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Distribution and Dispersal in Populations Capable of Resource Depletion

A Simulation Model

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Summary. A simulation model has been used to investigate the influence of animal (insect) distribution and dispersal among exhaustable resource units (food plants). Population size and stability were used as measures of success. The results showed that population size and stability are highest when egg batch size is as large as can be supported by the average food plant or slightly larger if larval dispersal occurs. Clumping of egg batches on food plants increases population stability when egg batches are small by insuring that some food plants will not be overcrowded. Increasing the proportion of larval dispersers or the success of dispersers can increase or decrease population size and stability depending on the original egg batch distribution, but individuals which produce offspring some of which disperse, generally have a selective advantage. Density dependent larval dispersal decreases population stability. Finally, individuals with lower reproductive capacities can have a selective advantage over those with higher reproductive capacities under certain conditions of egg batch size and larval dispersal.

Introduction

Animal populations are often subdivided because their food resources occur in distinct units. This type of ecological situation is commonly found between insects and their food plants. The number of animals on an individual plant is determined originally by the egg distribution, and secondly by dispersal of the developing animals after hatching. Resource exploitation may be severe in many insect species, and I attempt to analyze in this paper how an insect population might tailor its life history parameters to a situation in which food plants can be overexploited.

The theoretical basis for this consideration of insect distribution and resource utilization comes from the study of Monro (1967) on resource exploitation by insect populations. Monro suggests that maximum utilization of food plants will be selected for if the resource utilization of one generation does not influence the resource availability to the next generation. However, if mechanisms for preventing overcrowding per unit do not occur, populations will become extinct unless food refuges are maintained. This can be achieved by laying eggs in a random or alternatively, a contagious distribution.

The complex interactions between the distribution of eggs, subsequent larval dispersal, and mortality can be analyzed most easily with a simulation model. This paper describes a model which illustrates how population density might be affected by egg distribution, larval dispersal, and subsequent mortality.

The Model

The system simulated by the model consists of 100 plants which support on the average 10 larval insects to adulthood. The model was intended to be specific to insects on isolated food plants. The mean carrying capacity of the plants was normally distributed with a standard deviation of 2.5. The plants were renewed at the beginning of each generation independent of their defoliation history. Parameters which were investigated are listed in Table 1 and the sequence of steps is shown in Figure 1.

In most cases the initial population consisted of 5 females in each of two categories, dispersers and nondispersers. The disperser phenotype was characterized by the movement of a portion of the offspring from the original plant (parameter 4 in Fig. 1). The inheritance of this trait was complete and the same proportion of the offspring of surviving disperser types also left the plant in the next generation. Nondisperser phenotypes remained on the original plant as did their offspring in following generations. No interbreeding between the two types occurred.

Dispersing offspring were subjected to a mortality factor (parameter 5 in Fig. 1) and survivors placed randomly on plants. The only other mortality in the model occurred when the number of larvae on a plant exceeded the carrying capacity. All larvae were eliminated in this situation.

Table 1. Parameters which could be varied in the simulation model and the range of values investigated in this study.

Variable parameters							
Eggs per female	5	10	15	20			
Number eggs per batch	1	2	4	5	10	15	20
Distribution of eggs among plants (Variance/mean)	1	1.2	1.4	1.8	2.2	–	–
Proportion of offspring dispersing	0	0.2	0.4	0.5	0.6	0.8	–
Probability of surviving a dispersal episode	0.2	0.4	0.5	0.6	–	–	–
Dispersal	Density dependent and density independent						

