

Optimal Rates of Dispersal. III. Parent–Offspring Conflict¹

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Received October 22, 1980

The question of whether an offspring should migrate or stay near its parents is investigated in a model in which this decision is made by the offspring itself. Although migration is hazardous, the model presented here shows the existence of an optimal migration strategy which implies, under certain circumstances, a positive probability of choosing migration. Also briefly discussed is the relationship of the migration strategy to the parent–offspring conflict.

1. INTRODUCTION

This is the third in a series of three papers, which examine the question of optimal rates of dispersal. In these works we investigate the existence of an optimal division of the progeny of an individual into migrating and nonmigrating descendants, where the survival probability of a migrating offspring is smaller than that of an offspring which remains near the parent.

In the first paper (Motro, 1982a) we studied haploid populations. In the second paper (Motro, 1982b) we treated models of diploid populations, in which the division of the progeny is determined by the parent's genotype, while in this paper we investigate a diploid model in which the tendency to migrate is determined by the genotype of the offspring itself.

A similar question was investigated by Hamilton and May (1977). Referring to kin selection arguments, they used evolutionarily stable strategy (ESS) considerations to find the optimal rate of migration. The attempt here is to develop a more rigorous model, based on changes in gene frequencies. Unlike the haploid case, where identical results are obtained by the ESS methods of Hamilton and May and by the gene frequency models (Motro, 1982a), the results in the present case are different for these two different approaches.

¹ This work has been supported in part by National Institutes of Health Grant 1 R01 HD 12731.

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2. THE MODEL

This model deals with a migration strategy in which the decision of whether to migrate or to stay near the parent is made by the offspring itself. We investigate the existence of an optimal strategy—a single strategy which is stable against any mutant strategy, and which, if it appears as a mutant, will be established in any population.

The assumptions of the model are as follows:

(1) We consider an infinite population of diploid and monoecious organisms, which reproduce by random mating.

(2) Each individual in the population has the same expected number (μ) of descendants.

(3) Each descendant either remains near the parent, with probability $1 - \alpha$ ($0 \leq \alpha \leq 1$), or leaves its birth site and migrates (with probability α), in an attempt to establish itself in another living site. The number α is genetically determined (by a single locus), and the decision of whether to migrate or to stay at home is made according to the genotype of the descendant.

(4) Those progeny which migrate are uniformly dispersed over the entire population range.

(5) Generations are discrete and nonoverlapping. After reproduction, the previous generation is eliminated, and each living site is reoccupied by a single individual.

(6) The successor is chosen at random from among all the young individuals present at that site, which are either the nonmigrating descendants of the former occupant, or the immigrating descendants of other previous generation individuals, which occupied other living sites.

(7) Migration involves a risk to the migrating individual, so we assume that the probability of a migrating offspring to withstand the hazards of migration, and finally reach the state of competition on a living site, is only a fraction β ($0 < \beta \leq 1$) of that probability for a nonmigrating one. The smaller β is, the more stringent are the environmental conditions endured by the migrating young.

The model considered here differs from the simple diploid model (Motro, 1982b) in that in the present model the probability of migration is determined by the genotype of the offspring, whereas in the simple diploid model the division of the progeny into dispersed and nondispersed descendants was determined by the parent's genotype. Apart from that, the assumptions of both models are the same.

It should be noted that the model presented here can also be expanded to

include dioecious populations. (Please see the remark at the end of this section.)

To find the optimal rate of migration, we consider the locus which determines the migration rate α to have two alleles, A and B , so that the population can consist of three genotypes, AA , AB , and BB , with migration rates α_1 , α_2 , and α_3 , respectively.

If u , v , and w ($u + v + w = 1$) are the frequencies in the population of the three genotypes, then, assuming random mating, the expected number of immigrating descendants per living site is $\lambda = \mu\beta (\alpha_1 p^2 + 2\alpha_2 pq + \alpha_3 q^2)$. The expected number of AA 's among the immigrants is $\lambda_1 = \mu\beta\alpha_1 p^2$, the expected number of AB 's is $\lambda_2 = 2\mu\beta\alpha_2 pq$ and that of BB is $\lambda_3 = \mu\beta\alpha_3 q^2$, where $p = u + \frac{1}{2}v$ is the frequency of allele A among the genes and $q = w + \frac{1}{2}v$ is the frequency of B . This is summarized in Table 1.

