	C4	EARLY	0
15	C3	EARLY	0

15	C1	EARLY	0
15	C2	EARLY	0
15	M1	EARLY	0
16	I1	EARLY	0
16	I2	EARLY	0
16	M2	EARLY	0
16	M3	EARLY	0
16	C4	EARLY	0
16	C3	EARLY	0
16	C1	EARLY	0
16	C2	EARLY	0
16	M1	EARLY	0
17	I2	EARLY	0
18	C2	EARLY	0
18	C1	EARLY	0
18	C3	EARLY	0
18	C4	EARLY	0
18	M3	EARLY	0
18	M1	EARLY	0
18	M2	EARLY	0
18	I1	EARLY	0
23	I1	EARLY	0
23	I2	EARLY	0
23	M2	EARLY	0
23	M1	EARLY	0
23	M3	EARLY	0
23	C4	EARLY	0
23	C3	EARLY	0
23	C1	EARLY	0
23	C2	EARLY	0
28	I1	EARLY	0
28	I2	EARLY	0
28	M2	EARLY	0
28	M3	EARLY	0
28	C4	EARLY	0
28	C3	EARLY	0
28	C1	EARLY	0
28	C2	EARLY	0
28	M1	EARLY	0
30	I1	EARLY	0
30	I2	EARLY	0
30	M2	EARLY	0
30	M3	EARLY	0
30	C4	EARLY	0
30	C3	EARLY	0
30	C1	EARLY	0
30	C2	EARLY	0
30	M1	EARLY	0
34	I1	EARLY	0
34	I2	EARLY	0
34	M2	EARLY	0
34	M3	EARLY	0

34	C4	EARLY	0
34	C3	EARLY	0
34	C1	EARLY	0
34	C2	EARLY	0
34	M1	EARLY	0
36	I1	EARLY	1
36	I2	EARLY	0
36	M2	EARLY	0
36	M3	EARLY	0
36	C4	EARLY	0
36	C3	EARLY	0
36	C1	EARLY	0
36	C2	EARLY	0
36	M1	EARLY	0
38	I1	EARLY	0
38	I2	EARLY	0
38	M2	EARLY	0
38	M3	EARLY	0
38	C4	EARLY	0
38	C3	EARLY	0
38	C1	EARLY	0
38	C2	EARLY	0
38	M1	EARLY	0
39	M2	EARLY	0
39	M3	EARLY	0
39	C4	EARLY	0
39	C3	EARLY	0
39	C1	EARLY	0
39	C2	EARLY	0
39	M1	EARLY	0
39	I2	EARLY	0
39	I2	EARLY	0
43	I1	EARLY	2
43	I2	EARLY	4
43	M2	EARLY	2
43	M3	EARLY	1
43	C4	EARLY	0
43	C3	EARLY	0
43	C1	EARLY	1
43	C2	EARLY	3
43	M1	EARLY	3
48	C4	EARLY	9
48	C3	EARLY	4
48	C1	EARLY	4
48	C2	EARLY	11
48	M1	EARLY	3
48	M3	EARLY	8
48	M2	EARLY	4
48	I2	EARLY	5
48	I1	EARLY	18
50	M1	LATE	1
50	I2	LATE	0

50	M2	LATE	0
50	M3	LATE	0
50	C4	LATE	1
50	C3	LATE	0
50	C1	LATE	0
50	C2	LATE	0
50	I1	LATE	0
51	M1	EARLY	23
51	C3	EARLY	4
51	C1	EARLY	2
51	C2	EARLY	14
51	C4	EARLY	5
51	M3	EARLY	74
51	M2	EARLY	23
51	I2	EARLY	33
51	I1	EARLY	28
53	I1	LATE	1
53	I2	LATE	0
53	M2	LATE	3
53	M3	LATE	0
53	C4	LATE	3
53	C3	LATE	1
53	C1	LATE	0
53	C2	LATE	1
53	M1	LATE	0
55	M2	EARLY	20
55	M3	EARLY	149
55	C4	EARLY	9
55	C3	EARLY	18
55	C1	EARLY	4
55	C2	EARLY	34
55	M1	EARLY	16
55	I2	EARLY	76
55	I1	EARLY	64
57	C3	LATE	6
57	C1	LATE	7
57	C2	LATE	6
57	C4	LATE	12
57	M3	LATE	6
57	I1	LATE	1
57	M2	LATE	0
57	I2	LATE	0
57	I1	LATE	0
58	M1	EARLY	32
58	C3	EARLY	45
58	C1	EARLY	56
58	C2	EARLY	82
58	C4	EARLY	56
58	M3	EARLY	214

