

Optimal Rates of Dispersal I. Haploid Populations

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Received December 12, 1978

The problem of how an individual should divide its progeny into dispersed and non-dispersed descendants is investigated for a number of haploid models. In each model, a unique optimal ratio of dispersed to non-dispersed has been found, where the type with this optimal strategy has a selective advantage over all other types. Although the survival ability of a dispersed offspring is reduced (compared to that of a non-dispersed offspring), the optimal strategy implies that a substantial part of the progeny will be dispersed.

1. INTRODUCTION

Many organisms have special devices adapted for proper dispersal of their progeny. Usually the dispersal mechanisms are morphological, but in the animal kingdom, behavioral patterns, such as hierarchy and territorial behavior, are also common dispersal means (see e.g. Christian, 1970).

The varied dispersal mechanism guarantees that only part of the progeny will remain near the parent, while the rest will be scattered away and compete for other living sites.

It is interesting to note that in many species, division between those progeny which remain near the parent and those which are dispersed is made in advance. There are plants which produce two kinds of fruits or seeds (heterocarpy)—one kind possessing a dispersal apparatus and the other lacking such a device. In other plants (amphicarpous), the above-mentioned division is made by producing some of the fruit below the ground, the seeds of which sprout near the parent, and the others above the ground, the seeds being easily dispersed. A similar phenomenon is exhibited by basicarpous plants, in which some of the fruit are produced close to the ground, while others grow higher on the plant, thus scattering the seeds over a wider

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distance. In many plants, and also in animals, vegetative and sexual reproduction are combined; usually the offspring produced by vegetative reproduction remain near the parent, while those reproduced sexually are scattered away. More detailed descriptions and examples can be found in the botanical and in the zoological literature.

The present work is concerned with the ratio between that part of the progeny which remains near the parent and that part which disperses. An interesting question here is whether such a ratio has an optimal value and, if so, is this optimal ratio unique, and which value does it assume. Assuming that the dispersal rate is genetically determined, it is demonstrated that in each of the various models treated, there exists a single optimal ratio, and the type possessing this optimal ratio has a selective advantage over all other types resembling it in all other respects.

It is worth clarifying what we mean by an "optimal" characteristic. In this work we are not concerned with traits which are of value to the existence of the population as a whole but rather traits which endow their owner with a selective advantage over other types. The existence of a single optimum in this respect means that the type possessing the optimal characteristic has the best chance of winning the struggle for survival, but this does not necessarily mean that the chances of survival of the entire population are maximized.

The present paper deals with models of haploid populations. Diploid populations will be dealt with in later papers—one paper in which the proportion of the progeny which disperses is determined by the parent's genotype (Motro, 1982a) and another in which the probability of an offspring to migrate is determined by the genotype of the offspring itself (Motro, 1982b).

Hamilton and May (1977) considered the same question of optimal rate of dispersal and examined it in several situations which are also treated in this paper (Sections 2 and 4) and in Motro (1982b). Their approach to the problem was to use evolutionarily stable strategy (ESS) arguments, whereas the attempt here and in the following papers is to develop more traditional-type models, based on changes in gene frequencies.

2. THE SIMPLE HAPLOID MODEL

In this, and in the following sections, we investigate the optimal dispersal rate for various models of haploid populations. The models vary in some of their assumptions, but in each case we assume that the dispersed descendants suffer a greater mortality than those which are not dispersed.

The assumptions of the model of this section, the simple haploid model, are as follows.

(1) We consider an infinite population of haploid organisms, in which each individual has the same expected number (μ) of descendants (or seeds). A fraction $1 - \alpha$ ($0 \leq \alpha \leq 1$) of the progeny remains near the parent, whereas a fraction α is scattered uniformly across the entire population range. The number α , the dispersal rate, is assumed to be genetically determined at a single locus.

(2) Generations are discrete and non-overlapping. At the end of each season, the previous generation is eliminated, and each site is reoccupied by a single individual.

(3) The successor at a site is chosen at random from among all the young individuals at that place, which consist of the non-dispersed descendants of the previous occupant, or the immigrant descendants of other individuals of the previous generation.

(4) Due to extra expenditure of energy and other risks concomitant to dispersal, the probability of acquiring a site is assumed to be less for a dispersed offspring than for a non-dispersed one. Thus, the probability of a dispersed descendant to attain the state of competition on a living site is only a fraction β ($0 < \beta \leq 1$) of that probability for a sessile descendant. A reduced β signifies that more stringent environmental conditions are endured by the dispersed descendants.

Under these assumptions, we establish the existence of an optimal dispersal rate, which will be fixed in the population.

In order to find the optimal rate of dispersal, we consider a population consisting of two types, characterized by their intrinsic dispersal rates: Type *A* has a fraction α_1 of its progeny that disperses and a fraction $1 - \alpha_1$ that does not depart the parental site, while for Type *B*, the corresponding fractions are α_2 and $1 - \alpha_2$, respectively.

If p ($0 \leq p \leq 1$) is the frequency of Type *A* in the population and q ($q = 1 - p$) the frequency of *B*, then the expected number of immigrating descendants per living site is $\lambda = \mu\beta(\alpha_1 p + \alpha_2 q)$, where $1 - \beta$ is the proportion lost during dispersal. The expected number of *A*'s among the immigrants is $\mu\beta\alpha_1 p$ and the corresponding expected number of *B*'s is $\mu\beta\alpha_2 q$. These assumptions and consequences are summarized in Table 1.

The frequency of Type *A* in the next generation is

$$p' = pP_{AA} + qP_{BA},$$

where P_{ij} is the probability that a Type *i* individual will be replaced, in the next generation, by a Type *j* individual. (Note that $P_{AB} \neq P_{BA}$.)