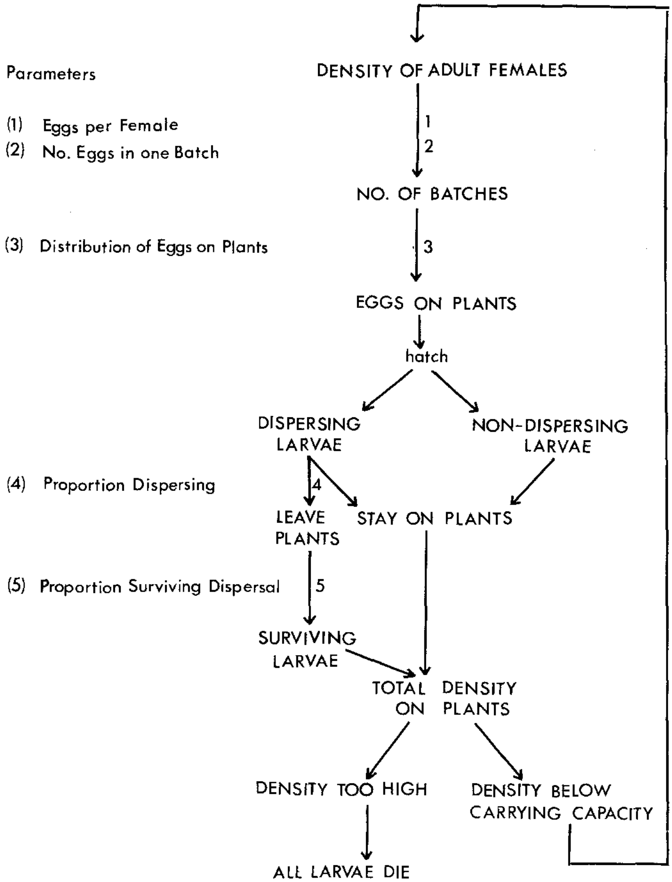

Fig. 1. Flow diagram for the simulation model

Population success was measured in two ways; by the average population per generation and by the degree of population fluctuation from generation to generation. The first measurement was obtained by taking the average of the mean population sizes from 5 separate runs of 20 generations each. Stability was estimated by dividing the mean population size by its standard error for each run of 20 generations. The stability coefficients obtained from 5 runs of 20 generations were averaged to yield a stability index. Obtaining an unbiased estimate of stability is difficult (Watt, 1964). Means and standard errors were only weakly correlated ($r=0.26$, $N=196$ runs of 20 generations each) for the range of values which occurred and therefore this measure was judged to be sufficiently unbiased for it to be useful as an indicator of population stability. The relation of the stability index to the number of generations before extinction is shown in Figure 2.

The egg distributions could be varied in the model by changing the probability that eggs would be deposited on a plant if eggs were not already present.

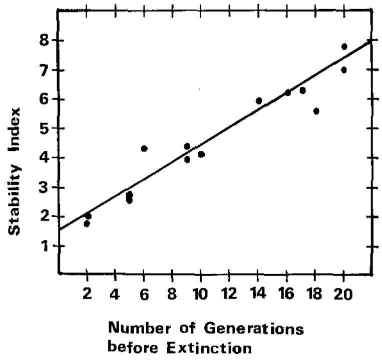

Fig. 2. The relation between the stability index (mean population/standard error) and the time until extinction of the population ($r=0.96$)

I only considered random and contagious distributions of eggs since these are the most common among insects.

Model Robustness

The plants in the simulated system were not arranged in a spatial pattern. Therefore, dispersing larvae were equally likely to find any of the 100 plants. This simplification eliminates complications with edge effects and simulates a situation in which larval dispersal into the population equals that lost from the population. However, the lack of a spatial pattern of the plants means that larvae from one plant are not more likely to move onto adjacent plants. Consideration for spatial patterns would only be important if the number of larvae or the number of overcrowded plants were low. On the average 45 to 65% of the plants were overcrowded per generation. Therefore, all plants would be in the vicinity of a plant with larvae or of an overcrowded plant. Since larvae from different plants are not distinguished, random distribution of larvae to all plants would have the same result as random distribution of larvae among neighboring plants.

Varying the number of plants in the population from 100 to 50 or to 150 changed the mean population size but not the stability of the populations. The mean population could also be varied by changing the carrying capacity of the plants. Since the value of interest is the ratio between the number of eggs laid and plant size, one of these factors must be kept constant to reveal relationships. Therefore, this study considers only one average plant size. The choice of these values is arbitrary and influences the size of resulting populations but not the relationships between animal distribution and plant exploitation.

In the original model there was no density dependent component to larval dispersal. Therefore, the model simulates innate, predefoliation dispersal tendency. A second version included density dependent dispersal in addition to innate dispersal. All larvae dispersed from a plant if the carrying capacity of that plant was exceeded. These larvae were exposed to the same probability of death as the innate dispersers and survivors were distributed randomly on plants. All larvae which were then on overcrowded plants were eliminated.