58	M2	EARLY	38
58	I2	EARLY	93
58	I1	EARLY	55
60	M1	LATE	3
60	C3	LATE	11
60	C1	LATE	7
60	C2	LATE	8
60	C4	LATE	12
60	M3	LATE	2
60	M2	LATE	6
60	I2	LATE	0
60	I1	LATE	0
61	I1	EARLY	36
61	I2	EARLY	48
61	M2	EARLY	37
61	M3	EARLY	129
61	C4	EARLY	43
61	C3	EARLY	45
61	C1	EARLY	49
61	C2	EARLY	102
61	M1	EARLY	26
65	M1	LATE	10
65	C3	LATE	10
65	C1	LATE	12
65	C2	LATE	12
65	C4	LATE	18
65	M3	LATE	14
65	M2	LATE	3
65	I2	LATE	6
65	I1	LATE	4
66	I1	EARLY	17
66	I2	EARLY	33
66	M2	EARLY	55
66	M3	EARLY	64
66	C4	EARLY	58
66	C3	EARLY	32
66	C1	EARLY	28
66	C2	EARLY	42
66	M1	EARLY	42
78	I1	EARLY	7
78	I1	LATE	5
78	I2	EARLY	9
78	I2	LATE	4
78	M2	EARLY	33
78	M2	LATE	37
78	M1	EARLY	32
78	M3	LATE	16
78	M3	EARLY	9
78	M3	LATE	40
78	C3	EARLY	32
78	C3	LATE	37
78	C1	EARLY	53

78	C1	LATE	38
78	C2	EARLY	45
78	C2	LATE	35
78	C4	EARLY	77
78	C4	LATE	38
85	M3	LATE	184
85	C3	LATE	257
85	C1	LATE	178
85	C2	LATE	168
85	C4	LATE	186
85	M1	LATE	251
85	M2	LATE	292
85	I2	LATE	187
85	I1	LATE	159
89	I1	LATE	171
89	I2	LATE	155
89	M2	LATE	365
89	M3	LATE	173
89	C3	LATE	429
89	C1	LATE	253
89	C4	LATE	215
89	C2	LATE	254
89	M1	LATE	441
99	I1	LATE	141
99	M2	LATE	443
99	C4	LATE	244
99	C3	LATE	549
100	I2	LATE	90
100	C2	LATE	174
100	C1	LATE	132
100	M1	LATE	515

Appendix 8. Analysis of Variance of Data on Effects of Patch Spatial Arrangement on Local Cabbage Butterfly Populations

Analysis of Variance of Residuals of Regression of Egg Density on day^2 and day^3 (see Chapter 6).

Note: *fldtp* indicates the category of cabbage patch (i.e., C, M, or I).

indfld indicates the specific cabbage patch within *fldtp* (i.e., C1, C2, C3, C4 within C, M1, M2, M3 within M, and I1, I2 within I).

Source	Degrees of Freedom	Sum of Squares	F	Prob.>F
<i>fldtp</i>	2	18000	3.92	0.0212
<i>indfld (fldtp)</i>	6	2090	0.91	0.4882
Error	215	494000		
Total	223	525000		

$R^2=0.058$

Means Tests for Significant Differences Among *fldtp* Categories

<i>fldtp</i>	N	Mean	Tukey	Bonferroni	Scheffe
M	74	10.47	a	a	a
C	100	-0.72	ab	ab	ab
I	50	-14.06	b	b	b