Assuming a large number of seeds per site and random sampling, we have

$$p' = p \frac{\mu(1 - \alpha_1) + \mu\beta\alpha_1 p}{\mu(1 - \alpha_1) + \lambda} + q \frac{\mu\beta\alpha_1 p}{\mu(1 - \alpha_2) + \lambda}.$$

TABLE 1
The Simple Haploid Model

	Type A Site	Type B Site
Frequency	p	q
Mean progeny size	μ	μ
Fraction of progeny dispersed	α_1	α_2
Expected number of descendants which remain near the parent	$\mu(1 - \alpha_1)$	$\mu(1 - \alpha_2)$
Expected number of A's among immigrants	$\mu\beta\alpha_1 p$	$\mu\beta\alpha_1 p$
Expected number of B's among immigrants	$\mu\beta\alpha_2 q$	$\mu\beta\alpha_2 q$
Expected total number of immigrants per site	$\lambda = \mu\beta(\alpha_1 p + \alpha_2 q)$	$\lambda = \mu\beta(\alpha_1 p + \alpha_2 q)$
Expected number of A's among competing young	$\mu(1 - \alpha_1) + \mu\beta\alpha_1 p$	$\mu\beta\alpha_1 p$
Expected number of B's among competing young	$\mu\beta\alpha_2 q$	$\mu(1 - \alpha_2) + \mu\beta\alpha_2 q$
Expected total number of competing young per site	$\mu(1 - \alpha_1) + \lambda$	$\mu(1 - \alpha_2) + \lambda$

After some algebraic manipulations, we obtain

$$\Delta p = p' - p = \frac{\mu^2 \beta^2 p q (\alpha_1 - \alpha_2)^2 (p - \bar{p})}{[\mu(1 - \alpha_1) + \lambda][\mu(1 - \alpha_2) + \lambda]}, \quad (1)$$

where $\bar{p} = (1 - \alpha_1 - (1 - \beta)\alpha_2)/\beta(\alpha_2 - \alpha_1)$.

The equilibrium points are determined by solving the third degree polynomial $\Delta p = 0$. There always exist two fixation equilibria $p = 0$ and $p = 1$, and if \bar{p} falls between 0 and 1, then \bar{p} is a third equilibrium point.

From Eq. (1) it follows that if $\bar{p} \leq 0$, then $\Delta p > 0$ for every p ($0 < p < 1$), which entails a global fixation of Type A; if $\bar{p} \geq 1$, then $\Delta p < 0$ for every p ($0 < p < 1$), implying global fixation of Type B; and if $0 < \bar{p} < 1$, then $\Delta p > 0$ for p exceeding \bar{p} and $\Delta p < 0$ for p less than \bar{p} .

The results are graphically summarized in Fig. 1.

In view of the dynamics described above, we define:

- (1) A dispersal rate α_1 (for Type A) is *better* than α_2 (the dispersal rate for Type B), if for every p ($0 < p < 1$) Type A is fixed in the population.
- (2) α_1 is the *optimal* rate of dispersal, if it is *better* than any $\alpha \neq \alpha_1$.

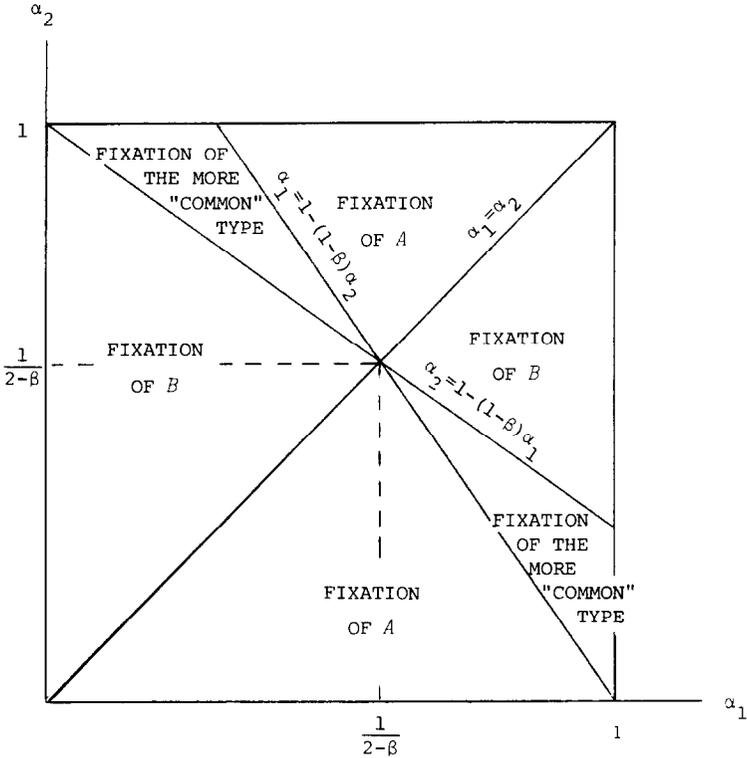


FIG. 1. The simple haploid model. On the line $\alpha_1 = 1 - (1 - \beta)\alpha_2$, except for the point $(1/(2 - \beta), 1/(2 - \beta))$, $\bar{p} = 0$. On the line $\alpha_2 = 1 - (1 - \beta)\alpha_1$, except for the point $(1/(2 - \beta), 1/(2 - \beta))$, $\bar{p} = 1$.

Set $\alpha^* = 1/(2 - \beta)$. We have proved

THEOREM. Each $\alpha_1 \neq \alpha^* = 1/(2 - \beta)$ determines an interval I (containing α^* on its interior and having α_1 as an open end bound), such that each α in I is better than α_1 , and also determines an interval J (containing I), such that if $\alpha \notin J$, then α_1 is better than α . (For $\alpha \in J - I$, the allele fixed in the population depends on the initial frequency p_0 .)

When $\alpha_1 = \alpha^*$, then I is an empty set and J reduces to the single point α^* , implying that $\alpha^* = 1/(2 - \beta)$ is the optimal rate of dispersal. ■

What are the intervals I and J ?

If $\alpha_1 < \beta$, then $I = (\alpha_1, 1 - (1 - \beta)\alpha_1]$ and $J = [\alpha_1, 1]$.

If $\beta \leq \alpha_1 < \alpha^*$, then $I = (\alpha_1, 1 - (1 - \beta)\alpha_1]$ and $J = [\alpha_1, (1 - \alpha_1)/(1 - \beta))$,

And, if $\alpha^* < \alpha_1$, then $I = [1 - (1 - \beta)\alpha_1, \alpha_1)$ and $J = ((1 - \alpha_1)/(1 - \beta), \alpha_1]$. (See Fig. 1.)

