



## **Dispersal: Population Consequences and Evolution**

Madhav Gadgil

*Ecology*, Vol. 52, No. 2. (Mar., 1971), pp. 253-261.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28197103%2952%3A2%3C253%3ADPCAE%3E2.0.CO%3B2-Y>

*Ecology* is currently published by The Ecological Society of America.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

# DISPERSAL: POPULATION CONSEQUENCES AND EVOLUTION<sup>1</sup>

MADHAV GADGIL

*The Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138*

*Abstract.* Most animal and plant populations are divided into a number of local populations with some dispersal of individuals from one site to another. A theoretical investigation of the phenomenon of dispersal suggests the following consequences: Isolated and poorly accessible sites will tend to become less crowded than an average site as a result of dispersal. An episode of dispersal will result in uneven crowding at the various sites. Variation in the degree of crowding resulting from dispersal will depress the total population size of a species over its entire range. Variation in the carrying capacity with time will lead to an analogous depression of the mean population size. Spatial variation in the carrying capacities of the sites will favor a sensitive response leading to a rapid increase in the emigration rate with crowding, while variation with time will disfavor a response very sensitive to crowding. Variation in space will favor the emigration of a small fraction of the population, while variation in time will favor the emigration of a larger fraction.

Dispersal is one of the most important and amongst the least understood factors of population biology. There has been a fair amount of work on gene flow through populations (reviewed in Moran 1962), but such work uniformly neglects population dynamics. Skellam (1951) has considered the rate of spread of epibiotics and Lidicker (1962) has some interesting suggestions about population consequences of dispersal. Cohen (1967) has investigated the properties of proximate factors which could serve as signals to trigger seasonal migrations. Levins (1969b, 1970) has recently published some very interesting work on the basis of considerations of the number of sites within the total range of a species which may be occupied by local populations as a function of dispersal and extinction rates. He goes on to deduce results on population control strategies and group selection.

The stable statistical properties of the populations subject to dispersal need to be investigated in much greater depth. This paper is an attempt to explore two aspects of this; the amount of crowding at any site and the total population size of the species over its entire range. The magnitude of the dispersal rate and its density response have not been separated in previous studies. The present investigation attempts to relate the spatial and temporal heterogeneity in the environment of the species to the evolution of these two components of dispersal.

## THE APPROACH TO CONSTRUCTION OF THEORY

The theory presented in this paper is based not on a single model, but on a hierarchy of models. The simpler models in the hierarchy are of course based on more general assumptions. However, all the models have two kinds of restrictions. We do not consider the possibility of an organism indulging in a search for a suitable site and accepting one when

it is unlikely that a continued search would take it into a better site. Also, we do not take into account the possibility of an organism physiologically detecting an impending deterioration of its habitat. We will continually refer to crowding, not in the sense of population density by itself, but in the sense of pressure on resources, expressed as the ratio of population size to the carrying capacity of the habitat.

The simplest of the models is algebraic in form, and is the most general, involving very few assumptions. It can, however, suggest results only about crowding at the various sites. As more assumptions are made, the models apply to fewer systems and become more complex, but also yield a richer variety of results about these systems. Thus the computer simulations with a system of difference equations represent a much more specific model, but yield results about total population size and evolution of dispersal rates as well as crowding. There is thus a trade-off between the generality of a model and the richness of its consequences. A more complex model embodies assumptions which have to be chosen from amongst several biologically interesting alternatives, resulting in an array of analogous models. The obvious solution is to investigate more than one analogous model and compare their consequences so as to isolate those results which have a greater generality than is implied by the restrictive assumptions of a single model. This is why we present two different models of regulation of total population, and base the later discussion on results common to over 100 simulations, utilizing different relationships and parameters.

In addition there is always a possibility with the more complex models that the results of the model are a consequence, not of a desirable and interesting feature of the model but of an unimportant simplification. Therefore, any result of a complex model should be considered of interest only when the fea-

<sup>1</sup> Received April 29, 1970; accepted September 5, 1970.

ture of the model which yields that particular result is identified as being an interesting feature. This is why I have furnished extensive verbal interpretations of all the theoretical results presented. I therefore believe that the results presented in this paper, though mostly derived from rather specific models, are quite general with the exception of the two restrictive assumptions mentioned above.

#### DISPERSAL AND CROWDING

Consider a species whose total population is made up of  $q$  local populations occupying  $q$  sites over the entire range of the species. Let  $N_i$  be the size of the  $i$ th local population, and  $k_i$  the carrying capacity of the  $i$ th site. We may define the degree of crowding for the  $i$ th local population,  $\rho_i$ , as:

$$\rho_i = N_i/k_i$$

Let us consider a single dispersal episode, such that there is no addition to the population through births, nor any deaths except those of dispersives over the duration of the episode. Let  $\alpha_i \cdot N_i$  be the total number of emigrants leaving site  $i$ . Further, let  $\beta_i \cdot N_i$  be the total number of immigrants arriving at site  $i$ . Then the size of the local population at site  $i$  has changed from  $N_i$  to  $N_i(1 - \alpha_i + \beta_i)$  as a result of the dispersal episode. The degree of crowding at site  $i$  has therefore changed from  $N_i/k_i$  to  $N_i(1 - \alpha_i + \beta_i)/k_i$ . If we designate the change in the degree of crowding at site  $i$  by  $\Delta\rho_i$ , then  $\Delta\rho_i = N_i(\beta_i - \alpha_i)/k_i$ .