Appendix 9. Computer Program of Organisms in Patchy Habitats (in FORTRAN)

```
C
C   THIS IS A PROGRAM OF POPULATIONS IN PATCHY HABITATS.
C
```

```

INTEGER P, I, T, RELAX
INTEGER NNN, CNT, KPT, IID, CZ1, CZ2
PARAMETER (P=10)
PARAMETER (T=150)
PARAMETER (ITER=2000)
PARAMETER (RELAX=50)
CHARACTER*1 CH(2)
REAL D(P,P), WW(P), ZZ(P), W, Z, RNOMA, RNOMB
REAL RAND, IMEM
REAL AREA(P,P), RAD(P), DIAM(P), LAP(P)
REAL KK(P), R(P), DISP(P), DIST(P), DET(P)
REAL XBARN(T), POOL(P), MEANM
REAL VKK(P), VR(P), VDR(P), VDD(P), VDET(P)
REAL KKM, RM, DISTM, DETM, VIM, VSURV
REAL KKS, RS, DRS, DDS, DETS, IMS
REAL SDRK, SDR, SDDR, SDDD, SDDET, SDIM
REAL DMEAN, MOV, SDMOV, CIRC, DFAR, DCLOS, MFRAC
REAL Z1, Z2, MVD(P,P), M(P,P), CURM
REAL N(T,P), NM(P), OPOOL(T), MNOSP, PLTOT, COVER
REAL SUMPL, SURV, SD(P), CV(P), CVCVS, MNCVS, SDCVS
REAL MNMNS, SDMNS, CVMNS, MNCV(20), PMEAN(P)
DIMENSION XI(500), PHI(500), CAPPHI(401), CC(500)
OPEN (1, FILE='\\LENORE\\SIMOUT')
DATA KKM/10000.0/, RM/0.10/, DETM/0.3/
DATA DISTM/2.0/
DATA SDRK/0.10/, SDR/0.10/
DATA SDDR/0.10/, SDDD/0.10/, SDDET/0.10/
DATA NN/400/, DXI/0.01/
DATA DI/1.0/
DATA SDMOVA/0.2/
DATA B/100.0/
DATA SDPOOL/0.10/
DATA SURVS/0.5/, SDIM/0.10/, SDSURV/0.10/
DATA NNN/164574444/
```

```
C
C   IN THIS SECTION THE STANDARD NORMAL VALUES ARE
C   CALCULATED.
```

```

RR = 1.0/(SQRT(2.0*3.14159))
NP1 = NN+1
DO 13 JF1=1,NP1
CC(JF1) = JF1
```

```

FJ = JP1 - 1
X1(JP1) = FJ*DX1
13 PHI(JP1) = RR*EXP(-X1(JP1)*X1(JP1)/2.0)
   CAPPHI(1) = 0.50
   DO 14 JP1 = 3, NP1, 2
14   CAPPHI(JP1) = CAPPHI(JP1 - 2) +
      1 (PHI(JP1-2) + 4.0*PHI(JP1-1) +
      2 PHI(JP1))*DX1/3.0
   DO 24 I=1, NP1
   IF (CAPPHI(I) .EQ. 0.) THEN
   CAPPHI(I) = (CAPPHI(I-1) + CAPPHI(I+1)) / 2.
   ENDIF
24 CONTINUE
C
C   OPOOL(1) = 0.
C
C   HERE THE INITIAL VALUES OF N (POPULATION SIZES)
C   ARE ENTERED, F IS THE NUMBER OF PATCHES.
C
DO 2 I = 1, F
N(I, I) = B
2 CONTINUE
C
DO 67 IRUNS=1, ITER
C   IRUNS IS THE NUMBER OF RUNS OF THE MODEL.
C
PLTOT = 0.
C   PLTOT IS THE NUMBER OF INDIVIDUALS IN THE DISPERSAL
C   POOL.
C   HERE I CHOOSE VALUES FOR DISPERSAL RATE (DRS),
C   DISPERSAL DISTANCE (DDS), DETECTION RADIUS (DETS),
C   IMMIGRATION RATE (IMS), INTRINSIC GROWTH RATE WITHIN
C   PATCHES (RS), CARRYING CAPACITY OF PATCHES (KKS).
C
CALL RANDOM(NNN, RNOM)
DRS = RNOM
CALL RANDOM(NNN, RNOM)
DDS = -RNOM*DISTM
CALL RANDOM(NNN, RNOM)
DETS = RNOM*DETM
CALL RANDOM(NNN, RNOM)
IMS = RNOM*B*F
CALL RANDOM(NNN, RNOM)
RS = RNOM*RM
CALL RANDOM(NNN, RNOM)
KKS = RNOM*KKM
IF (KKS.LE.0.) THEN
KKS = 0.
ENDIF
VIM = (SDIM*IMS)*(SDIM*IMS)

```

```

VSURV = (SDSURV*SURVS)*(SDSURV*SURVS)

C   VIM IS THE VARIANCE AROUND THE ESTIMATE OF THE
C   IMMIGRATION RATE (FROM OUTSIDE THE AREA)
C   VSURV IS THE VARIANCE AROUND THE SURVIVAL RATE
C   OF ORGANISMS IN THE DISPERSAL POOL.
C
C   IN THIS SECTION THE LOCATIONS OF 10 RANDOMLY
C   PLACED PATCHES ARE DETERMINED.
C   THE GRID IS 1000*1000.
C   THE PATCH CO-ORDINATES ARE ZZ(I) AND WW(I) WHERE
C   I IS THE PATCH.
C
DO 33 I = 1,P
  CALL RANDOM(NNN,RNOMA)
  RNOMA = RNOMA * 1000.
  ZZ(I) = RNOMA
  CALL RANDOM(NNN,RNOMB)
  RNOMB = RNOMB * 1000.
  WW(I) = RNOMB
33  CONTINUE
DO 34 J = 1,P
  DO 34 I = 1,P
    W = (WW(J) - WW(I)) * (WW(J) - WW(I))
    Z = (ZZ(J) - ZZ(I)) * (ZZ(J) - ZZ(I))
    D(I,J) = SQRT (W + Z)
    IF (D(I,J) .EQ. 0.) THEN
      D(I,J) = 1.
    ENDIF
    IF (I .EQ. J) THEN
      D(I,J) = 1.
    ENDIF
34  CONTINUE
  DMEAN = 0.
  DO 8 I = 1,P
    DO 8 J = 1,P
      DMEAN = D(I,J) + DMEAN
8  CONTINUE
  DMEAN = (DMEAN-P)/((P*P)-P)
C   DMEAN IS THE MEAN DISTANCE BETWEEN PAIRS OF PATCHES.
C
C   THIS IS THE BEGINNING OF THE INDIVIDUAL RUN.
C   EACH PARAMETER CHANGES WITH EACH TIME STEP.
C
DO 11 K = 2,T
  T IS THE NUMBER OF TIME STEPS.
C
C   HERE I CALCULATE THE AVERAGE OF ALL PATCH
C   POPULATION SIZES AT TIME PERIOD K-1.
C
  XBARN(K-1) = 0.
  DO 56 I = 1,P