Thus, the type with the strategy $\alpha^* = 1/(2 - \beta)$ (i.e., which disperses a fraction $1/(2 - \beta)$ of its progeny) carries a selective advantage over all types following other dispersal strategies.

$\alpha^* = 1/(2 - \beta)$ is an increasing function of β ($0 < \beta \leq 1$), $\alpha^*(1) = 1$, and $\lim_{\beta \rightarrow 0} \alpha^*(\beta) = \frac{1}{2}$. Thus, the more stringent the ecological conditions for the dispersed descendants (relative to the conditions encountered by the non-dispersed ones), the smaller the optimal rate of dispersal, yet even if environmental conditions are very harsh (β is small), the optimal strategy is still to scatter more than half of the progeny ($\alpha^* \geq \frac{1}{2}$).

Remarks. (1) In the above model we have assumed equal investment in the production of a dispersed and of a non-dispersed descendant. The results obtained are also valid for more general situations, if we ascribe to the parameters μ , α , and β the following interpretations.

μ : The expected magnitude of reproductive investment of an individual.

α and $1 - \alpha$: The fractions of the reproductive investment in producing dispersed and non-dispersed descendants, respectively.

β : The fraction of a unit of reproductive investment which, if invested in non-dispersed descendants, is equivalent (from the viewpoint of the chances to occupy a site the following season) to a unit invested in producing dispersed descendants.

(2) The results obtained above are also valid for a certain type of perennial population. Suppose following reproduction, the parent continues to live with probability γ ($0 < \gamma < 1$). In this case, $\hat{P}_{AA} = \gamma + (1 - \gamma)P_{AA}$ and $\hat{P}_{BA} = (1 - \gamma)P_{BA}$. Hence $\hat{\Delta}p = (1 - \gamma)\Delta p$, which yields the same evolutionary realization as for annual populations, only the rates of change in gene frequencies are diminished.

3. THE OPTIMAL DISPERSAL RATE UNDER CONDITIONS OF TEMPORALLY VARYING ENVIRONMENT

Many studies have investigated the distribution of gene frequencies in a population exposed to a temporally varying environment. Some authors have considered the effect of varying selection parameters on infinite populations (e.g., Kimura, 1954; Haldane and Jayakar, 1963; Gillespie, 1973; Hartl and Cook, 1973; Karlin and Lieberman, 1974). Models which include sampling variations due to a finite population size, as well as temporal variations in selection intensities, were treated by Ohta (1972), Jensen (1973), Karlin and Levikson (1974), and others.

In this section we investigate the optimal rate of dispersal in an infinite

haploid population, where the survival ability of a dispersed descendant changes randomly from generation to generation. More specifically, β (of Section 2) is a random variable (having a distribution $F(\beta)$). In each generation, a value of β is sampled from the distribution $F(\beta)$, and this value indicates the probability of a dispersed descendant to withstand the dispersal hazards. We assume that the values of β in successive generations are uncorrelated. Except for the variability of β , the other assumptions of the present model are identical to those of the model in Section 2.

In the varying environment model, the optimal rate of dispersal is defined as that unique rate which will become fixed (with probability 1). Provided that the expectation of the (random) change in type frequency exists (for every α_1 and α_2 in $[0, 1]$), we show (in Appendix 1) that there exists a unique rate α^* , such that the type having α^* as its dispersal rate will be fixed in the population (with probability 1). Thus, according to the above definition, α^* is the optimal rate of dispersal.

4. UNOCCUPIED LIVING SITES

This section examines the existence of an optimal dispersal rate in a model in which there is the possibility of potential sites to stay vacant after their occupant's death. Whereas in the previous models each living site was reoccupied in the following generation, in the present model each young individual (or seed) has a positive probability u ($0 < u < 1$) of failing to mature (or sprout). Hence an occupied site is effectively vacant in the next generation if all the descendants that compete for this place (either non-dispersed or immigrants) are not viable.

Apart from the possibility of vacancies, all other assumptions of the present model are the same as those of the simple haploid model of Section 2.

In the first part of this section we develop conditions for the survival of a population. We assume that the number of competitors per site has a Poisson distribution. Let r ($0 \leq r \leq 1$) be the fraction of vacant sites ($1 - r$, the fraction of those occupied). Employing the same notation as in the previous sections, the expected number of competitors on a previously vacant site is $\lambda = \mu\beta\alpha(1 - r)$, and that for a previously occupied site is $\mu(1 - \alpha) + \lambda$. Again, μ is the average progeny size of an individual, α ($0 \leq \alpha \leq 1$) the fraction of the progeny scattered, and β ($0 < \beta \leq 1$) the probability that a dispersed offspring will reach a state of competition on a living site, relative to that of a non-dispersed one.

The frequency of vacancies in the next generation is

$$r' = re^{-\lambda(1-u)} + (1-r)e^{-[\mu(1-\alpha)+\lambda](1-u)}.$$

In order to determine the fixed points of this transformation, we examine the equation $r' = r$. The function $f(r) = re^{-\lambda(1-u)} + (1-r)e^{-(\mu(1-\alpha)+\lambda)(1-u)}$ is an increasing and convex function of r over the interval $0 \leq r \leq 1$; also, $f(0) = e^{-\mu(1-\alpha+\beta\alpha)(1-u)} > 0$, $f(1) = 1$ and $f'(1) = 1 + \mu\beta\alpha(1-u) - e^{-\mu(1-\alpha)(1-u)}$.