Other elaborations of the model were used to compare the success of females with different egg laying tactics. In these versions the simulation was initiated with females which produced different numbers of eggs, size of batches, distribution of batches, or proportion of dispersing larvae. The superior egg laying tactic was determined by the female type which became fixed in the population.

Results

The influence of the parameters listed in Table 1 are discussed in the following section. The simplest appropriate versions of the model were used in each case.

Total Number of Eggs Produced

The number of eggs produced by each female determined the rate at which the "habitat" could become saturated. Because the only mortality factor in the model was that arising from overcrowding of plants, high egg production led to greater overexploitation yielding smaller mean populations and reduced population stability (Table 2). The highest mean population densities and greatest stability of numbers occurred when females laid all their eggs in one batch. This maintains the greatest number of unexploited food refuges. The laying of individual eggs at fecundities of 10 or 20 eggs resulted in instability and extinction within several generations. This is explained by all plants receiving eggs and becoming overexploited. If those females which produced 20 eggs had laid these in one batch, all plants with eggs would have been overcrowded and the insect population would have gone extinct during the first generation.

Distribution of Eggs

Egg batches were placed on plants in 5 distributions ranging from random to clumped (see Table 1). When there was no dispersal, the clumped distribution

Table 2. Relation of mean population density and coefficient of stability to number and division of eggs produced. Asterisk indicates populations that were unstable and did not persist 20 generations. Distribution of eggs random and dispersal lacking

Total number of eggs per female	Population density			Population stability		
	Number of eggs per batch					
	1	5	10	1	5	10
5	327	348	–	8	12	–
10	*	285	306	*	12	19
20	*	193	229	*	6	9

Table 3. Mean population density and coefficient of stability for a computer simulation with 5 runs as a function of the clumping of egg batch distribution and the total egg production. No dispersal. Batch size = 5

Total number of eggs per female	Population density			Population stability		
	Variance mean ratio for egg distribution					
	1 (random)	1.4	1.8 (clumped)	1	1.4	1.8
5	348	272	186	12.4	13.1	13.9
10	285	253	188	11.9	18.2	19.1
20	193	183	153	6.3	9.6	16.3

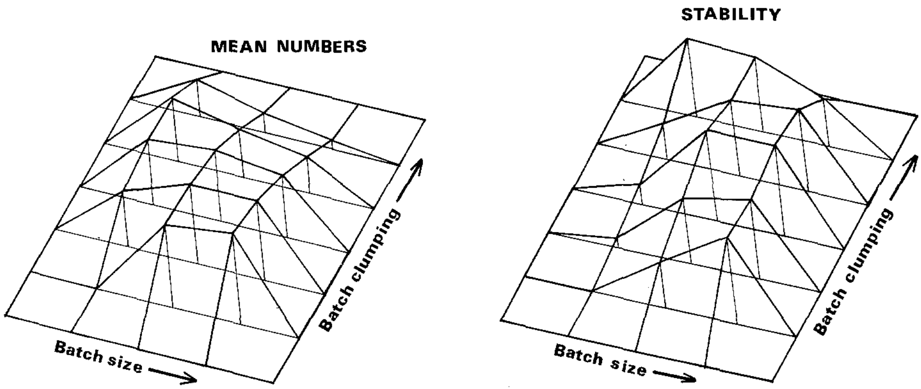

Fig. 3. The relation of egg batch size to mean population numbers and population stability with changing egg batch distribution. Egg batch sizes were 2, 5, and 10. Egg distribution ranges from random to clumped (variance/mean = 2.2). There was no dispersal and egg production was 10 eggs for every female