The frequencies of the three genotypes in the next generation are

$$(u', v', w') = (u, v, w) \begin{bmatrix} P_{11} & P_{12} & P_{13} \\ P_{21} & P_{22} & P_{23} \\ P_{31} & P_{32} & P_{33} \end{bmatrix},$$

where, assuming a large number of competing young per living site,

$$P_{11} = \frac{\mu(1 - \alpha_1)p + \lambda_1}{\mu(1 - \alpha_1)p + \mu(1 - \alpha_2)q + \lambda},$$

$$P_{12} = \frac{\mu(1 - \alpha_2)q + \lambda_2}{\mu(1 - \alpha_1)p + \mu(1 - \alpha_2)q + \lambda},$$

$$P_{13} = \frac{\lambda_3}{\mu(1 - \alpha_1)p + \mu(1 - \alpha_2)q + \lambda},$$

$$P_{21} = \frac{\frac{1}{2}\mu(1 - \alpha_1)p + \lambda_1}{\frac{1}{2}\mu(1 - \alpha_1)p + \frac{1}{2}\mu(1 - \alpha_2) + \frac{1}{2}\mu(1 - \alpha_3)q + \lambda},$$

$$P_{22} = \frac{\frac{1}{2}\mu(1 - \alpha_2) + \lambda_2}{\frac{1}{2}\mu(1 - \alpha_1)p + \frac{1}{2}\mu(1 - \alpha_2) + \frac{1}{2}\mu(1 - \alpha_3)q + \lambda},$$

$$P_{23} = \frac{\frac{1}{2}\mu(1 - \alpha_3)q + \lambda_3}{\frac{1}{2}\mu(1 - \alpha_1)p + \frac{1}{2}\mu(1 - \alpha_2) + \frac{1}{2}\mu(1 - \alpha_3)q + \lambda},$$

$$P_{31} = \frac{\lambda_1}{\mu(1 - \alpha_2)p + \mu(1 - \alpha_3)q + \lambda},$$

$$P_{32} = \frac{\mu(1 - \alpha_2)p + \lambda_2}{\mu(1 - \alpha_2)p + \mu(1 - \alpha_3)q + \lambda},$$

$$P_{33} = \frac{\mu(1 - \alpha_3)q + \lambda_3}{\mu(1 - \alpha_2)p + \mu(1 - \alpha_3)q + \lambda}.$$

TABLE 1
The Diploid Model in Which the Probability of Dispersal Is
Determined by the Genotype of the Offspring