The equation $r' = r$ is always satisfied for $r = 1$. It has an additional solution (\tilde{r}) in the interval $0 < r < 1$ if, and only if, $f'(1) > 1$, or, equivalently, if and only if

$$\mu\beta\alpha(1-u) - e^{-\mu(1-\alpha)(1-u)} > 0. \quad (2)$$

The function $g(\alpha) = \mu\beta\alpha(1-u) - e^{-\mu(1-\alpha)(1-u)}$ exhibits an absolute maximum of value $\beta[\mu(1-u) + \ln \beta - 1]$ at $\alpha = 1 + (\ln \beta / \mu(1-u))$. It follows that only when $\ln \beta > 1 - \mu(1-u)$ does there exist an open interval, containing $1 + (\ln \beta / \mu(1-u))$ on its interior, such that for each α in this interval, inequality (2) holds. If α lies in this interval, then $r = \tilde{r}$ is the exclusive stable equilibrium. Otherwise, $r = 1$ is the only equilibrium point.

To sum up, a necessary and sufficient condition for the survival of the population is (1) $\ln \beta > 1 - \mu(1-u)$, and (2) α is "close enough" to $1 + (\ln \beta / \mu(1-u))$ (i.e., α is in the above-mentioned interval, in which inequality (2) holds).

In the remaining part of this section we investigate the existence of an optimal dispersal rate. In fact, there exists a single dispersal rate which is stable against any mutant strategy; this rate is defined as the optimal rate of dispersal for the present model.

To prove the foregoing assertion, we again distinguish two types, characterized by their dispersal fractions: Type *A*, with fraction α_1 of its progeny that is dispersed, and Type *B*, with dispersal fraction α_2 . Let p be the proportion of living sites that are occupied by Type *A* individuals, q the proportion occupied by *B*'s, and r ($p + q + r = 1$) the proportion of vacant sites. The proportions in the next generation are

$$(p', q', r') = (p, q, r) \begin{bmatrix} P_{AA} & P_{AB} & P_{A0} \\ P_{BA} & P_{BB} & P_{B0} \\ P_{0A} & P_{0B} & P_{00} \end{bmatrix},$$

where

$$P_{AA} = (1 - P_{A0}) \frac{\mu(1 - \alpha_1) + \mu\beta\alpha_1 p}{\mu(1 - \alpha_1) + \lambda}, \quad P_{AB} = (1 - P_{A0}) \frac{\mu\beta\alpha_2 q}{\mu(1 - \alpha_1) + \lambda}$$

$$P_{A0} = e^{-[\mu(1 - \alpha_1) + \lambda](1 - u)}$$

$$\begin{aligned}
 P_{BA} &= (1 - p_{B0}) \frac{\mu\beta\alpha_1 p}{\mu(1 + \alpha_2) + \lambda}, & P_{BB} &= (1 - p_{B0}) \frac{\mu(1 - \alpha_2) + \mu\beta\alpha_2 q}{\mu(1 - \alpha_2) + \lambda} \\
 P_{B0} &= e^{-[\mu(1 - \alpha_2) + \lambda](1 - u)} \\
 P_{0A} &= (1 - p_{00}) \frac{\mu\beta\alpha_1 p}{\lambda}, & P_{0B} &= (1 - p_{00}) \frac{\mu\beta\alpha_2 q}{\lambda} \\
 P_{00} &= e^{-\lambda(1 - u)}
 \end{aligned}$$

and $\lambda = \mu\beta(\alpha_1 p + \alpha_2 q)$.

The equilibrium points are as follows.

There always exists the trivial (extinction) equilibrium state $(p, q, r) = (0, 0, 1)$. A monomorphic equilibrium $(\tilde{p}, 0, \tilde{r})$ exists if, and only if, $\mu\beta\alpha_1(1 - u) - \exp\{-\mu(1 - \alpha_1)(1 - u)\} > 0$. Similarly, a necessary and sufficient condition for the existence of the other monomorphic equilibrium $(0, \tilde{q}, \tilde{r})$ is $\mu\beta\alpha_2(1 - u) - \exp\{-\mu(1 - \alpha_2)(1 - u)\} > 0$. The stability conditions of these equilibria are determined in Appendix 2.

The optimal rate of dispersal in this model is defined to be the rate α^+ for which the monomorphic equilibrium of its possessor exists and is stable against any mutant. By the analysis of Appendix 2, we have numerically searched for an optimal α for various values of β and $\mu(1 - u)$. The results are presented in Table 2.

The numerical results suggest that

- (1) the optimal rate of dispersal (α^+) increases with β ,
- (2) \tilde{p} (the proportion of sites occupied by the α^+ type in the steady state) increases with β and with $\mu(1 - u)$.
- (3) In each case, α^+ is smaller than $\alpha^* = 1/(2 - \beta)$, which we recall is the optimal rate of dispersal in the simple haploid model (in which all the potential sites are constantly occupied).

(4) In each case, α^+ is larger than $\hat{\alpha}$ (the maximum-occupancy strategy) and, of course, \tilde{p} is smaller than \hat{p} , which means that the optimal α , in the sense in which we are concerned (stability of the monomorphic equilibrium against any mutant), is not identical with the α for which the population assumes its greatest size. In other words, the optimal type pays for its intraspecies success in that it cannot exploit the environmental conditions in the most efficient way. Thus we encounter here an example of a trait which is advantageous for the individual carrying it, but not necessarily beneficial to the population as a whole. This result is in qualitative agreement with the findings of Hamilton and May (1977), Comins *et al.* (1980), and Roff (1975).