```

```

      XBARN(K-1) = XBARN(K-1) + N(K-1,I)
56  CONTINUE
      XBARN(K-1) = XBARN(K-1)/P
C
C   IN THE FOLLOWING SECTION STOCHASTIC VARIATION
C   IN CARRYING CAPACITIES (K), GROWTH RATES (R),
C   DISPERSAL RATES (DR),
C   DISPERSAL DISTANCES (DD), AND DETECTION DISTANCES
C   (DET) ARE INCLUDED.
C
      DO 40 J=1,P
      KK(J) = KLS
      R(J) = RS
      DISP(J) = DRS
      DIST(J) = DDS
      DET(J) = DETS*DMEAN
      VKK(J) = (SDKK*KK(J))*(SDKK*KK(J))
      VR(J) = (SDR*R(J))*(SDR*R(J))
      VDR(J) = (SDDR*DISP(J))*(SDDR*DISP(J))
      VDD(J) = (SDDD*DIST(J))*(SDDD*DIST(J))
      VDET(J) = (SDDET*DET(J))*(SDDET*DET(J))
C
C   THE V*(J) VALUES ARE THE VARIANCE ASSOC. WITH THE
C   STOCHASTIC VARIATION IN * IN PATCH J. IN ALL CASES
C   THE DISTRIBUTION IS NORMAL WITH MEAN *S AND VARIANCE
C   V*.
      DIAM(J) = DI
C   DIAM(J) IS THE DIAMETER OF PATCH J.
40  CONTINUE
C
C   HERE STOCHASTIC VARIATION IS IMPOSED ON THE PARAMETERS
C   FOR IM AND SURV. ONE VALUE IS CHOSEN FOR EACH TIME
C   STEP. FOR KK, R, DR, DD, DET A SEPARATE VALUE IS
C   CHOSEN FOR EACH PATCH IN EACH TIME STEP.
      CALL NORMAL(NNN,IMS,VIM,RNOM)
      IM = RNOM
      IF (IM .LE. 0.) THEN
        IM = 0.
      ENDIF
      CALL NORMAL(NNN,SURVS,VSURV,RNOM)
      SURV = RNOM
      IF (SURV .LE. 0.) THEN
        SURV = 0.
      ENDIF
      DO 10 J = 1,P
      CALL NORMAL(NNN,KK(J),VKK(J),RNOM)
      KK(J) = RNOM
      IF (KK(J) .LE. 0.) THEN

```

```

      KK(J) = 1.
      ENDIF
      CALL NORMAL(NNN, R(J), VR(J), RNOM)
      R(J) = RNOM
      CALL NORMAL(NNN, DISP(J), VDR(J), RNOM)
      DISP(J) = RNOM
      IF (DISP(J) .LT. 0.) THEN
        DISP(J) = 0.
      ENDIF
      CALL NORMAL(NNN, DIST(J), VDD(J), RNOM)
      DIST(J) = RNOM
      IF (DIST(J) .LE. 0.0001) THEN
        DIST(J) = 0.0001
      ENDIF
      CALL NORMAL(NNN, DET(J), VDET(J), RNOM)
      DET(J) = RNOM
      IF (DET(J) .LE. 0.01) THEN
        DET(J) = 0.01
      ENDIF
10    CONTINUE
C
      MNDSP = 0.
      DO 80 J = 1, P
        MNDSP = MNDSP + DISP(J)
80    CONTINUE
      MNDSP = MNDSP / P
C      MNDSP IS THE AVERAGE DISPERSAL RATE FROM ALL PATCHES.
C
C      IN THE FOLLOWING SECTION THE OVERLAP AREAS OF THE
C      PATCH DETECTION AREAS ARE CALCULATED.
C
      DO 28 I = 1, P
        RAD(I) = DET(I)
C      RAD(I) IS THE RADIUS FROM THE PATCH CENTRE TO THE
C      EDGE OF THE DETECTION ZONE. IT IS THE SAME AS THE
C      DETECTION RADIUS.
28    CONTINUE
      DO 29 I = 1, P
        DO 29 J = 1, P
          IF (I .NE. J) THEN
            IF ((RAD(I) + RAD(J)) .LE. D(I, J)) THEN
              AREA(I, J) = 0.
C      AREA(I, J) IS THE OVERLAP AREA OF THE DETECTION
C      ZONES OF PATCHES I AND J.
            ENDIF
            IF ((D(I, J) + RAD(I)) .LE. RAD(J)) THEN
              AREA(I, J) = 3.14159 * (RAD(I) * RAD(I))
            ENDIF
          ENDIF
        END DO
      END DO