	Site AA	Site AB	Site BB
Frequency	u	v	w
Mean progeny size	μ	μ	μ
Fraction of progeny dispersed	$\alpha_1 p + \alpha_2 q$	$\frac{1}{2}\alpha_1 p + \frac{1}{2}\alpha_2 + \frac{1}{2}\alpha_3 q$	$\alpha_2 p + \alpha_3 q$
Expected number remaining near parent	$\mu(1 - \alpha_1)p + \mu(1 - \alpha_2)q$	$\frac{1}{2}\mu(1 - \alpha_1)p + \frac{1}{2}\mu(1 - \alpha_2) + \frac{1}{2}\mu(1 - \alpha_3)q$	$\mu(1 - \alpha_2)p + \mu(1 - \alpha_3)q$
Expected number of AA's among immigrants	$\lambda_1 = \mu\beta\alpha_1 p^2$	$\lambda_1 = \mu\beta\alpha_1 p^2$	$\lambda_1 = \mu\beta\alpha_1 p^2$
Expected number of AB's among immigrants	$\lambda_2 = 2\mu\beta\alpha_2 pq$	$\lambda_2 = 2\mu\beta\alpha_2 pq$	$\lambda_2 = 2\mu\beta\alpha_2 pq$
Expected number of BB's among immigrants	$\lambda_3 = \mu\beta\alpha_3 q^2$	$\lambda_3 = \mu\beta\alpha_3 q^2$	$\lambda_3 = \mu\beta\alpha_3 q^2$
Expected total number of immigrants per site	$\lambda = \mu\beta(\alpha_1 p^2 + 2\alpha_2 pq + \alpha_3 q^2)$	$\lambda = \mu\beta(\alpha_1 p^2 + 2\alpha_2 pq + \alpha_3 q^2)$	$\lambda = \mu\beta(\alpha_1 p^2 + 2\alpha_2 pq + \alpha_3 q^2)$
Expected number of AA's among competing young	$\mu(1 - \alpha_1)p + \lambda_1$	$\frac{1}{2}\mu(1 - \alpha_1)p + \lambda_1$	λ_1
Expected number of AB's among competing young	$\mu(1 - \alpha_2)q + \lambda_2$	$\frac{1}{2}\mu(1 - \alpha_2) + \lambda_2$	$\mu(1 - \alpha_2)p + \lambda_2$
Expected number of BB's among competing young	λ_3	$\frac{1}{2}\mu(1 - \alpha_3)q + \lambda_3$	$\mu(1 - \alpha_3)q + \lambda_3$
Expected total number of competing young per site	$\mu(1 - \alpha_1)p + \mu(1 - \alpha_2)q + \lambda$	$\frac{1}{2}\mu(1 - \alpha_1)p + \frac{1}{2}\mu(1 - \alpha_2) + \frac{1}{2}\mu(1 - \alpha_3)q + \lambda$	$\mu(1 - \alpha_2)p + \mu(1 - \alpha_3)q + \lambda$

We consider the conditions for the stability of the monomorphic equilibrium points $(u, v, w) = (1, 0, 0)$ and $(u, v, w) = (0, 0, 1)$. The detailed analysis is presented in Appendix 1, and the results are summarized below.

Set

$$\alpha^* = 0 \quad \text{if } 0 < \beta \leq \frac{3}{4}$$

$$= \frac{\beta - \frac{3}{4}}{(\beta - \frac{1}{2})(\frac{3}{2} - \beta)} \quad \text{if } \frac{3}{4} < \beta \leq 1.$$

Using the results of Appendix 1, we have proved

THEOREM. *Each $\alpha_2 \neq \alpha^*$ determines an interval I (containing α^* as an interior point, and having α_2 as an open end bound), such that if $\alpha_1 \in I$, then $(1, 0, 0)$ is stable, and if $\alpha_1 \notin \bar{I}$ (\bar{I} is the closure of I), then $(1, 0, 0)$ is unstable. Likewise, if $\alpha_3 \in I$ or if $\alpha_3 \notin \bar{I}$, $(0, 0, 1)$ is stable or unstable, respectively.*

If $\alpha_2 = \alpha^$, then I is the null set.*

(The bounds of the interval I are presented in Appendix 2.)

Let us define α_i ($i = 1, 3$) is "closer" to α^* than α_2 , if $\alpha_i \in I$; α_i is "further" from α^* than α_2 , if $\alpha_i \notin \bar{I}$. Thus, the results of our theorem can be put as follows.

(1) If one of the homozygotes has a rate of migration which is "closer" to α^* than α_2 (which is the rate of migration of the heterozygote) and the α of the other homozygote is "further" from α^* than α_2 , then the monomorphic equilibrium of the former homozygote is stable, whereas that of the latter is unstable.

(2) If the α 's of both homozygotes are "closer" to α^* than the rate of migration of the heterozygote, both monomorphic equilibria are stable.

(3) If both homozygotes have α 's which are "further" from α^* than α_2 , both monomorphic equilibria are unstable, and a coexistence of both alleles is maintained in the population (a protected polymorphism).

Hence the type with the strategy α^* has a selective advantage over all types having other strategies—a population consisting of α^* -type individuals is stable against the appearance of any mutant, whereas mutants with the strategy α^* will be established in any population with $\alpha \neq \alpha^*$.

Remark. In our model we considered a monoecious population. We get also similar results for a dioecious population, under the following assumptions.