An episode of dispersal may bring about significant changes in the degree of crowding at the various sites. Its simplest effect could be a general reduction in crowding at all of the sites if the dispersives are subject to high rates of mortality; i.e. if the term  $\alpha$  is much greater than  $\beta$ . Under this condition, the changes in crowding at different sites,  $\Delta\rho$ 's will vary importantly with the differences in the fraction of individuals emigrating, i.e. in  $\alpha$ 's. Sites which are located such that agents of dispersal have a strong impact on them may become relatively less crowded as a result of a greater fraction of their population leaving them.

If the total number of immigrants arriving at a site is comparable in magnitude with the population left at the site after dispersal, i.e. if  $\beta$  is of the same order as  $(1 - \alpha)$ , then immigration will also have a significant effect on the degree of crowding at the various sites. Isolated and poorly accessible sites may be expected to resemble other sites in  $\alpha$ 's, but to have low  $\beta$ 's. Such sites will tend to become less crowded than others.

Another interesting effect may arise if the ability of a site to intercept dispersives is independent of, or at least does not increase as rapidly as its carrying capacity,  $k$ . Then the sites with higher carrying capacities will receive a number of immigrants lower

relative to their populations, i.e. will tend to have smaller  $\beta$ 's. The sites with lower  $k$ 's will then tend to become more crowded than the sites with higher  $k$ 's. If this condition were to hold, then the lower crowding at larger sites, i.e. sites with higher  $k$ , will distribute a species more uniformly over its range than the limiting agents determining its carrying capacity. If, on the other hand, the ability of a site to intercept dispersives increases at a rate higher than its  $k$ , then high  $k$  sites will become more crowded and low  $k$  sites less crowded as a result of dispersal. Under these conditions, the species will be less uniformly distributed over its range than the limiting agents determining its carrying capacity.

However, so long as the ability of interception of dispersives by a site does not increase exactly in proportion to its carrying capacity, a dispersal episode will result in some sites becoming more crowded than others. The first case, viz., that the ability of interception increases less rapidly than  $k$ , has been used in the models presented further on in the paper. The conclusions from these models are, however, not dependent on that particular assumption, but merely on the more general consequence that dispersal would result in uneven crowding of the various sites.

#### TOTAL POPULATION SIZE

The way in which the range of a species is divided up into habitable sites is expected to be of significance in determining the total population size of the species in relation to the sum of the carrying capacities of all the sites. We may distinguish three aspects of this problem. Firstly, the total size of the range over which the sites are distributed, widely separated or close together; secondly, the number of local populations, few large or many small; and thirdly, the extent of variation in the accessibility, in isolation or in the value of the carrying capacities of the various sites; whether the various sites are more or less equal or highly unequal in these respects. Territoriality will introduce special effects not considered in the discussion below.

#### *Size of the range*

The size of the range over which the sites are distributed will have distinct effects on the total population size. The larger the size of the range, the greater the distances that must be traversed by dispersives before reaching another site, and hence the greater the chance of deaths during dispersal. This stepping up of death rate should lead to a reduction in the total population density. A possible experimental verification of this prediction is furnished by Huffaker's (1958) studies on mite populations. Huffaker cultured herbivorous mite species on oranges. The experimental set-up comprised a number of oranges interspersed with rubber balls on a tray. The amount

of feeding area per orange was adjusted by coating a part of the orange and leaving only a fraction of the area exposed. He could thus adjust the total amount of food made available on a single tray. The same amount of food could be offered by exposing large areas on a few oranges or small areas on many. The size of the range could be adjusted by clumping the oranges or distributing them widely amongst the rubber balls. When a 2-orange feeding area was distributed over a 4-orange range the total population density had a mean of about 8,000; when an equal feeding area was distributed over a 40-orange range, the mean total population density was reduced to 5,500. In both cases the number and feeding areas of the sites were the same. Field studies of the populations of the psyllid *Cardiospina albitextura* show a similar pattern (Johnson 1969). This insect feeds on leaves of *Eucalyptus* trees in Australia. The mean population density of the insect is higher when the host trees are more closely planted.

In this context, Levins (pers. comm.) makes the interesting suggestion that the decline in mean population density with increasing distance between sites leads to a limiting density of local populations compatible with the species' survival. Thus, the boundary of a species might come at some threshold density and could be quite a sharp boundary.

*Number of sites*

Even with the same size of the range, a given total carrying capacity may be distributed amongst few large or many small sites. If these sites do not vary in accessibility, isolation or the value of *k*, the extent of crowding is expected to be about equal for all sites, with none very over- or undercrowded.

The extent of deaths during dispersal may depend either on the mean distance between the different sites, or on the total size of the range. In the former case the total population size will be greater if the same carrying capacity of the entire range is divided up amongst more sites each with smaller *k*. In the latter case, the total population size may be expected to be independent of the number of sites. Huffaker's (1958) mites seem to exemplify the latter case. He made available a total of 2 orange feeding areas divided up equally amongst 4 large or 20 small areas dispersed over an approximately equal range. The mean total population density was about 5,500 in both the cases.