TABLE 2
Numerical Results for the Unoccupied Living Sites Model^a

β	$\mu(1-u)$				The simple haploid model (no vacancies)
	1.25	1.50	2.20	3.00	
0.20	—	—	—	$\alpha^+ = 0.381$ ($\hat{a} = 0.346$) $\bar{p} = 0.343$ ($\hat{p} = 0.347$)	$\alpha^+ = 0.556$ $\bar{p} = 1.000$
0.37	—	—	$\alpha^+ = 0.498$ ($\hat{a} = 0.474$) $\bar{p} = 0.218$ ($\hat{p} = 0.219$)	$\alpha^+ = 0.503$ ($\hat{a} = 0.384$) $\bar{p} = 0.667$ ($\hat{p} = 0.681$)	$\alpha^+ = 0.613$ $\bar{p} = 1.000$
0.63	—	$\alpha^+ = 0.683$ ($\hat{a} = 0.678$) $\bar{p} = 0.053$ ($\hat{p} = 0.054$)	$\alpha^+ = 0.674$ ($\hat{a} = 0.576$) $\bar{p} = 0.613$ ($\hat{p} = 0.619$)	$\alpha^+ = 0.683$ ($\hat{a} = 0.476$) $\bar{p} = 0.833$ ($\hat{p} = 0.846$)	$\alpha^+ = 0.730$ $\bar{p} = 1.000$
0.66	—	$\alpha^+ = 0.704$ ($\hat{a} = 0.694$) $\bar{p} = 0.116$ ($\hat{p} = 0.117$)	$\alpha^+ = 0.696$ ($\hat{a} = 0.592$) $\bar{p} = 0.640$ ($\hat{p} = 0.645$)	$\alpha^+ = 0.705$ ($\hat{a} = 0.491$) $\bar{p} = 0.845$ ($\hat{p} = 0.857$)	$\alpha^+ = 0.746$ $\bar{p} = 1.000$
0.70	—	$\alpha^+ = 0.732$ ($\hat{a} = 0.716$) $\bar{p} = 0.193$ ($\hat{p} = 0.193$)	$\alpha^+ = 0.727$ ($\hat{a} = 0.616$) $\bar{p} = 0.671$ ($\hat{p} = 0.677$)	$\alpha^+ = 0.734$ ($\hat{a} = 0.514$) $\bar{p} = 0.860$ ($\hat{p} = 0.870$)	$\alpha^+ = 0.769$ $\bar{p} = 1.000$
0.80	$\alpha^+ = 0.817$ ($\hat{a} = 0.814$) $\bar{p} = 0.043$ ($\hat{p} = 0.044$)	$\alpha^+ = 0.810$ ($\hat{a} = 0.783$) $\bar{p} = 0.351$ ($\hat{p} = 0.351$)	$\alpha^+ = 0.807$ ($\hat{a} = 0.690$) $\bar{p} = 0.740$ ($\hat{p} = 0.744$)	$\alpha^+ = 0.813$ ($\hat{a} = 0.588$) $\bar{p} = 0.891$ ($\hat{p} = 0.898$)	$\alpha^+ = 0.833$ $\bar{p} = 1.000$
0.90	$\alpha^+ = 0.902$ ($\hat{a} = 0.893$) $\bar{p} = 0.223$ ($\hat{p} = 0.223$)	$\alpha^+ = 0.898$ ($\hat{a} = 0.871$) $\bar{p} = 0.478$ ($\hat{p} = 0.478$)	$\alpha^+ = 0.897$ ($\hat{a} = 0.801$) $\bar{p} = 0.796$ ($\hat{p} = 0.798$)	$\alpha^+ = 0.900$ ($\hat{a} = 0.709$) $\bar{p} = 0.918$ ($\hat{p} = 0.920$)	$\alpha^+ = 0.909$ $\bar{p} = 1.000$

^a The first row of each group gives the optimal rate of dispersal (α^+). In the steady state, a monomorphic α^+ -type population occupies a frequency \bar{p} (in the third row) of the living sites. The second row (in parentheses) gives the maximum-occupancy rate of dispersal (denoted by \hat{a}). For a monomorphic \hat{a} -type population, the steady-state frequency of occupied living sites is \hat{p} (in the fourth row).

5. THE ISLAND MODEL

In this section we study a haploid population which is divided into an infinite number of demes. We consider the island model (Wright, 1943), along the lines formulated by Eshel (1972), with relevant modifications.

We assume that a fraction $1 - \alpha$ of the progeny of an individual remains in the parent's deme, whereas a fraction α is scattered uniformly over the entire population range.

To simplify, we consider equal-sized demes, each consisting of N individuals. (In the previous sections we had $N = 1$.) All other assumptions are the same as those of the simple haploid model of Section 2.

In the present model, we define the optimal rate of dispersal as the only rate (where such exists) which is stable against mutants. In order to investigate its existence and to find its value, we distinguish between two types A and B having dispersal rates α_1 and α_2 , respectively. The expected progeny size of each individual is μ .

Each deme may be characterized by the number of A -Type individuals in it. We denote by ξ_k ($k = 0, 1, 2, \dots, N$) the frequency of demes with k A 's (and $N - k$ B 's); $\xi = (\xi_0, \xi_1, \dots, \xi_N)$ and $\sum_{k=0}^N \xi_k = 1$. The mean number of A 's per deme is $\bar{x} = \sum_{k=0}^N k \xi_k$ and the mean number of B 's is $N - \bar{x}$.

The next generation demes are formed following the Wright-Fisher random sampling scheme. Assuming a large number of descendants per individual, the proportion of A 's among the competing young, in a deme previously occupied by k A 's, is

$$p_k = \frac{\mu(1 - \alpha_1)k + \mu\beta\alpha_1\bar{x}}{\mu(1 - \alpha_1)k + \mu(1 - \alpha_2)(N - k) + \lambda},$$

and the proportion of B 's is

$$q_k = \frac{\mu(1 - \alpha_2)(N - k) + \mu\beta\alpha_2(N - \bar{x})}{\mu(1 - \alpha_1)k + \mu(1 - \alpha_2)(N - k) + \lambda},$$

where β ($0 < \beta \leq 1$) is the probability of a dispersed offspring to withstand the risks of dispersal, and $\lambda = \mu\beta[\alpha_1\bar{x} + \alpha_2(N - \bar{x})]$ is the mean number of immigrants per deme.

The probability that a deme with k A 's will turn into a deme with j A 's in the next generation is

$$P_{k,j} = \binom{N}{j} p_k^j q_k^{N-j}, \quad k = 0, 1, 2, \dots, N, \quad j = 0, 1, 2, \dots, N.$$

Thus, in the next generation, the frequency of demes with k A 's will be

$$\xi'_j = \sum_{k=0}^N \xi_k P_{k,j}.$$

The optimal rate of dispersal α^* is defined as that value for which the monomorphic equilibrium of the type possessing it is stable against any mutant. That is to say, for any β ($0 < \beta \leq 1$) we look for a unique $\alpha^* = \alpha^*(\beta)$ so that if $\alpha_2 = \alpha^*$, then for all α_1 ($\alpha_1 \neq \alpha^*$) the monomorphic equilibrium $\mathbf{e}_0 = (1, 0, 0, \dots, 0)$ (i.e., fixation of B) is stable, and if $\alpha_1 = \alpha^*$, then for all α_2 ($\alpha_2 \neq \alpha^*$) \mathbf{e}_0 is unstable. (α_1 and α_2 are the strategies of A and B , respectively.)