(1) The young individuals of one sex (the "females") always migrate, and are uniformly dispersed over the entire population range.

(2) The young individuals of the other sex (the "males"), either migrate (with probability α) or stay near the parent (with probability $1 - \alpha$). The number α is determined by the genotype of the offspring itself.

(3) Each living site is occupied by a single couple, consisting of one male and one female. The young males are those which compete for the living sites, and after a male establishes itself in a site, it is joined by a random female.

It turns out that the same optimal rate of migration (α^*), obtained in the monoecious model, is also valid for the dioecious model. Here, α^* is the optimal strategy for the males (the females always migrate).

3. DISCUSSION

In our model, the descendants are those which decide whether to migrate or stay near the parent. Since migration is risky, it was interesting to find that, in certain circumstances, the optimal strategy implies a positive probability that the offspring will decide to migrate (a probability that increases as a function of the survival chances of the migrants). More specifically, the optimal rate of migration is

$$\alpha^* = 0 \quad \text{if } 0 < \beta \leq \frac{3}{4}$$

$$= \frac{\beta - \frac{3}{4}}{(\beta - \frac{1}{2})(\frac{3}{2} - \beta)} \quad \text{if } \frac{3}{4} < \beta \leq 1,$$

where β is the survival probability of the migrating offspring. Thus, if migration is too risky ($\beta \leq \frac{3}{4}$), the optimal strategy is to stay at home. But if the chances of surviving migration are large enough, the optimal strategy is to choose to migrate with probability $\alpha^* > 0$. It should be noted that by choosing to migrate, the migrating descendant reduces its own survival probability. Yet, its migration increases the survival chances of its brothers, with which the migrant is more likely to share the same genotype.

On the other hand, the optimal rate of migration obtained by Hamilton and May (1977), using ESS techniques based on the maximization of the inclusive fitness, is different than the rate obtained in our model, which has the same basic assumptions. The ESS strategy of Hamilton and May's inclusive fitness model is (using the same notation as in this work)

$$\alpha^* = 0 \quad \text{if } 0 < \beta \leq \frac{1}{2}$$

$$= \frac{2\beta - 1}{4\beta - \beta^2 - 1} \quad \text{if } \frac{1}{2} < \beta \leq 1,$$

a migration probability which is greater than the probability in our gene frequency model. Hence, the optimal rate of migration, which will be selected for in the population, neither maximizes the Fisherian fitness (i.e., the expected number of surviving descendants in the next generation) of the migrants, nor does it maximize their inclusive fitness.

Also interesting to note is that the optimal rate of migration, in the model treated here, is always smaller than the optimal rate $(1/(2 - \beta))$, $0 < \beta \leq 1$ obtained in the case in which the parents are those that decide about the division of the progeny (Motro, 1982b). This clearly illustrates the contrast inherent in dispersal, a contrast between the interests of the parents and those of their progeny. Whenever the decision is made by the parent, it would disperse a larger fraction of its progeny than would be dispersed if the decision is made by the offspring themselves. The parents prefer that their progeny will be more altruistic toward each other than the offspring are willing to be. In most cases, especially in plants, this contrast of interest cannot lead to a real conflict—the progeny is dispersed according to its morphological phenotype, which is determined either by the genotype of the parent or by the genotype of the offspring itself.

As for animals, in those of the cases in which the dispersal mechanism is behavioral, the parent-offspring conflict can be expressed. Generally, it seems more likely that the parents, which are stronger than their progeny and usually control the resources essential for the growth of the descendants, are those which enforce their strategy on their progeny. Thus, the parents may compel their descendants to be more altruistic, a situation suitably termed by West-Eberhard (1975) as *imposed altruism*. But while Alexander (1974) views this situation to be the only possible one, Trivers (1974) claims that sometimes the offspring can prevail. Zahavi (1977) suggests that a way by which the seemingly weak offspring can impose their wishes on their parents is by threats of self-destruction.