*Variation amongst sites*

However, if the different sites vary in their accessibility, isolation from other sites or in their *k*'s, different local populations are expected to be crowded to different extents with some under- and others overcrowded relative to the average. The greater the variation amongst the different sites in their accessi-

bility, isolation or *k*, the greater will be the extent of under- and overcrowding. It is therefore pertinent to investigate how such under- or overcrowding of the various local populations will affect the total population size. We need to postulate some mechanism of population regulation in order to investigate this problem. It is widely accepted that population regulation must be negatively density dependent; i.e. the growth rate of the population declines with an increase in population size relative to *k*.

$$\frac{1}{N} \frac{dN}{dt} \propto f(N,k)$$

where *f(N,k)* is a monotonically decreasing function of *N/k*. In particular, for the logistic model:

$$\frac{1}{N} \frac{dN}{dt} \propto \left(1 - \frac{N}{k}\right)$$

In general, it is reasonable to assume that the degree of regulation depends on *N/k*. But if the degree of regulation (i.e. change in population size in terms of the fraction of population size) is dependent on *N/k*, the magnitude of regulation (i.e. the change in terms of actual numbers) is dependent on *N × (N/k) = N<sup>2</sup>/k*. Hence the magnitude of regulation is greater for a given degree of overcrowding in comparison with the same degree of undercrowding (where the degree of under- or overcrowding is specified by  $|1 - (N/k)|$ ). This leads, as shown below, to the consequence that overcrowding of some local populations and undercrowding of others leads to the maintenance of a total population size lower than the total *k*.

This argument can be verified on the basis of two different analytic models. The first model can be represented by the following system of a pair of coupled difference equations:

$$N_1(t + 1) = (1 - p_1) \left\{ N_1(t) + rN_1(t) \left(1 - \frac{N_1(t)}{k_1}\right) \right\} + p_2 \left\{ N_2(t) + rN_2(t) \left(1 - \frac{N_2(t)}{k_2}\right) \right\} \quad (1a)$$

$$N_2(t + 1) = (1 - p_2) \left\{ N_2(t) + rN_2(t) \left(1 - \frac{N_2(t)}{k_2}\right) \right\} + p_1 \left\{ N_1(t) + rN_1(t) \left(1 - \frac{N_1(t)}{k_1}\right) \right\} \quad (1b)$$

These equations represent the following model: there exist two local populations between which organisms may disperse. The generations are nonoverlapping. The number of offspring produced is related to the initial density for the local population in a logistic fashion. A fraction *p<sub>i</sub>* of the offspring born

disperses to the other local population,  $p_i$  being characteristic of a given local population. There are no deaths during dispersal.

If we assume the system to be in a steady state,

$$N(t+1) = N(t).$$

For such a steady state situation it can be shown that the total population ( $N_1 + N_2$ ) can never exceed the total carrying capacity ( $k_1 + k_2$ ), but can equal it if and only if  $N_1 = k_1$  and  $N_2 = k_2$ , otherwise the total population is less than the sum of  $k_1$  and  $k_2$  and declines as  $k_1$  and  $k_2$  become more and more unequal. Proof of this result is presented in Appendix 1. Computer simulation of the behavior of a similar system, but with the number of local populations greater than two showed that this result holds in general for any number of local populations.

As suggested earlier, we consider it important to verify that these results are not unique to the logistic model. Therefore, we investigated a second model which includes the possibility of deaths during dispersal. This model is represented by the following system of equations:

$$N_1(t+1) = hN_1(t) - \frac{hbN_1^2(t)}{u_1} + hbcN_2^2(t)/u_2 \quad (2a)$$

$$N_2(t+1) = hN_2(t) - hbN_2^2(t)/u_2 + hbcN_1^2(t)/u_1 \quad (2b)$$

This model assumes a constant birth rate ( $h$ ). A fraction of the offspring produced emigrates. This fraction increases with the degree of crowding,  $u$  being some linear function of the carrying capacity of the site. The term ( $hbN^2/u$ ) represents this emigration. A constant fraction ( $1 - c$ ) of the emigrants dies during dispersal; the survivors settle in the other site. It is possible to show that for this system as well the total number maintained at steady state ( $N_1 + N_2$ ) declines as the carrying capacities of the sites become more disparate (see Appendix 2).

*Summary.*—Thus any undercrowding and overcrowding which is very likely to result from dispersal of organisms between different sites will depress the total population size. The extent of such under- and overcrowding will be greater, the greater the variation between the sites. The reduction in the total population size is therefore enhanced with an increase in the variability amongst the sites.

#### *Analogy of temporal variation*

The effects of variation in  $k$  with time on the mean population size are analogous to the effects of variation in  $k$  in space. Let us assume that there is only one population with no emigration and immigration and a logistic population control. Let  $k$  vary with time such that it takes the values  $k(1)$  and  $k(2)$  alternately. At steady state the population size will

take two values,  $N(1)$  and  $N(2)$  at alternate time intervals. Let  $N(1)$  be the population size when  $k$  equals  $k(1)$  and  $N(2)$  when  $k$  equals  $k(2)$ . Then:

$$N(2) = N(1) + rN(1) \left(1 - \frac{N(1)}{k(1)}\right) \quad (3a)$$

$$N(1) = N(2) + rN(2) \left(1 - \frac{N(2)}{k(2)}\right) \quad (3b)$$

This system gives rise to equations identical to those arising from 1a and 1b. Hence it follows that  $N(1) + N(2) \leq k(1) + k(2)$  and  $(N(1) + N(2))$  decreases as  $k(1)$  becomes progressively different from  $k(2)$  (see Appendix 3).