```

```
IF ((D(I,J)+RAD(J)).LE.RAD(I)) THEN
  AREA(I,J) = 3.14159*(RAD(J)*RAD(J))
ENDIF
```

```
IF (((RAD(I) + RAD(J)) .GT. D(I,J))
1  .AND. ((D(I,J)+RAD(I)).GT.RAD(J))
2  .AND. ((D(I,J)+RAD(J)).GT.RAD(I)) THEN
  ALPHA = ACOS(((RAD(I)*RAD(I)) + (D(I,J)*D(I,J))
1  - (RAD(J)*RAD(J))) / (2.*RAD(I)*D(I,J)))
  BETA = ACOS (((RAD(J)*RAD(J)) + (D(I,J)*D(I,J))
1  - (RAD(I)*RAD(I))) / (2.*RAD(J)*D(I,J)))
  C1 = 2.*ALPHA
  C2 = 2.*BETA
  A1 = 0.5 * (RAD(I)*RAD(I)) * (C1-SIN(C1))
  A2 = 0.5 * (RAD(J)*RAD(J)) * (C2-SIN(C2))
  IF (((RAD(I).LE.D(I,J)) .AND. (RAD(J).LE.D(I,J))) .OR.
1  ((RAD(I).GE.D(I,J)) .AND. (RAD(J).GE.D(I,J))) .OR.
2  ((RAD(I).LT.D(I,J)) .AND. (RAD(J).GT.D(I,J)) .AND.
3  (ALPHA.LE.1.5708)) .OR.
4  ((RAD(I).GT.D(I,J)) .AND. (RAD(J).LT.D(I,J)) .AND.
5  (BETA.LE.1.5708))) THEN
    AREA(I,J) = A1 + A2
  ENDIF
  IF ((RAD(I).LT.D(I,J)) .AND. (RAD(J).GT.D(I,J)) .AND.
1  (ALPHA.GT.1.5708)) THEN
```

```
  AREA(I,J) = ((3.14159*(RAD(I)*RAD(I)))-A1)+A2
  ENDIF
```

```
IF ((RAD(I).GT.D(I,J)) .AND. (RAD(J).LT.D(I,J)) .AND.
1  (BETA.GT.1.5708)) THEN
  AREA(I,J) = ((3.14159*(RAD(J)*RAD(J)))-A2)+A1
  ENDIF
```

```
ENDIF
ENDIF
```

```
29 CONTINUE
```

```
DO 71 I = 1,P
DO 71 J = 1,P
M(I,J) = 0.
```

```
71 CONTINUE
```

C
C
C
C

IN THE FOLLOWING SECTION THE PROPORTIONS OF
SUCCESSFUL DISPERSAL ARE CALCULATED.

```
DO 12 I = 1,P
MOV = DMEAN*DIST(I)
```

C
C

MOV IS THE DISPERSAL DISTANCE RELATIVE TO THE
AVERAGE DISTANCE BETWEEN PATCHES.

```
SDMOV = SDMOVA*MOV
```

```

C      SDMOV IS THE STANDARD DEVIATION ASSOCIATED WITH THE
C      MEAN DISPERSAL DISTANCE FROM PATCHES. IT DETERMINES
C      THE DEGREE TO WHICH DISPERSERS ARE SPREAD OUT OVER
C      SPACE.

      DO 12 J = 1, P
      IF (I .NE. J) THEN
      CIRC = 6.283*D(I,J)

C      CIRC(I,J) IS THE CIRCUMFERENCE OF THE CIRCLE WHOSE
C      RADIUS IS THE DISTANCE FROM PATCH I TO J.

      DFAR = D(I,J) + RAD(J)

C      DFAR(I,J) IS THE DISTANCE FROM THE CENTRE OF PATCH
C      I TO THE FARTHEST EDGE OF THE DETECTION ZONE OF
C      PATCH J.

      DCLOS = D(I,J) - RAD(J)

C      DCLOS(I,J) IS THE DISTANCE FROM THE CENTRE OF PATCH
C      I TO THE CLOSEST EDGE OF THE DETECTION ZONE OF PATCH J

      MFRAC = (2*RAD(J))/CIRC
C      MFRAC(I,J) IS THE FRACTION OF CIRC(I,J) OF WHICH
C      PATCH J OVERLAPS.

      Z1 = ABS(((DCLOS - MOV)/SDMOV))
      Z2 = ABS(((DFAR - MOV)/SDMOV))

C      Z1 AND Z2 ARE THE STANDARD TRANSFORMATIONS OF
C      DCLOS AND DFAR RELATIVE TO THE MEAN DISPERSAL
C      DISTANCE FROM I.

      CZ1 = INT(1.5 + (Z1*100.))
      IF (CZ1 .GT. 401) THEN
      CZ1 = 401
      ENDIF
      CZ2 = INT(1.5 + (Z2*100.))
      IF (CZ2 .GT. 401) THEN
      CZ2 = 401
      ENDIF

C      HERE I USE THE STANDARD NORMAL VALUES (TABLE
C      CALCULATED ABOVE) TO DETERMINE THE AREA
C      UNDER THE NORMAL CURVE WHICH IS OVERLAPPED BY
C      J.

      IF (((DFAR .GT. MOV) .AND. (DCLOS .LT. MOV)) THEN
      MVD(I,J) = CAPPHI(CZ1) + CAPPHI(CZ2)
      ENDIF
      IF (((DFAR .LE. MOV) .AND. (DCLOS .LE. MOV)) .OR.