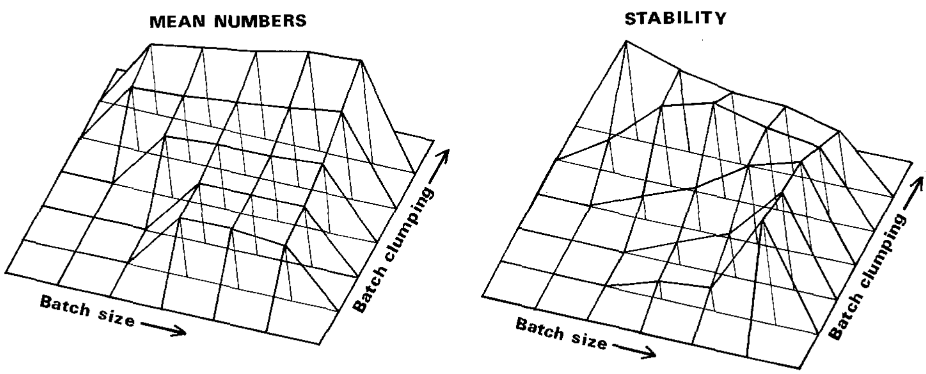

Fig. 4. The relation of egg batch size to mean population numbers and population stability with changing egg batch distribution. Egg batch sizes were 2, 5, 7, 10 and 15. Fifty percent of the offspring of the dispersing phenotype left the plants and of these 50% were successful in finding new food plants. Egg distributions as in Figure 1. Egg production was 20 eggs for every female

of eggs decreased the mean population size but increased the stability of the population (Table 3). Changing the distribution of egg batches had the most dramatic effect on the mean population size when the number of eggs produced per female was small and equal to the size of the egg batch. When egg production per female was high, the stability of the population was increased markedly with a more clumped egg distribution.

In contrast to the data shown in Table 2, when egg distributions are more clumped than random, the mean population size does not increase with an increase in batch size (Fig. 3). However, this relationship is reestablished when dispersal is added (Fig. 4). Therefore, there is an intricate association between the distribution of the eggs and the batch size. Laying eggs in a more clumped pattern is a means of stabilizing populations when production of eggs per female is high and batch size is small (see Table 3, eggs produced=20, and Fig. 3) regardless of whether larvae disperse or not.

Dispersal – Proportion of Dispersers

I began each computer run with equal numbers of females with dispersing offspring and females with nondispersing offspring. The dispersing phenotype displaced the nondispersing type in almost every combination. The only exceptions occurred when the frequency of dispersers was high and mortality of dispersers also high (50% dispersers and 80% mortality). Females with dispersing offspring were favored whenever plants became overexploited and movement to another plant was possible.

Dispersal only strongly influenced population size when the egg distribution was highly clumped (Fig. 5), and here higher levels of dispersal resulted in higher population densities. The same general pattern as that demonstrated in Figure 5, held for the different levels of egg production and for different batch sizes.

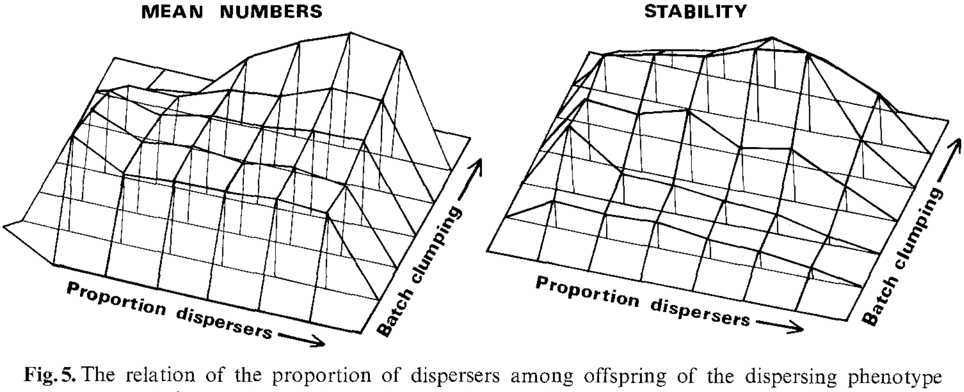

Fig. 5. The relation of the proportion of dispersers among offspring of the dispersing phenotype to mean population numbers and population stability with changing egg batch distribution. Proportion dispersers from 0 to 60%. Disperser success was 50%, egg batch size 10 and egg production 20 eggs per female. Egg distributions as in Figure 1

When egg batches were distributed in a random or slightly contagious manner, increasing the proportion of dispersers resulted in a gradual decrease in population stability. At more contagious egg distributions higher levels of dispersal were necessary before population stability was reduced (Fig. 5). Therefore, just as a more contagious distribution of eggs increases the stability of populations when the production of eggs per female is high (Table 3), increased dispersal breaks down this advantage and causes instability.