*Summary.*—Increasing variation in  $k$  with time thus depresses the mean population size increasingly below the mean  $k$ . For a more detailed discussion of the effects of variation with time on population size, see Levins (1969a).

#### EVOLUTION OF DISPERSIBILITY

So far we have considered the parameters of dispersibility as being given. We must now investigate how these parameters themselves evolve. Any dispersive stage is very vulnerable to risks of death. Hence, there must be some overriding advantages which favor the tendency to disperse. Any increase in vulnerability to death during dispersal would tend to disfavor dispersibility. Thus, we find that the incidence of dispersive pelagic larval phase decreases in prosobranch mollusks and echinoderms as we pass from the temperate latitudes towards the poles. This has been explained as a result of decrease in the time over which larval food supply persists, rendering the dispersive larval stages more vulnerable (Thorson 1936, 1950).

#### *Crowding and fitness*

In spite of the heavy toll of death exacted during dispersal a very strong tendency to disperse obtains in a large number of groups of plants and animals. In a very general way, the factor favoring dispersal would be the chance of colonizing a site more favorable than the one that is presently inhabited. In the population dynamic formulation, such a more favorable site is defined to be one which is less crowded; i.e. has a lower  $N/k$  ratio than the site presently inhabited. An organism should disperse if the expected gain from the chance of reaching a better site exceeds the expected loss from the risk of death during dispersal or the chance of reaching a poorer habitat. In many cases a mixed strategy of a proportion of organisms staying on in the same habitat, while the rest disperse could be the most advantageous strategy.

#### *The model*

The problem of determining the fittest strategy of dispersal for some species for any specified environ-

mental regime necessitates the investigation of a model complex enough to be tractable only through numerical experiments on a digital computer. Of course, the quantitative predictions of such numerical experiments are of no value, because no precise quantitative estimates of the parameters of the model are available for any natural populations. However, the results of such numerical experiments can suggest qualitative trends. Thus the fittest strategy of dispersal may always change towards higher dispersal rates when the amplitude of fluctuation in the  $k$ 's of the various sites is increased. If such a trend holds without exception in a large number of simulations employing different sets of values for the parameters of the model, it is reasonable to suspect such a trend as being a rather general trend. Further, if one can find an interpretation for the trend in very general terms, one's confidence in the validity of the trend is strengthened.

The model employed is one of competition amongst noninterbreeding types which differ from each other only in their strategy of dispersal, and are identical in all other ways. The equations describing the model are the difference form of competition equations, modified to include dispersal, with all the competition coefficients equalling one. If there are  $q$  habitable sites, and  $m$  competing types, the model is a system of  $m \times q$  difference equations of the following type:

$$N_{ij}(t + 1) = (1 - p_{ij}(t)) \left[ N_{ij}(t) + rN_{ij}(t) \left( 1 - \frac{\sum_{u=1}^m N_{uj}(t)}{k_j(t)} \right) \right] + \sum_{\substack{s=1 \\ s \neq j}}^q p_{is}(t) \cdot z_{sj} \left[ N_{is}(t) + rN_{is}(t) \times \left( \frac{1 - \sum_{u=1}^m N_{us}(t)}{k_s(t)} \right) \right] \quad (4)$$

where the first subscript denotes the type and the second subscript the site for all doubly subscripted variables and where

$N_{ij}(t)$  = population size of  $i$ th type on site  $j$  at time  $t$ .

$p_{ij}(t)$  = fraction of the local population of the  $i$ th type dispersing from site  $j$  at time  $t$ .

$k_j(t)$  = carrying capacity of the site  $j$  at time  $t$ , assumed to be equal for all types at that site for any given time interval.

$z_{sj}$  = fraction of the dispersives leaving site  $s$  which settle on site  $j$ . The value of  $z$  is assumed to be the same for all types and at all times for any pair of sites concerned.

$r$  = intrinsic rate of natural increase, considered to

be the same for all types, over all sites, for all time intervals.

$k$ , the carrying capacity is considered to vary both with site and with time. In general,  $k$  for any site  $j$  was considered to vary in the manner of a sine curve with time.

$$k_j(t) = y_j \cdot [1 + v_j \cdot \sin(\pi(t - \psi_j)/\Theta)] \quad (5)$$

where  $1 \geq v_j \geq 0$  for all  $j$ . Then  $y_j$  specifies the mean carrying capacity, and  $v_j$  the amplitude of variation in  $k_j$  with time.  $\Theta$ , common to all  $k$ 's specifies the frequency of fluctuation in the  $k$ 's.  $\psi_j$  specifies the difference in phase of fluctuations in  $k$ 's for the various sites.