The stability of the equilibrium point will be examined using the local stability analysis technique. For that purpose we consider the eigenvalues of the matrix $(\partial \xi'_j / \partial \xi_i |_{\mathbf{e}_0})$, $j = 0, 1, \dots, N-1$, $i = 0, 1, \dots, N-1$.

By differentiating and setting $\xi = \mathbf{e}_0$, we get

$$\begin{aligned} \partial \xi'_0 / \partial \xi_i |_{\mathbf{e}_0} &= 1 - q_N^N + N\beta r, & i = 0 \\ &= q_i^N - q_N^N + (N-i)\beta r, & 1 \leq i \leq N-1 \end{aligned}$$

$$\begin{aligned} \partial \xi'_i / \partial \xi_i |_{\mathbf{e}_0} &= -Np_N q_N^{N-1} - N\beta r, & i = 0 \\ &= Np_i q_i^{N-1} - Np_N q_N^{N-1} - (N-i)\beta r, & 1 \leq i \leq N-1 \end{aligned}$$

$$\begin{aligned} \partial \xi'_j / \partial \xi_i |_{\mathbf{e}_0} &= -\binom{N}{j} p_N^j q_N^{N-j}, & i = 0 \\ &= \binom{N}{j} p_i^j q_i^{N-j} - \binom{N}{j} p_N^j q_N^{N-j}, & 1 \leq i \leq N-1 \end{aligned}$$

$$j = 2, 3, \dots, N-1,$$

where $r = \alpha_1 / (1 - \alpha_2 + \beta \alpha_2)$.

We have examined numerically the case $N = 2$, and found for values of β ($0 < \beta \leq 1$) a single $\alpha^* = \alpha^*(\beta)$ which, according to the definition of this section, is the optimal dispersal rate. (The values of α^* corresponding to values of β are listed in Appendix 3.) α^* is an increasing function of β , $\alpha^*(1) = 1$, and $\lim_{\beta \rightarrow 0} \alpha^*(\beta) = \frac{1}{4}$, i.e., even if environmental conditions are very harsh for the dispersed descendants (β is small), the type which scatters a fraction α^* ($\alpha^* > \frac{1}{4}$) of its progeny carries an advantage over any mutant.

For $N = 3$ we restricted our research to the limit case $\beta \rightarrow 0$ ($\beta \neq 0$). We have numerically found that $\alpha_2 = \frac{1}{6}$ is a necessary condition for the stability of \mathbf{e}_0 and $\alpha_1 = \frac{1}{6}$ is a sufficient condition for the instability of \mathbf{e}_0 . We have also ascertained that $\alpha_1 = \frac{1}{8}$ is sufficient for the instability of \mathbf{e}_0 when $N = 4$

and $\beta \rightarrow 0$ ($\beta \neq 0$). It is conjectural that for the general case the optimal α is $\alpha^* = (1/2N) + o(\beta)$ (where $o(\beta)$ approaches zero when $\beta \rightarrow 0$).

It is noteworthy that selection in favor of the type with the optimal dispersal rate is somewhat different from the classical fitness selection. Whereas the latter acts to increase the frequency of the advantageous type each generation, selection in our case does not necessarily increase the frequency of the preferred type in the next generation, as demonstrated if we take, for example, $N = 2$, $\alpha_1 = 0$, and $\xi = (1 - V, V, 0)$, $0 < V \leq 1$. If $\beta < (2 - V)^{-1}$, then for any $\alpha_2 > 0$ (certainly for $\alpha_2 = \alpha^*$) $\Delta \bar{x} > 0$. In this sense the selection process described in this section resembles the selection process induced by the neighbor effect in Eshel's island model (Eshel, 1972).

6. DISCUSSION

In this work we were concerned with a strategy of progeny dispersal. We examined the existence of an optimal division of the progeny of an individual into those which remain near the parent and those which are dispersed; optimal in the sense that the type with the optimal division has a selective advantage over other types.

Generally, progeny dispersal is considered to be advantageous in that it enables the occupation of vacant living sites. Most of the cases treated here were such that all possible living sites for the population are always occupied. Yet, in each case, a single strategy of progeny division, which implies a substantial fraction of dispersed descendants, was found to be the optimal strategy. As expected, the optimal rate of dispersal increases as the risks involved in dispersal decrease.

When there is a possibility of living sites being vacant after the death of the occupant, the optimal rate of dispersal was found to be smaller than that obtained in the full-occupancy case. This conclusion is somewhat different than that of Van Valen (1971). Also, in this case, the optimal strategy, which will be selected for in the population, is not identical with the dispersal rate which, if adopted by the population, would maximize the population size in the given environment (cf. Roff, 1975; Hamilton and May, 1977; Comins *et al.*, 1980).

All the models treated in this paper were of haploid populations. Diploid populations are treated in two succeeding papers—Motro (1982a, b). Surprisingly, we get values for the optimal dispersal rate in the diploid model of random mating and in the diploid model of mixed selfing and random mating (Motro, 1982a) which coincide with the value obtained here in the simple haploid model.

It is noteworthy that optimization, in the context of this work, does not necessarily coincide with maximal fitness (in the classical sense; the mean

number of surviving descendants in the next generation). Moreover, the existence of an optimal strategy is not self-evident—the genetical structure is such that optimization is not always possible. For example, Oster *et al.* (1977), in analyzing the behavior of social *Hymenoptera* workers according to the degree of sterility and the distribution of resources among male and female larvae, have concluded that for each behavioral pattern, if genetically determined, there exists another pattern, which, at least when it appears, is more advantageous.