Dispersal was of the greatest advantage when the number of eggs per clutch exceeded that number which a single plant could support. In this case high dispersal levels were necessary for persistence of the population.

Disperser Survival

The influence of increased disperser survival on population parameters was variable. When half the individuals dispersed, increasing disperser survival decreased the mean population size in most cases. The effect of higher survival of dispersing individuals varied with the original egg distribution (Fig. 6). When the eggs were contagiously distributed, improvement of disperser survival to intermediate levels increased the mean population size, further improvement decreased population size. If the egg batch size was larger than the number of organisms which could be supported by the average plant, intermediate to high dispersal and intermediate to low disperser survival raised both the mean population size and the population stability.

In conclusion, the survival of dispersers has a stronger and more variable influence on population stability than on population size. The original distribution of the egg batches strongly influences the outcome of increased disperser survival. Figure 6 demonstrates that increasing the success of dispersers can either stabilize or destabilize populations.

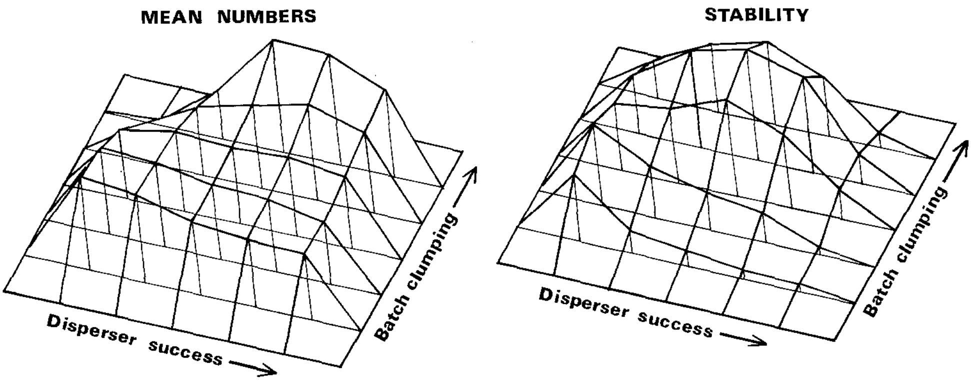

Fig. 6. The relation of the success of dispersers to mean population numbers and population stability with changing egg batch distribution. Success of dispersers from 0 to 80%. Proportion of dispersers among offspring of the dispersing phenotype was 50%. Egg batch size 15 and egg production 20 eggs for every female. Egg distributions as in Figure 1

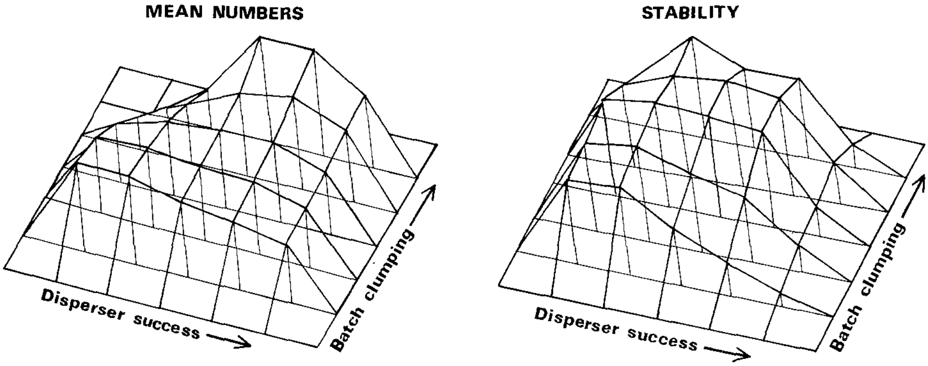

Fig. 7. Similar to Figure 6 but with the addition of density dependent dispersal. Disperser success is from 0 to 40%. Success rates above 40% caused population instability and extinction

Density Dependent Dispersal

All of the previous results have been obtained without the dispersal rate being influenced by population density on the plants. Since it is reasonable that larvae would not stay on a defoliated plant, the influence of dispersal from overcrowded plants was investigated with the density dependent model described previously. Populations often went extinct when all larvae on overcrowded plants dispersed. This was particularly the case when batch size was small (5 or 10) and/or if the survival of the dispersers was high (greater than 0.4). Small changes in the probability of success of dispersers had a major effect on the mean population size when egg distributions were clumped (Fig. 7). When eggs were randomly distributed, complete mortality of dispersing individuals resulted in the highest population densities and stability. When egg distributions were clumped, a low survival rate (20 to 30% for dispersing individuals) produced the highest average density and the greatest stability (Fig. 7).