$z_{sj}$  is the fraction of dispersers from site  $s$  reaching site  $j$ . For most simulations  $z_{sj}$  was taken to be  $(1/[q - 1])$  for all  $s$  and  $j$ , where  $s \neq j$ . This implies the assumption of no dispersal deaths and equal distance and accessibility for all the sites. However, other assumptions, e.g.  $z$  a function of distance between sites disposed around a circle were tried out, but led to no differences in the conclusions presented below.

The most crucial part of the model is that pertaining to rates of dispersal. The various types were assumed to differ from each other in this respect. The fraction of the local population of a type dispersing was given by the following expression:

$$p_{ij}(t) = a_i \cdot \left( \frac{\sum_{u=1}^m N_{uj}(t)}{k_j(t)} \right)^{x_i} \quad (6)$$

where  $a_i$  and  $x_i$  are constants characteristic of the type  $i$ . The dispersal response of any type is thus specified by two component parameters:  $a$  is the fraction of the population dispersing at any given degree of crowding and takes values between zero and one. It will be referred to as the magnitude of dispersal.  $x$  specifies the response to crowding. Note that the factor to which  $x$  serves as an exponent in the expression (6) is the degree of crowding as defined before, but now including the local populations of all types at a site. When  $x = 0$ , a constant fraction of the local population disperses. When  $x > 0$  the fraction dispersing increases with crowding. We neglect the case of  $x < 0$ .

The complete equation derived by substituting the equations (5) and (6) for  $k$ 's and  $p$ 's in equation (4) specifies the transition in the size of local population of one type, at one site, from one time interval to the next. For each time transition we thus need ( $m$  $q$ ) such equations to completely specify the system. Given these, and given all the initial values, and the constraint that no population can take negative values, the simulations could be carried over as many time intervals as desirable. We carried out a large number of simulations for various sets of parameter values, initiating them with the local pop-

ulations of each type equal in size over all the sites. As any simulation progressed one of the several competing types increased in population size, while the others gradually decreased. The pattern was quite smooth, with types having values of  $a$  and  $x$  closest to the fittest type decreasing slowly, while those types with values of  $a$  and  $x$  most different from the fittest type decreasing most rapidly. Generally, the simulations were carried over approximately one hundred complete periods of fluctuation in  $k$  with time. By this time, one of the types was clearly displacing all others and the simulation was stopped.

A total of over 100 different simulations were thus carried out, trying out a wide variety of parameter sets. From these simulations a very clear pattern of the relation of fitness of type with certain magnitude of dispersal and certain density response to the environmental regime could be discerned. This is the pattern presented in Table 1.

TABLE 1. Characteristics of the type with superior fitness for different kinds of environmental regimes

		Variability in space	
		Low	High
Variability in time	High	Sensitivity of response low; magnitude of dispersal high	Sensitivity of response medium; magnitude of dispersal medium
	Low	Sensitivity of response medium; magnitude of dispersal medium	Sensitivity of response high; magnitude of dispersal low

I have omitted presenting the numerical results of any simulation as serving no particular purpose, but the mechanism at operation during the simulations leading to the pattern presented in Table 1, is explained in the interpretations of the results which make up the rest of this section.

#### Consequences of dispersal parameters

The rest of this section is devoted to presenting a somewhat informal verbal interpretation of the results presented in Table 1, which themselves were derived rigorously from the simulations explained above. Results of these simulations are essentially explicable on the basis of the role of parameters  $a$  and  $x$  of equation (6) in determining the distribution of a given type in colonies with different degrees of crowding. Let us consider dispersal during one time interval over which the values of  $k$  remain constant. Firstly, let us compare two types with the same value of  $x$ , but different values of  $a$ ,  $a_1$  and  $a_2$  with  $a_1 > a_2$ . Let us for the purpose of all further discussion assume that the various sites differ only in  $k$ . Analogous results would follow if they differed in accessibility or isolation instead. For our particular

TABLE 2. Effect of magnitude of dispersal on the distribution of type amongst more or less crowded sites

Type	Site	1	2	3	
all together	Carrying capacity	300	600	900	
	Population before dispersal	300	600	900	
	$\rho$ before dispersal	1	1	1	
	Population after dispersal	420	600	780	
	$\rho$ after dispersal	1.4	1	0.87	
$1^a$	Before dispersal	Numbers Fraction <sup>b</sup>	100 .17	200 .33	300 .5
	After dispersal	Numbers Fraction <sup>b</sup>	175 .29	200 .33	225 .38
	Before dispersal	Numbers Fraction <sup>b</sup>	100 .17	200 .33	300 .5
	After dispersal	Numbers Fraction <sup>b</sup>	130 .22	200 .33	270 .45
$2^a$	Before dispersal	Numbers Fraction <sup>b</sup>	100 .17	200 .33	300 .5
	After dispersal	Numbers Fraction <sup>b</sup>	130 .22	200 .33	270 .45
	Before dispersal	Numbers Fraction <sup>b</sup>	100 .17	200 .33	300 .5
	After dispersal	Numbers Fraction <sup>b</sup>	115 .19	200 .33	285 .48

<sup>a</sup> $a=0$  for type 1, 0.2 for type 2, 0.1 for type 3,  $x=0$  for all three types. The distributions shown represent the outcome of a single dispersal episode, uncomplicated by births and deaths.