```

```

1      ((DFAR .GE. MOV) .AND. (DCLOS .GE. MOV))) THEN
      MVD(I,J) = AIS(CAPPHI(CZ2) - CAPPHI(CZ1))
      ENDIF

C
C      HERE I MULTIPLY BY .7854 (PI/4) TO ACCOUNT FOR
C      THE FACT THAT I WANT A CIRCULAR DETECTION ZONE,
C      NOT A SQUARE ONE.
C
      H(I,J) = 0.7854*MVD(I,J)*MFRAC

      ENDIF
12     CONTINUE

C      HERE I ACCOUNT FOR THE POSSIBILITY OF DETECTION
C      OF ONE PATCH (J) FROM WITHIN ANOTHER PATCH (I)

      DO 33 I = 1,P
      TOTAR = 0.

C      TOTAR IS THE TOTAL AREA OF ALL PATCHES (MINUS THEIR
C      OVERLAPS WITH EACH OTHER) WHICH CAN BE DETECTED FROM
C      WITHIN I.

      NP = P

C      NP IS THE PATCH WHICH CAN BE DETECTED FROM WITHIN
C      I AND FOR WHICH THE OUTERMOST EDGE OF ITS DETECTION
C      ZONE IS FARTHEST FROM I.
C      THIS DISTANCE DETERMINES THE RADIUS AROUND I
C      WITHIN WHICH DISPERSERS ARE "DIRECTED" TO ONE
C      OF THE PATCHES WHICH CAN BE DETECTED FROM WITHIN
C      I. ONLY DISPERSERS WHICH WOULD DISPERSE WITHIN THIS
C      DISTANCE ARE AFFECTED.

      DO 44 J = 1,P
      IF (D(I,J) .LE. RAD(J)) THEN
      TOTAR = TOTAR+(3.14159*RAD(J)*RAD(J))
      IF (RAD(J) .GT. RAD(NP)) THEN
      NP = J
      ENDIF
      ENDIF
44     CONTINUE

C      HERE WE CALCULATE THE FRACTION OF DISPERSERS FROM
C      I WHICH END UP WITHIN THE ZONE IN WHICH THEY WILL
C      BE "DIRECTED" TO THE PATCHES WHICH CAN BE DETECTED
C      FROM WITHIN I.

      IF (TOTAR .GT. 0.) THEN
      TOTM = M(I,NP) * ((3.14159*(D(I,NP)+RAD(NP))*
1          (D(I,NP)+RAD(NP)))/(3.14159*RAD(NP)
2          *RAD(NP)))

```

```

DO 77 J = 1,F
  IF (D(I,J) .LE. RAD(J)) THEN
    N(I,J) = TOTN * ((3.14159*RAD(J)*RAD(J))/TOTAR)
  ENDIF
77 CONTINUE
ENDIF
55 CONTINUE
DO 56 I=1,F
  LAP(I) = 0.
  DO 58 J=J,F
    LAP(I) = LAP(I) + AREA(I,J)
  58 CONTINUE

C   LAP(I) IS THE TOTAL OF ALL OVERLAP AREAS BETWEEN
C   THE DETECTION ZONES OF I AND OTHER PATCHES.

56 CONTINUE

C   N(I,J) IS THE FRACTION OF ORGANISMS DISPERSING
C   FROM I TO J.

DO 57 J=1,F
  DO 57 J=1,F
    IF (I .EQ. J) THEN
      N(I,J) = -1.*DISP(I)
    ENDIF
    IF (I .NE. J) THEN
      N(I,J) = (DISP(I) * M(I,J)) * (1. -
        (0.5*(LAP(J)/(3.14159*RAD(J)*RAD(J))))
    )

    IF (M(I,J) .GT. 1.) THEN
      N(I,J) = 1.
    ENDIF
    IF (N(I,J) .LE. 0.) THEN
      M(I,J) = 0.
    ENDIF
  57 CONTINUE
  MEANN=0.
  DO 20 I=1,F
    DO 55 J=1,F
      IF (I .NE. J) THEN
        MEANN=MEANN+M(I,J)
      ENDIF
    55 CONTINUE
  20 MEANN=MEANN/(F*F-F)
85 CONTINUE

C   MEANN IS THE AVERAGE FRACTION OF ORGANISMS DISPERSING
C   BETWEEN PATCHES. IT MEASURES SUCCESSFUL DISPERSAL
C   RATE.
C   LAPTOT IS THE TOTAL OF ALL OVERLAP AREAS BETWEEN
C   PATCHES.
C   COVER IS THE TOTAL AMOUNT OF AREA IN THE REGION THAT

```

IS COVERED BY THE DETECTION ZONES OF ALL PATCHES.

```

LAPTOT = 0.
COVER = 0.
DO 81 I = 1,P
  LAPTOT = LAPTOT+LAP(I)
  COVER = COVER+(3.14159*RAD(I)*RAD(I))
81 CONTINUE
LAPTOT = LAPTOT/2.
COVER = COVER-LAPTOT
IF (COVER .LE. 0.) THEN
  COVER = .001
ENDIF

```

PLTOT = (OPOOL(I-1)*SUR(V)+IN.

C ~~THE NUMBER OF ORGANISMS IN THE DISPERSAL POOL~~
C ~~IS NEGATIVELY RELATED TO COVER (AND THEREFORE~~
C ~~THE NUMBER THAT SUCCESSFULLY DISPERSE BETWEEN~~
C ~~PATCHES. XBARN IS THE AVERAGE PATCH POPULATION~~
C ~~SIZE.~~

```

PLTOT = PLTOT + (MNDSF*XBARN(I-
1) *R)*(((1500.**2.)-COVER)/(1500.**2.))