The relation of egg batch size to egg batch distribution was similar to that described previously. A comparison of Figures 6 and 7 (note difference in scale) shows that the addition of density-dependent dispersal to this particular system has little effect on population parameters but makes them more sensitive to smaller changes in the success rate of dispersers. In Figure 7 an increase in the success of dispersers from 20 to 30% had a similar influence to an increase from 20 to 40% in the model lacking density dependent dispersal.

In conclusion, the addition of density dependent dispersal reduced population stability and caused extinction unless the survival of dispersing individuals was low.

Selection for Lowered Fecundity

In a finite environment, high fecundity can cause habitat destruction and population instability. To determine if individuals with reduced egg production could

Table 4. Interaction of batch size and dispersal in determining competitive superiority of individuals with different reproductive capabilities. Dispersal applies to A type only = 50% dispersers and 50% survival. No density dependent dispersal. "?" indicates that the winner was not consistent. Each combination was run 5 times for 20 generations

Batch size A	Batch size B	Dispersal Type A	Winner
A Type = 10 eggs/female		B Type = 20 eggs/female	
10	10	no	B
5	10	no	B
2	10	no	A
10	10	yes	B
5	10	yes	A
A Type = 8 eggs		B Type = 10 eggs	
4	5	no	B
8	10	no	B
8	10	yes	A
A Type = 8 eggs		B Type = 12 eggs	
4	6	no	?
4	6	yes	A

be competitively superior under certain conditions of egg batch size, or larval dispersal, simulations were run starting with two distinct groups of females with different fecundities, egg batch sizes and dispersal characteristics. The combinations investigated and the outcomes are given in Table 4. It is clear that in this simulation model dispersal and egg batch sizes can be manipulated so that individuals with reduced fecundities have a selective advantage. However, this is a simplification since no consideration is given for a genetic mechanism to maintain this system.

Selection for a Clumped Egg Distribution

A contagious egg distribution can be inefficient since it results in the wasting of eggs on overcrowded plants. To determine if individuals with more contagious egg distributions could have a selective advantage over those with random egg distributions, simulations were run using two types of females: those with random egg distributions and those with contagious egg distributions (M/V = 1.2). The contagious phenotype was competitively superior to the random phenotype when the batch size was reduced (7 to 10, 8 to 10, or 9 to 10) using the density dependent dispersal model with low survival of dispersers (20%), or if dispersal were associated with the contagious phenotype and the batch size reduced for this phenotype as well. The contagious phenotype could still be competitively superior even if the fecundity were slightly reduced (17 eggs/female for the contagious type and 20 eggs for the random type).

Therefore, in this simple situation it is possible to demonstrate combinations of characteristics which can lead to selection for individuals which lay eggs contagiously.

Discussion

The purpose of this model was to investigate the population consequences of insects laying eggs in different patterns on food plants which can be overutilized. If too many eggs are laid on a single plant, that subpopulation is killed, unless there is dispersal to other plants. Thus, dispersal works to smoothout "mistakes" of egg laying.

It is the characteristic of overexploitation which distinguishes this model from earlier models designed to investigate the relation of dispersal to population stability (Gadgil, 1971; Levins, 1970; Reddingius and den Boer, 1970; Roff, 1974a, b; Van Valen, 1971). While in these studies subpopulations could reach the carrying capacity, they could not overexploit their habitat to their own demise. The general conclusion arising from these studies was that dispersal of individuals among population subunits increases the temporal stability of the total population.

The summarized conclusions from the overexploited model are given in Table 5. *Factors which lead to resource exploitation (high fecundity, low batch size and density dependent dispersal) all tend to destabilize the populations and reduce the average population size.* On the other hand those traits which lead to the maintenance of resource refuges (large batch size and clumped egg batch distribution) stabilize population densities.