<sup>b</sup>Fraction of the total population of a given type on that site. Dispersives distribute themselves equally amongst the other two sites.

model the lower  $k$  sites should become more crowded compared to higher  $k$  sites as a result of dispersal. For a given distribution of  $k$  over the sites, this effect will be more pronounced for  $a_1$  than  $a_2$ . The high  $k$  sites become less crowded because they send off relatively more emigrants than they receive immigrants. Since a higher  $a$  implies greater proportions being sent off from each local population, this over- and undercrowding of the various sites is more pronounced. When  $a$  is very low, very few emigrate and the numerical changes through dispersal are quite small. Hence the over- and undercrowding following dispersal will also be very small. A more pronounced overcrowding of low  $k$  sites and undercrowding of high  $k$  sites implies a greater proportion of the population in more crowded sites and a smaller proportion in less crowded sites.

*Summary.*—Therefore a greater magnitude of dispersal leads to a greater proportion of the total population occupying more crowded sites provided that  $k$ 's have remained unchanged. (See Table 2.)

The effect of higher values of  $x$ , i.e. more sensitive density response is quite the opposite for small values of  $x$ . A more sensitive response implies emigrating in larger proportions with increasing crowding. This can then serve as a corrective response leading to equitable crowding. Very high values of  $x$  can lead to tremendous emigrations with even slight overcrowding and produce instabilities. We will deal only with the range of moderate values of  $x$  from zero to two. Over this range a higher  $x$  type ends with greater

TABLE 3. Effect of the sensitivity to density response on the distribution of the population of a type amongst more or less crowded sites

Type	Site	1	2	3	
A together	Carrying capacity	100	200	300	
	Population before dispersal	160	200	240	
	$\rho$ before dispersal	1.6	1	0.8	
	Population after dispersal	160	206	234	
	$\rho$ after dispersal	1.6	1.03	0.78	
1 <sup>a</sup>	Before dispersal	Numbers Fraction <sup>b</sup>	80 .27	100 .33	120 .4
	After dispersal	Numbers Fraction <sup>b</sup>	95 .32	100 .33	105 .35
	Before dispersal	Numbers Fraction <sup>b</sup>	80 .27	100 .33	120 .4
	After dispersal	Numbers Fraction <sup>b</sup>	65 .22	106 .35	129 .43

<sup>a</sup>The distributions shown represent the outcome of a single dispersal episode uncomplicated by births and deaths.  $a = 0.5$  for both types 1 and 2.  $x = 0$  for type 1 and  $x = 1$  for type 2.

<sup>b</sup>Fraction of the total population of a given type on that site. Dispersives distribute themselves equally amongst the other two colonies.

tendency to stay put in undercrowded and leave overcrowded environments.

*Summary.*—Hence a more sensitive density response leads to a greater proportion of the total population occupying less crowded sites, provided that  $k$ 's have remained unchanged. (See Table 3.)

*Environment constant with time*

As suggested above, a greater proportion of the population occupying more crowded sites will imply a lowering of fitness for that type. This is the result of higher values of  $a$  and lower values of  $x$  for a type, provided that  $k$ 's remain unchanged. The overcrowding of certain sites, and undercrowding of others is enhanced by an increase in the variation in values of  $k$  for different sites. Hence the fitness of higher  $a$  and lower  $x$  types will be more drastically lowered as the variation in  $k$  amongst the sites increases. These conclusions were supported by the results of simulations.

*Summary.*—Hence, selective forces will always favor a low magnitude of dispersal, but a more sensitive density response in an environment constant with time. These selective forces will be accentuated as the environment, constant in time, becomes more variable in space.

*Variation with time in phase*

The pattern is entirely different when variations in  $k$ 's of different sites with time are taken into consideration. With an environment variable in time, a site which is very overcrowded in this time interval may have its  $k$  markedly increased, and become a very undercrowded site. On the other hand, a site which is quite undercrowded may have its  $k$  markedly

decreased and become overcrowded. This will, however, not be the case if the  $k$ 's for various colonies change in time, but completely in phase with each other. In that case, all the sites may become more or less crowded than previously but the relative degrees of crowding amongst the colonies will be maintained. In this case, the type which has the tendency to maintain a greater proportion of its total population in more crowded environments will continue to do so and will be selected against. This conclusion was supported by simulations.

*Summary.*—Therefore, selective forces will always favor a low magnitude of dispersal, but a more sensitive density response in an environment which varies with time, but completely in phase over its entire spatial range. These selective pressures will, as for environment constant in time, be accentuated as the environment becomes more variable in space at any given time.

*Variation with time out of phase*

If, on the other hand the variation in  $k$  with time is out of phase with each other for the various sites, different results follow. In that case there are excellent chances of a site which is undercrowded at this time interval becoming overcrowded at the next, and a site which is overcrowded at this time interval becoming undercrowded at the next. By dispersing an organism can gain in the former eventuality and lose in the latter. Since the fitness of an individual is greater in the undercrowded colony, there is apt to be more gain from going away from an undercrowded site of this time to another site, which, though overcrowded now, may become undercrowded the next time. The exact magnitude of this gain will depend on the phase difference and the extent of the variation of  $k$  between the different sites. The only point to be made is that selective forces may favor dispersibility, in contrast to environments constant with time.