The same problem of progeny dispersal strategies was examined by Hamilton and May (1977), using the ESS approach, a technique different from the gene frequency method used in our work. It is, perhaps, both surprising and reassuring that though different approaches have been used, the results obtained by the ESS methods and those of the gene frequency models are identical in most of the cases. This fact supports the use of ESS techniques in population genetics. Yet, in one case (Motro, 1982b), the more rigorous gene frequency model yielded a result different from that of Hamilton and May.

Recently, Comins *et al.* (1980), using ESS concepts, investigated cases in which there is the possibility that living sites will become extinct.

APPENDIX 1: THE MATHEMATICS FOR THE VARYING ENVIRONMENT MODEL

In this appendix we show the existence of a single dispersal rate α^* which, with probability one, will be fixed in the population.

We assume that $E(\Delta p)$ exists (for all α_1 and α_2 in $[0, 1]$). Using Eq. (1), we have

$$E(\Delta p) = \mu p q (\alpha_1 - \alpha_2) E \left\{ \frac{\beta [\mu (1 - \alpha_1 - \alpha_2) + \lambda]}{[\mu (1 - \alpha_1) + \lambda][\mu (1 - \alpha_2) + \lambda]} \right\},$$

where $\lambda = \mu \beta (\alpha_1 p + \alpha_2 q)$. Denoting

$$g(\alpha_1, \alpha_2) = E \left\{ \frac{\beta [\mu (1 - \alpha_1 - \alpha_2) + \lambda]}{[\mu (1 - \alpha_1) + \lambda][\mu (1 - \alpha_2) + \lambda]} \right\},$$

we observe that for $\alpha_1 = \alpha^*$ to assure $E(\Delta p) > 0$ (for all $0 < p < 1$), it is necessary and sufficient that $g(\alpha^*, \alpha_2) > 0$ if $\alpha_2 < \alpha_1 = \alpha^*$, and that $g(\alpha^*, \alpha_2) < 0$ if $\alpha_2 > \alpha_1 = \alpha^*$. Since $g(\alpha^*, \alpha_2)$ is continuous in α_2 , we must have $g(\alpha^*, \alpha^*) = 0$.

The equation $g(\alpha^*, \alpha^*) = 0$ has a single solution in the interval

$0 \leq \alpha^* \leq 1$: $g(0, 0) = E(\beta/\mu) > 0$, $g(1, 1) = E(-(1 - \beta)/\mu\beta) \leq 0$ and $g(\alpha^*, \alpha^*)$ is a continuous and decreasing function of α^* in $[0, 1]$, since

$$\frac{d}{d\alpha^*} g(\alpha^*, \alpha^*) = -E \left\{ \frac{\beta[(2 - \beta)(1 - \beta)\alpha^* + \beta]}{\mu(1 - \alpha^* + \beta\alpha^*)^3} \right\} < 0 \quad (0 \leq \alpha^* \leq 1).$$

Letting $\alpha_1 = \alpha^*$, we get

$$\begin{aligned} g(\alpha^*, \alpha_2) &= E \left\{ \frac{\beta[\mu(1 - \alpha^* - \alpha_2) + \lambda]}{[\mu(1 - \alpha^*) + \lambda][\mu(1 - \alpha_2) + \lambda]} \right\} \\ &= E \left[\frac{\beta\mu(1 - 2\alpha^* + \beta\alpha^*)}{\mu^2(1 - \alpha^* + \beta\alpha^*)^2} + d \right] = g(\alpha^*, \alpha^*) + E(d) = E(d), \end{aligned}$$

where

$$\begin{aligned} d &= \frac{\beta[\mu(1 - \alpha^* - \alpha_2) + \lambda]}{[\mu(1 - \alpha^*) + \lambda][\mu(1 - \alpha_2) + \lambda]} - \frac{\beta\mu(1 - 2\alpha^* + \beta\alpha^*)}{\mu^2(1 - \alpha^* + \beta\alpha^*)^2} \\ &\quad - \frac{\beta(\alpha^* - \alpha_2)\{\mu(1 - \beta q)\alpha^*(1 - \alpha^* + \beta\alpha^*) + \beta q(1 - 2\alpha^* + \beta\alpha^*)[\mu(1 - \alpha_2) + \lambda]\}}{(1 - \alpha^* + \beta\alpha^*)^2[\mu(1 - \alpha^*) + \lambda][\mu(1 - \alpha_2) + \lambda]}. \end{aligned}$$

Since $1 - 2\alpha^* + \beta\alpha^* = 1 - \alpha^* - (1 - \beta)\alpha^* \geq -(1 - \beta)\alpha^* \geq (1 - \beta q)\alpha^*$, the expression in the braces in the numerator of d is larger than or equal to $(1 - \beta q)\alpha^*\{\mu(1 - \alpha^* + \beta\alpha^*) - \beta q[\mu(1 - \alpha_2) + \lambda]\}$, which equals $(1 - \beta q)^2\alpha^*[\mu(1 - \alpha^*) + \lambda]$. Because this last expression is non-negative, we see that $\text{sign}(d) = \text{sign}(\alpha^* - \alpha_2)$, thus proving that for α^* , defined by the single solution of $g(\alpha^*, \alpha^*) = 0$ in $[0, 1]$, we always have $E(\Delta p) > 0$, where $0 < p < 1$ is the frequency of the α^* -type in the population.

The sequence $\{p_n\}_{n=0}^\infty$ (p_n is the frequency of α^* in generation n) forms a submartingale. By applying the probability convergence theorem for submartingales (see Feller, 1971), this sequence converges, with probability one, to the number 1. Hence the type with the strategy α^* will be fixed in the population (with probability one).

APPENDIX 2: STABILITY ANALYSIS OF THE EQUILIBRIUM POINTS IN THE UNOCCUPIED LIVING SITES MODEL

We investigate the stability of the equilibrium points by considering the eigenvalues of the matrix

$$\begin{bmatrix} \partial p' / \partial p & \partial p' / \partial q \\ \partial q' / \partial p & \partial q' / \partial q \end{bmatrix},$$

where the derivatives are calculated at the corresponding points.