Table 5. Summarized results from simulation model. ↑ indicates increasing, ↓ indicates decreasing, ∩ indicates highest at intermediate levels. Question marks indicate trend with exceptions

Parameter	Stability	Mean population
Increasing # eggs/female	↓ ?	↓
Increasing # eggs/batch	↑	↑
Egg distribution more clumped		
No dispersal	↑ or ∩	↓
Dispersal	∩	↑
Increased dispersal		
Random egg distribution	↓ ?	∩ ?
Clumped egg distribution	∩	∩ ?
Increased disperser survival		
Random egg distribution	↓ ?	↓ ?
Clumped egg distribution	∩ ?	∩ ?
Density dependent dispersal[a] increased disperser survival		
Random egg distribution	↓	↓
Clumped egg distribution	∩	∩

[a] All populations become unstable when survival of dispersing individuals is above 40%

The results of the model show that while the proportion and success of dispersers can influence population levels, the interactions are complicated so that generalizations about optimum levels are not made easily. For example, increased mortality to dispersers can increase or decrease mean population size or population stability depending on egg batch size, distribution, and proportion of dispersers.

This result means that for insect populations on host plants it is not possible to make blanket statements about the relationship of dispersal to population stability. In general increased disperser survival and tendency to disperse decrease population stability, but there are many exceptions. When egg distributions are clumped, an increase from low to intermediate levels of dispersal or disperser survival can increase population density and stability (Figs. 5–7). High rates of dispersal or disperser success have a destabilizing influence.

In a field situation where external factors can be variable, it is difficult to imagine that fine tuning will maintain a maximum mean population size and level of stability through the adjustment of dispersal tendency. Probably, if parameters of animal distribution and dispersal are adaptive characteristics which can be adjusted through selection, field populations will adopt characteristics (egg distribution and disperser tendency) which will allow them to survive in a variable environment. These characteristics are (1) a moderately clumped egg distribution, (2) egg batches which are larger than that which can be supported by the average plant, and (3) intermediate levels of dispersal. Examples of advantageous combinations of characteristics are shown in Figures 4 and 5.

In this analysis I have concentrated on population density and population stability as measures of the influence of egg distribution and larval dispersal. It is not clear that characteristics which benefit populations will be those which benefit individuals. For example, high individual fecundity leads to overexploitation and unstable populations. However, individuals with higher fecundities replace those with reduced fecundity unless the reduced fecundity is associated with differences in dispersal patterns, egg batch sizes, or egg batch distributions. Similarly contagious egg distributions stabilize populations but are only advantageous at the individual level if associated with other modifications of egg distribution or dispersal. The contradiction between individual and population advantages should be analyzed further by a genetic model to consider possible mechanisms of inheritance of egg distribution and dispersal traits as has been done for dispersal without resource depletion by Roff (1975).

To consider some of the constraints on individuals which could influence their distribution and dispersal patterns, one must think in terms of specific organisms. Lepidoptera fit the characteristics of the model well. In most cases females deposit eggs on the larval food plant, and the larvae hatch and develop there. Food plant choice is often very specific and suitable resource units represent individual plants. Some Lepidoptera lay eggs individually while others lay eggs in batches. Examples from this group of insects can be used to investigate the conclusions of the model.

Most butterflies lay eggs singly, although some members of the subfamily Nymphalinae lay eggs in batches of several to many (Labine, 1968). On the other hand, more moth species seem to lay eggs in batches (Gruys, 1970). With the simulation model it was seen that if females with high reproductive rates deposit eggs singly, food exploitation and population extinction are likely to occur. Therefore, one would like to know if butterflies which lay eggs individually produce fewer eggs than moths or other butterflies which lay eggs in batches. I could find no evidence that the total number of eggs produced by Lepidoptera which lay eggs singly is reduced in comparison to those which lay eggs in batches (Gilbert, 1972; R. Jones, personal communication, personal observation) although good data do not seem to be available. If egg production is not reduced it is likely that those species which lay eggs individually are prevented from overexploiting their food supply by other factors such as higher egg or larval mortality or cannabalism. For example Monarch and Queen butterfly larvae will eat other eggs on the same food plant (Brower, 1961). This mechanism could reduce overcrowding of individual food plants.