The degree of crowding in this time interval may be correlated with crowding in the next time interval sometimes negatively and sometimes positively in a time-dependent environment. There may therefore be no overall gain from a sensitive density response prompting the organism to leave an overcrowded environment more rapidly. The exact balance will of course depend on the precise regime of the phase difference in and the extent of variation of  $k$  with time. The results from the simulations agree with the expectation suggested above.

*Summary.*—For a given distribution of mean  $k$ 's (i.e. given  $y$ 's) for various colonies and for given phase differences in the variation of  $k$  with time, selective pressures favor an increasing magnitude of dispersal and a decreasing sensitivity of density response with an increase in the extent of variation



in  $k$  with time (i.e. higher  $v$ 's). Also, for a given regime of variation in  $k$  with time (i.e. given  $v$ 's), selective pressures favor a decreasing magnitude of dispersal and a more sensitive density response with an increase in the variability of mean  $k$ 's (higher variance of  $v$ 's) for the various colonies. (See Table 1.)

Many naturalists have intuited (e.g. Southwood 1962) and Cohen (1967) has formally proven that an increase in the variability of  $k$  with time will favor a higher magnitude of dispersal. Brown (1951) has obtained excellent field evidence for this, showing that the corixid water bugs of temporary water bodies are much more dispersible than those belonging to more permanent water bodies.

#### TESTS FOR NEW PREDICTIONS

The present study has led to five new conclusions pertaining to dispersal:

- (1) Variation in the carrying capacities of the various sites in time and space reduces the total population size.
- (2) An episode of dispersal results in more uneven crowding at the various sites.
- (3) A species which inhabits sites more variable in their carrying capacities will tend to have a lower dispersibility in terms of the proportion of the local population at a site which emigrates during a time interval.
- (4) Such a species which inhabits sites more variable in their carrying capacities will have a more sensitive density response in dispersal; i.e. the proportion of local population emigrating will rise more rapidly with increase in crowding.
- (5) A species inhabiting an environment more variable in time will have a less sensitive density response in dispersal.

It should be possible to test these conclusions either experimentally or in the field. Huffaker's (1958) experimental setup with the oranges, rubber balls and mites should be ideal for testing the first two conclusions. Quantitative field studies of spatial distribution of organisms have been very few indeed; the first two conclusions could provide concrete, testable hypotheses for such future studies. The most suitable subjects for such studies would probably be provided by inhabitants of disjunct habitat islands such as freshwater ponds. Conclusions (3) and (4) could be approached by a comparison of contrasting species, some of which colonize habitat islands over a more restricted size range of habitats than others. Thus there may be groups of aquatic insects or molluscs with some species restricted to only small or large ponds and other species occurring over the entire size range of ponds. The latter kind of species would be expected to be less dispersible in terms of propor-

tion emigrating, but more sensitive in their density response. The sensitivity of density response could be compared for species inhabiting more or less permanent habitats in order to test the fifth conclusion. It will be necessary to collect data on rates of immigration and emigration for a number of colonies of a given species to arrive at any valid inferences about the density response, though much more incomplete data could allow interesting conclusions about the magnitude of dispersal (e.g. Brown 1951). The variance of rates of emigration for a number of local populations of a given species will increase with the sensitivity of the density response of that species and this statistic can be used to compare various species. More elaborate experiments including artificial manipulation of densities will be necessary to specify the form of the density response in greater detail.

#### ACKNOWLEDGMENTS

I had stimulating discussions with W. H. Bossert, S. Gadgil, J. Roughgarden, and E. O. Wilson while the ideas presented in this paper were being developed. A first version of this paper was read by W. H. Bossert, R. Levins, R. H. MacArthur, I. C. T. Nisbet, J. Roughgarden, T. W. Schoener, M. Slatkin and E. O. Wilson, and their comments have considerably improved it. The editor made a number of valuable suggestions. This research was supported by a grant from the Milton Fund of Harvard University.

#### LITERATURE CITED

- Brown, E. S. 1951. The relation between migration rate and type of habitat in aquatic insects, with special reference to certain species of Corixidae. *Proc. Zool. Soc. Lond.* **121**: 529-545.
- Cohen, D. 1967. Optimization of seasonal migratory behaviour. *Amer. Naturalist* **101**: 1-17.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**: 343-383.
- Johnson, C. G. 1969. Migration and dispersal of insects by flight. London. Methuen and Co. 763 p.
- Levins, R. 1969a. The effect of random variations of different types on population growth. *Proc. Nat. Acad. Sci.* **62**: 1061-1065.
- . 1969b. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Amer.* **15**: 237-240.
- . 1970. Extinction. *In Mathematics in biology.* Amer. Math. Soc.
- Lidicker, W. Z. 1962. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. *Amer. Naturalist* **96**: 29-34.
- Moran, P. A. P. 1962. The statistical processes of evolutionary theory. Oxford. Clarendon. 200 p.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**: 196-218.
- Southwood, T. R. E. 1962. Migration of terrestrial arthropods in relation to habitat. *Biol. Rev.* **37**: 171-214.
- Thorson, G. 1936. The larval development, growth and metabolism of marine bottom invertebrates. *Medd. Gronland.* **100**: 1-155.
- . 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25**: 1-45.