APPENDIX 1: STABILITY OF THE MONOMORPHIC EQUILIBRIUM POINTS

We begin by considering the monomorphic equilibrium $(u, v, w) = (0, 0, 1)$. For $\alpha_2 \neq \alpha_3$, the stability of $(0, 0, 1)$ is determined using the local stability analysis technique. We consider the eigenvalues of the matrix

$$\begin{bmatrix} \left. \frac{\partial p'}{\partial p} \right|_{\substack{p=0 \\ v=0}} & \left. \frac{\partial p'}{\partial v} \right|_{\substack{p=0 \\ v=0}} \\ \left. \frac{\partial v'}{\partial p} \right|_{\substack{p=0 \\ v=0}} & \left. \frac{\partial v'}{\partial v} \right|_{\substack{p=0 \\ v=0}} \end{bmatrix}$$

$$p' = u' + \frac{1}{2}v' = (P_{11} + \frac{1}{2}P_{12})u + (P_{21} + \frac{1}{2}P_{22})v + (P_{31} + \frac{1}{2}P_{32})w$$

$$v' = P_{12}u + P_{22}v + P_{32}w.$$

Hence

$$\left. \frac{\partial p'}{\partial p} \right|_{\substack{p=0 \\ v=0}} = \frac{\frac{1}{2}(1-\alpha_2)}{1-\alpha_2+\beta\alpha_3} + \frac{\frac{1}{2}(1-\alpha_2)+\beta\alpha_2}{1-\alpha_3+\beta\alpha_3}$$

$$\left. \frac{\partial p'}{\partial v} \right|_{\substack{p=0 \\ v=0}} = \frac{-\frac{1}{4}(1-\alpha_2)}{1-\alpha_2+\beta\alpha_3} + \frac{\frac{1}{4}(1-\alpha_2)}{\frac{1}{2}(1-\alpha_2)+\frac{1}{2}(1-\alpha_3)+\beta\alpha_3}$$

$$\left. \frac{\partial v'}{\partial p} \right|_{\substack{p=0 \\ v=0}} = \frac{1-\alpha_2}{1-\alpha_2+\beta\alpha_3} + \frac{1-\alpha_2+2\beta\alpha_2}{1-\alpha_3+\beta\alpha_3}$$

$$\left. \frac{\partial v'}{\partial v} \right|_{\substack{p=0 \\ v=0}} = \frac{-\frac{1}{2}(1-\alpha_2)}{1-\alpha_2+\beta\alpha_3} + \frac{\frac{1}{2}(1-\alpha_2)}{\frac{1}{2}(1-\alpha_2)+\frac{1}{2}(1-\alpha_3)+\beta\alpha_3}.$$

The eigenvalues of our matrix are $x_1 = 0$ and

$$x_2 = \frac{\frac{1}{2}(1-\alpha_2)+\beta\alpha_2}{1-\alpha_3+\beta\alpha_3} + \frac{\frac{1}{2}(1-\alpha_2)}{\frac{1}{2}(1-\alpha_2)+\frac{1}{2}(1-\alpha_3)+\beta\alpha_3} > 0.$$

Hence, the monomorphic equilibrium is stable if $x_2 < 1$ and is unstable if $x_2 > 1$.

After some simple algebra we get

$$\text{sign}(1-x_2) = \text{sign}[(\alpha_2-\alpha_3)\{(\frac{1}{2}-\beta)\{(1-\beta)(1-\alpha_3) + \frac{1}{2}(1-\alpha_2)\} + \beta(1-\beta)\}].$$

The expression in braces, which we shall denote by D , is positive for $\beta \leq \frac{3}{4}$. As for $\frac{3}{4} < \beta \leq 1$,

$$D > 0 \quad \text{if} \quad \alpha_2 > \frac{4\beta-3}{2\beta-1} - 2(1-\beta)\alpha_3$$

$$D < 0 \quad \text{if} \quad \alpha_2 < \frac{4\beta-3}{2\beta-1} - 2(1-\beta)\alpha_3.$$