At the point $(p, q, r) = (0, 0, 1)$, the eigenvalues are

$$x_1 = 1 + \mu\beta\alpha_1(1-u) - \exp\{-\mu(1-\alpha_1)(1-u)\}$$

and

$$x_2 = 1 + \mu\beta\alpha_2(1-u) - \exp\{-\mu(1-\alpha_2)(1-u)\}.$$

Since both x_1 and x_2 are positive, $(0, 0, 1)$ is stable if $x_1 < 1$ and also $x_2 < 1$, i.e., if both $\mu\beta\alpha_i(1-u) - \exp\{-\mu(1-\alpha_i)(1-u)\} < 0$ ($i = 1, 2$). In other words, for the extinction equilibrium to be stable it is necessary that both monomorphic equilibria do not exist.

At the point $(p, q, r) = (\bar{p}, 0, \bar{r})$, the eigenvalues are

$$x_1 = \mu\beta\alpha_1\bar{r}(1-u) + \exp\{-\tilde{\lambda}(1-u)\} [1 - \exp\{-\mu(1-\alpha_1)(1-u)\}]$$

and

$$x_2 = \frac{\mu(1-\alpha_2)[1 - \exp\{-[\mu(1-\alpha_2) + \tilde{\lambda}](1-u)\}]}{\mu(1-\alpha_2) + \tilde{\lambda}} + \frac{\mu\beta\alpha_2[1 - \exp\{-\tilde{\lambda}(1-u)\}][1 - \exp\{-[\mu(1-\alpha_1) + \tilde{\lambda}](1-u)\}]}{[\mu(1-\alpha_1) + \tilde{\lambda}][1 - \exp\{-\tilde{\lambda}(1-u)\} + \exp\{-[\mu(1-\alpha_1) + \tilde{\lambda}](1-u)\}]} + \frac{\alpha_2 \exp\{-[\mu(1-\alpha_1) + \tilde{\lambda}](1-u)\}}{\alpha_1}$$

(where $\tilde{\lambda} = \mu\beta\alpha_1\bar{p}$). Both x_1 and x_2 are positive. If $(\bar{p}, 0, \bar{r})$ exists, then $x_1 < 1$ (since x_1 is the slope of $f(r)$ at $r = \bar{r}$). Hence a sufficient condition for the stability of $(\bar{p}, 0, \bar{r})$ is $x_2 < 1$, i.e.,

$$\frac{\tilde{\lambda} + \mu(1-\alpha_1) \exp\{-[\mu(1-\alpha_1) + \tilde{\lambda}](1-u)\}}{\alpha_1[\mu(1-\alpha_1) + \tilde{\lambda}]} < \frac{\tilde{\lambda} + \mu(1-\alpha_2) \exp\{-[\mu(1-\alpha_2) + \tilde{\lambda}](1-u)\}}{\alpha_2[\mu(1-\alpha_2) + \tilde{\lambda}]}.$$

(We have made use of the relation $\bar{r}[1 - \exp\{-\tilde{\lambda}(1-u)\}] = (1-\bar{r}) \exp\{-[\mu(1-\alpha_1) + \tilde{\lambda}](1-u)\}$ which is valid at $(\bar{p}, 0, \bar{r})$.)

The optimal rate of dispersal α^+ is defined, for the unoccupied living sites model, as that rate for which the monomorphic equilibrium of the α^+ type exists and is stable against any mutant. Hence α^+ has to (1) satisfy the relation $\bar{r}[1 - \exp\{-\tilde{\lambda}(1-u)\}] = (1-\bar{r}) \exp\{-[\mu(1-\alpha^+) + \tilde{\lambda}](1-u)\}$ (where $\tilde{\lambda} = \mu\beta\alpha^+\bar{p}$), and (2) minimize the value of the function

$$h(\alpha) = \frac{k + \mu(1-\alpha) \exp\{-[\mu(1-\alpha) + k](1-u)\}}{\alpha[\mu(1-\alpha) + k]}$$

(where k is a constant independent of α) in the interval $0 \leq \alpha \leq 1$.

APPENDIX 3: THE ISLAND MODEL, $N = 2$:
 α^* AS A FUNCTION OF β

β	α^*	β	α^*	β	α^*
.00	.2500	.34	.3474	.68	.5511
.01	.2521	.35	.3513	.69	.5602
.02	.2542	.36	.3554	.70	.5696
.03	.2564	.37	.3595	.71	.5791
.04	.2586	.38	.3637	.72	.5890
.05	.2609	.39	.3680	.73	.5991
.06	.2631	.40	.3725	.74	.6095
.07	.2655	.41	.3770	.75	.6202
.08	.2678	.42	.3816	.76	.6312
.09	.2702	.43	.3863	.77	.6425
.10	.2727	.44	.3911	.78	.6541
.11	.2752	.45	.3961	.79	.6660
.12	.2777	.46	.4012	.80	.6782
.13	.2803	.47	.4063	.81	.6908
.14	.2829	.48	.4116	.82	.7037
.15	.2856	.49	.4171	.83	.7170
.16	.2883	.50	.4226	.84	.7306
.17	.2910	.51	.4284	.85	.7445
.18	.2939	.52	.4342	.86	.7589
.19	.2967	.53	.4402	.87	.7736
.20	.2997	.54	.4463	.88	.7886
.21	.3027	.55	.4526	.89	.8041
.22	.3057	.56	.4591	.90	.8199
.23	.3088	.57	.4657	.91	.8362
.24	.3120	.58	.4725	.92	.8528
.25	.3152	.59	.4795	.93	.8698
.26	.3185	.60	.4866	.94	.8872
.27	.3218	.61	.4940	.95	.9050
.28	.3253	.62	.5015	.96	.9232
.29	.3288	.63	.5092	.97	.9418
.30	.3323	.64	.5172	.98	.9608
.31	.3360	.65	.5253	.99	.9802
.32	.3397	.66	.5337	1.00	1.0000
.33	.3435	.67	.5423		

ACKNOWLEDGMENTS

This work is based upon part of a Ph. D. thesis, carried out under the supervision of Professor Ilan Eshel of Tel Aviv University. I wish to thank also Professor Samuel Karlin for helpful advice and Professor Dan Cohen for stimulating discussions.

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