```

```

C WRITE(1,200) OPOOL(I-1), IN, MNDSF, COVER.
C 1 XBARN(I-1), PLTOT
C 200 FORMAT(F14.1,1X,F5.3,1X,F5.3,1X,F14.1,1X,F10.2,1X,
C 1 F14.1)

```

C POOL(I) IS THE POOL SIZE AS IT AFFECTS PATCH I.
C IT IS MULTIPLIED BY MEANN BECAUSE THE SUCCESS RATE
C OF DISPERSERS MOVING FROM THE DISPERSAL POOL TO
C PATCHES DEPENDS ON THE AREA COVERED BY THE DETECTION
C ZONES OF THE PATCHES.

```

SUMPL = 0.
DO 82 I = 1,P
  POOL(I) = MEANN*PLTOT

```

C DISPERSERS CAN ENTER A PATCH FROM THE DISPERSAL
C POOL ONLY IF THERE IS ROOM (THE PATCH IS BELOW
C CARRYING CAPACITY).

```

IF (POOL(I) .GE. (KK(I)-N(K-1,I))) THEN
  POOL(I) = KK(I)-N(K-1,I)
ENDIF
SUMPL = SUMPL+POOL(I)
82 CONTINUE
OPOOL(K) = PLTOT-SUMPL

```

```

DO 22 I = 1,P

```

```

      NM(I) = 0.
22  CONTINUE
C
C   HERE I ADD THE IMMIGRANTS FROM THE DISPERSAL POOL.
C
      DO 84 I = 1,P
      NK(I) = NK(I-1,J)+POOL(I)
C
C   HERE I CALCULATE THE CHANGE DUE TO DISPERSAL
C   AND INTERPATCH MOVEMENT.
C
84  CONTINUE
      DO 23 I = 1,P
      DO 83 J = 1,P
      NM(I) = NM(I) + (NK(I,J)*M(J,I))
83  CONTINUE
C
C   DISPERSERS BETWEEN PATCHES CAN ENTER PATCHES ONLY
C   THERE IS ROOM.

      IF (NM(I) .GT. (KK(I)-N(K,I))) THEN
      OPOOL(I) = OPOOL(I)+NM(I)-(KK(I)-N(K,I))
      NM(I) = KK(I)-N(K,I)
      ENDIF
23  CONTINUE
      DO 11 I = 1,P
      NK(I) = NK(I) + NM(I)
      IF (NK(I) .LT. 0.) THEN
      NK(I) = 0.
      ENDIF
C
C   IN THIS SECTION THE LOGISTIC GROWTH IS IMPOSED.
C
      NK(I) = INT(0.5 + NK(I)
1      + (NK(I)*(EXP(R(I)*
2      (1.0-(NK(I)/KK(I))))-1.0)))
      IF (NK(I) .LT. 0.) THEN
      NK(I) = 0.
      ENDIF

      CALL KEYCHK ( CH(1). )
      IF ( CH(1) .EQ. CHAR(27) ) STOP

11  CONTINUE
      XBARN(T) = 0.
      DO 61 I=1,P
      XBARN(T) = XBARN(T) + N(T,I)
61  CONTINUE
      XBARN(T) = XBARN(T)/P
      DO 89 I=1,P
      SD(I) = 0.
      CV(I) = 0.

```

```

89  CONTINUE

C  GRDMN IS THE MEAN TOTAL (POOL + PATCHES) POP.
C  AVERAGED OVER PATCHES AND TIME UNITS.
C  MNMNS IS THE MEAN PATCH POP.
C  CVMNS IS THE C.V. AMONG PATCH MEANS.
C  MNCVS IS THE AVERAGE C.V. (OVER TIME) OF ALL PATCHES.
C  CVCVS IS THE C.V. AMONG THE PATCH C.V.'S OVER TIME.

      MNMNS = 0.
      SDMNS = 0.
      CVMNS = 0.
      MNCVS = 0.
      SDCVS = 0.
      CVCVS = 0.
      DO 15 J = 1, P
      PMEAN(I) = 0.

C  RELAX IS THE "RELAXATION PERIOD" WHICH ALLOWS
C  THE DYNAMICS TO SETTLE DOWN.
C  VALUES FROM THIS PERIOD ARE NOT USED IN CALCULATIONS.
      DO 15 K = RELAX, T
      PMEAN(I) = PMEAN(I) + N(K, I)
15  CONTINUE
      DO 16 I = 1, P
      PMEAN(I) = PMEAN(I) / (T - RELAX + 1)
16  CONTINUE
      DO 88 I = 1, P
      DO 87 K = RELAX, T
      SD(I) = SD(I) + ((N(K, I) - PMEAN(I)) ** 2.)
87  CONTINUE
      SD(I) = SD(I) / (T - RELAX)
88  CONTINUE
      DO 90 I = 1, P
      IF (PMEAN(I) .LE. 0.) THEN
      CV(I) = 0.
      ENDIF
      IF (PMEAN(I) .GT. 0.) THEN
      CV(I) = SD(I) / PMEAN(I)
      ENDIF
90  CONTINUE
      DO 17 I = 1, P
      MNMNS = MNMNS + PMEAN(I)
      MNCVS = MNCVS + CV(I)
17  CONTINUE
      MNMNS = MNMNS / P
      MNCVS = MNCVS / P
      GRDMN = 0.
      DO 86 K = RELAX, T
      GRDMN = GRDMN + OPOOL(K)
86  CONTINUE