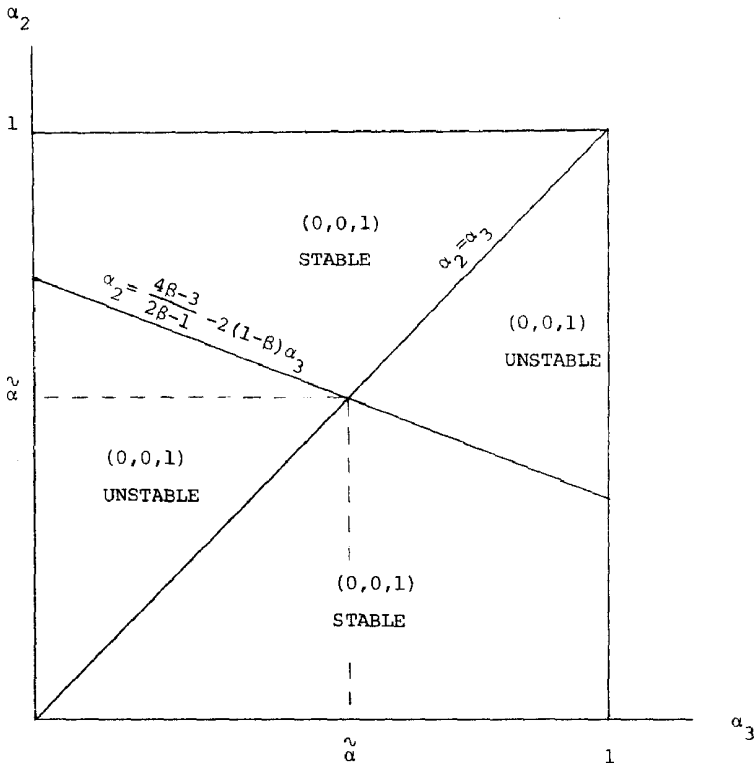


FIG. 1. Stability analysis of the monomorphic equilibrium $(u, v, w) = (0, 0, 1)$: the case $\frac{3}{4} < \beta \leq 1$.

The lines $\alpha_2 = (4\beta - 3)/(2\beta - 1) - 2(1 - \beta)\alpha_3$ and $\alpha_2 = \alpha_3$ intersect at the point $\alpha_2 = \alpha_3 = (\beta - \frac{3}{4})/((\beta - \frac{1}{2})(\frac{3}{4} - \beta))$, and we shall denote this value, which is a function of β , by $\tilde{\alpha}$. $\tilde{\alpha}(\beta)$ is a continuous and increasing function in the interval $\frac{3}{4} \leq \beta \leq 1$, $\tilde{\alpha}(\frac{3}{4}) = 0$, and $\tilde{\alpha}(1) = 1$.

Thus, for $\beta \leq \frac{3}{4}$, the monomorphic equilibrium $(0, 0, 1)$ is stable if $\alpha_2 > \alpha_3$ and is unstable if $\alpha_2 < \alpha_3$. For $\beta > \frac{3}{4}$, the situation is graphically summarized in Fig. 1.

Because of symmetry, the above results are also valid for the other equilibrium point $(1, 0, 0)$, provided we change α_3 into α_1 .

APPENDIX 2: THE INTERVAL I

$$\begin{aligned}
 I &= [0, \alpha_2] && \text{if } \beta \leq \frac{3}{4} \text{ and } \alpha_2 \neq \alpha^* \text{ or} \\
 & && \text{if } \beta > \frac{3}{4}, \alpha_2 > \alpha^* \text{ and } M < 0 \\
 &= (M, \alpha_2) && \text{if } \beta > \frac{3}{4}, \alpha_2 > \alpha^* \text{ and } M \geq 0 \\
 &= (\alpha_2, 1] && \text{if } \beta > \frac{3}{4}, \alpha_2 < \alpha^* \text{ and } M > 1 \\
 &= (\alpha_2, M) && \text{if } \beta > \frac{3}{4}, \alpha_2 < \alpha^* \text{ and } M \leq 1 \\
 &= \phi && \text{if } \alpha_2 = \alpha^*
 \end{aligned}$$

where

$$M = \frac{\frac{1}{2}(4\beta - 3)}{(2\beta - 1)(1 - \beta)} - \frac{\alpha_2}{2(1 - \beta)}.$$

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 also thank Professor Samuel Karlin, Professor Glenys Thomson, and the referees for important comments.

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