Certainly other constraints besides population density and stability can influence the oviposition pattern of insects. Larval aggregations can be important (Ford, 1962) for predator protection (concentrated defense secretions, etc.) or for environmental modification (tent caterpillars). If there are selective advantages to groups of larvae, laying eggs in batches is one way to achieve this goal. Egg batches do not, however, always give rise to gregarious larvae and in some cases larvae disperse shortly after they emerge from the egg mass (Gruys, 1970). Selection against laying eggs in groups might occur in response to parasitism. There is some evidence that the parasitism rate can be higher if several eggs are laid together (Kulman, 1965).

An aspect of egg distribution which has not been considered in this analysis is that of "spreading risk" (den Boer, 1970; Reddingius and den Boer, 1970). If a female lays more smaller egg batches she reduces the possibility that a disaster to one food plant will elimate all her offspring. The advantage of "spreading the risk" is difficult to measure in field populations but it is a factor which may well influence whether eggs are laid singly or in batches.

A contagious distribution of eggs or egg batches seems to be the rule among the Lepidoptera (Cinnabar Moth, Green, 1974, personal observation; Spruce Budworm, Morris, 1963; *Cactoblastis cactorum,* Monro, 1967; Diamond Back Moth, Harcourt, 1961a; Cabbage White Butterfly, Harcourt, 1961b; Cabbage Looper, Harcourt, 1965) and individual insects and their eggs in general are usually found to have contagious distributions (Southwood, 1966). While it has been argued that a clumped egg distribution is an "adaptive strategy" (Monro, 1967; Birch, 1970) it may be that this distribution is an artifact of a variety of other conditions. Characteristics such as size, exposure, age or physiological state of the food plant may influence its attractiveness to ovipositing butterflies or moths. Differential attractiveness of plants can lead to a contagious egg distribution. An interesting question is whether selection can act to enhance or reduce the expression of oviposition preferences of females.

Monro (1967) posed the question of what prevents individual female moths from improving the fate of their own offspring by laying eggs only on plants which have not previously received eggs. One answer to this is that as long as other individuals do not follow the same rules for oviposition, no advantage will accure to an individual which distributes her eggs uniformly. While a uniform distribution of eggs may prevent egg wastage on overcrowded plants, it requires that ovipositing females are capable of identifying plants which already have eggs. This would mean either that the eggs would have to be highly visible, which very likely would increase their susceptibility to predation, or that a chemical marking system would have to evolve. A random egg distribution is the simplest to achieve.

Increased mortality to dispersing individuals can be a population stabilizing mechanism but this does not explain why individuals should disperse when the probability of success is low. Kin selection is a possible explanation for the maintenance of larval dispersal when disperser mortality is high and if the animals on one plant are sibs. If stationary members of the family benefit from some siblings leaving the plant, families consisting of some dispersing individuals would have a selective advantage. However, it is likely that poor disperser success will select against the tendency of larvae to leave the plant. For example, *Cactoblastis* larvae rarely leave the food plant and if forced to leave, seldom find a new plant (Monro, 1967). Green (1974) stressed the importance of plant spacing in determining the probability of success of dispersing larvae. His hypothesis is based on the proposition that wide plant spacing will result in high disperser mortality and increased population stability. Selection against dispersal tendency when success is low would modify this situation.

The detailed information necessary to test predictions of the model are not available in the literature. Field studies are now underway (Myers and Campbell, M.S.) to investigate predictions from the model using the Cinnabar Moth, *Tyria jacobaeae* (L.). The explicit predictions are as follows: (1) Mean egg batch size should be larger than the number which can be supported by the average plant if larval dispersal occurs (see Fig. 4); (2) In high density populations, where the egg to plant biomass ratio is high, egg distributions should be more contagious to assure that some food refuges will survive (see Table 4); (3) Because selection will be stronger for a clumped egg batch distribution when egg batches are smaller, populations with smaller egg batches should deposit eggs in a more contagious manner (see Fig. 4); (4) Populations with very high disperser survival should be less stable than those with low disperser survival (see Fig. 7). In the future, species comparisons should be undertaken to describe patterns of egg distribution, food plant distribution, and dispersal patterns, and to elucidate the relationship of these characteristics to parameters of population density and stability.

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