APPENDIX 1

For steady state, addition and subtraction of the equations 1a and 1b yields

$$N_1 \left(1 - \frac{N_1}{k_1}\right) + N_2 \left(1 - \frac{N_2}{k_2}\right) = 0 \quad (1c)$$

and

$$r(1 - 2p_1)N_1 \left(1 - \frac{N_1}{k_1}\right) - r(1 - 2p_2)N_2 \left(1 - \frac{N_2}{k_2}\right) + 2(p_2N_2 - p_1N_1) = 0 \quad (1d)$$

Equation 1c can be solved to give  $N_2$  in terms of  $N_1$ .

$$N_2 = \frac{k_2 + [k_2^2 + 4N_1k_2(1 - N_1/k_1)]^{\frac{1}{2}}}{2} \quad (1e)$$

where only the positive root for  $N_2$  has been retained.

Using (1e)

$$(k_1 + k_2) - (N_1 + N_2) = \frac{1}{2} \left( [2(k_1 - N_1) + k_2] - [k_2^2 + 4k_2N_1(1 - N_1/k_1)]^{\frac{1}{2}} \right) \quad (1f)$$

Note that the term  $2(k_1 - N_1) + k_2$  can be expressed in terms of the quantity under the square root as

$$[2(k_1 - N_1) + k_2] = \left[ k_2^2 + 4k_2N_1 \left(1 - \frac{N_1}{k_1}\right) + 4(k_1 - N_1)^2 \left(1 + \frac{k_2}{k_1}\right) \right]^{\frac{1}{2}} \quad (1g)$$

This implies that  $(k_1 + k_2) - (N_1 + N_2)$  cannot be negative since the first term in (1f) either exceeds or equals the second. Moreover, from (1g) the two terms are equal only if  $N_1 = k_1$  which also implies  $N_2 = k_2$  from (1f). Thus the total population  $(N_1 + N_2)$  is less than or equal to the total carrying capacity  $(k_1 + k_2)$ . The point at which it equals  $(k_1 + k_2)$  is given by  $N_1 = k_1, N_2 = k_2$ . This point  $N_1 = k_1, N_2 = k_2$  is a solution of the set (1c, 1d) if  $p_1k_1 = p_2k_2$ . Any departure from this set of  $p_{1,2}, k_{1,2}$  will depress the total population below the value  $(k_1 + k_2)$ .

APPENDIX 2

At steady state, the equations 2a, 2b have the following solution for the case  $u_1 = u_2$

$$N_1 = N_2 = \frac{u_1(h-1)}{(1-c)hb} \quad (2c)$$

Let  $(u_1 + u_2)$  be constant. Then the change in total population  $(N_1 + N_2)$  produced by changing  $u_1$  from this value of  $(u_1 + u_2)/2$  is given at the point (2c) by

$$(1-h) \left[ \frac{\partial(N_1 + N_2)}{\partial u_1} \right] = (1-c) \left( \frac{N_2^2}{u_2} - \frac{N_1^2}{u_1} \right) = 0$$

Therefore the value  $u_1 = u_2$  is an extremum for  $N_1 + N_2$ . Evaluating the second derivative at this point

$$\left[ \frac{\partial^2(N_1 + N_2)}{\partial u_1^2} \right] = \frac{-4}{N_1 u_1} \left[ \frac{\partial N_1}{\partial u_1} - \frac{N_1}{u_1} \right]^2$$

which is always negative. Thus  $(N_1 + N_2)$  is maximum at  $u_1 = u_2$  and any departure from this causes a depression in the total population.

APPENDIX 3

At steady state, the equations 3a, 3b have the solution:

$$N(1) = N(2) = k(1) = k(2) \quad (3c)$$

for the case  $k(1) = k(2)$ .

Let  $[k(1) + k(2)]$  be constant. Then

$$\frac{\partial[N(1) + N(2)]}{\partial k(1)} = \frac{2 \cdot N(1)}{k(1)} \cdot \frac{\partial N(1)}{\partial k(1)} + \frac{2 \cdot N(2)}{k(2)} \frac{\partial N(2)}{\partial k(1)} - \left[ \frac{N(1)^2}{k(1)^2} - \frac{N(2)^2}{k(2)^2} \right] \quad (3d)$$

At the point of equilibrium (3c) the above reduces to:

$$\frac{\partial[N(1) + N(2)]}{\partial k(1)} = \frac{N(1)^2}{k(1)^2} - \frac{N(2)^2}{k(1)^2} \Big|_{N(1)=N(2)} = 0$$

Hence this point is an extremum of the sum  $[N(1) + N(2)]$  regarded as a function of  $k(1)$  where  $[k(1) + k(2)]$  is constant. Further differentiation of (3d) yields:

$$\frac{\partial^2 [N(1) + N(2)]}{\partial k(1)^2} = \frac{-2}{k(1)} \left[ \frac{\partial N(1)}{\partial k(1)} - 1 \right]^2 - \frac{2}{k(1)} \left[ \frac{\partial N(2)}{\partial k(1)} - 1 \right]^2 < 0$$

Therefore,  $[N(1) + N(2)]$  is maximum at  $k(1) = k(2)$  and any departure from this causes a depression in the mean population.