```

```

GRDMN = (GRDMN/(1-RELAX+1)) + (MINMNS*F)
DO 20 I = 1, P
SDMNS = SDMNS + ((PMEAN(I) - MINMNS)**2.0)
SDCVS = SDCVS + ((CV(I) - MNCVS)**2.0)
20 CONTINUE
SDMNS = SORT(SDMNS/(P-1))
SDCVS = SORT(SDCVS/(P-1))
IF (MINMNS .NE. 0.) THEN
CVMNS = SDMNS/MINMNS
ENDIF
IF (MNCVS .NE. 0.) THEN
CVCVS = SDCVS/MNCVS
ENDIF
IF (MINMNS .EQ. 0.) THEN
CVMNS = 0.
ENDIF
IF (MNCVS .EQ. 0.) THEN
CVCVS = 0.
ENDIF
C MNCV(1) = 1.
C JJ = 2 * P
C DO 27 I = 2, JJ, 2
C J = 1/2
C MNCV(I) = PMEAN(J)
C MNCV(I+1) = MNCV(I-1) + 1.
C 27 CONTINUE
WRITE (1,800) RS, KRS, DRS, DDS, DETS, IMS, GRDMN,
1 MINMNS, CVMNS, MNCVS, CVCVS
800 FORMAT(F6.4,1X,F7.0,1X,F6.4,1X,F7.4,1X,F6.4,
1 1X,F7.1,1X,F10.1,1X,F10.1,1X,F7.3,1X,F7.3,1X,
2 F7.3)
WRITE(*,200) IRUNS, ITER
200 FORMAT(1X,'CURRENT RUN NUMBER',15,'1X,14,1X,'OF',1X,14)

67 CONTINUE
STOP
END

```

SUBROUTINE RANDOM(IX,YFL)

C-RAND-

```

C PORTABLE RANDOM NUMBER GENERATOR
C USING THE RECURSION.
C IX = IX*A MOD P
C

```

```

C FROM: SCHRAGE, L. 1979. A MORE PORTABLE FORTRAN RANDOM NUMBER
C GENERATOR. ACM TRANS. ON MATH. SOFTWARE, 5:132-138
C ON INPUT IX MUST BE SET TO AN INTEGER 0<IX<2147483647
C RETURNS REAL NUMBER IN YFL (0.0<YFL<1.0) AND IX IS UPDATED

```

```

C -----
C      INTEGER A, P, IX, B15, B16, XH1, XALO, LEFTLO, FHI, K
C
C      7**5, 2**15, 2**16, 2**31-1
C      DATA A/16807/, B15/32768/, B16/65536/, P/2147483647/
C -----
C
C      GET 15 HI ORDER BITS OF IX
C      XH1 = IX/B16
C      GET 16 LO BITS OF IX AND FORM LO PRODUCT
C      XALO=(IX-XH1*B16)*A
C      GET 15 HI ORDER BITS OF LO PRODUCT
C      LEFTLO = XALO/B16
C
C      FORM THE 31 HIGHEST BITS OF FULL PRODUCT
C      FHI = XH1*A + LEFTLO
C      GET OVERFLO PAST 31ST BIT OF FULL PRODUCT
C      K = FHI/B15
C      ASSEMBLE ALL THE PARTS AND PRESUBTRACT P
C      THE PARENTHESES ARE ESSENTIAL
C      IX = (((XALO-LEFTLO*B16) - P) + (FHI-K*B15)*B16) + K
C      ADD P BACK IN IF NECESSARY
C      IF (IX .LT. 0) IX = IX + P
C      MULTIPLY BY 1/(2**31-1)
C      YFL = FLOAT(IX)*4.656612875E-10
C      RETURN
C      END

```

```

CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
C
C      THIS PROGRAM GENERATES RANDOM NUMBERS HAVING A
C      NORMAL DISTRIBUTION
C
C      THE BASIC UNIFORM RANDOM NUMBER GENERATOR IS
C      USED (AND THE CENTRAL LIMIT THEOREM)
C
C      AGAIN N IS THE SEED,
C      MEAN AND VAR ARE THE MEAN AND VARIANCE
C      OF THE RANDOM NUMBERS,
C      AND XN ARE THE RANDOM NUMBERS
C
CCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCCC
C      SUBROUTINE NORMAL (NA, MEAN, VAR, XN)
C      REAL MEAN, VAR, XN, U, SUM
C      INTEGER*4 NA, I
C      SUM=0.0
C      DO 100 I=1,6
C      CALL RANDOM(NA,U)
100 SUM=SUM+U
C      XN=MEAN+(SUM-3.0)*SQRT(2.0*VAR)
C      RETURN
C      END

```

END

0|4·0|3·8|9

FIN