Optimal Rates of Dispersal
II. Diploid Populations

Uzi Motro*

Department of Statistics, Tel Aviv University, Tel Aviv, Israel

The question of progeny division into dispersed and non-dispersed descendants is investigated in several diploid models. For each of these models, in which the division of the progeny is determined by the genotype of the parent, a single optimal strategy of dispersal has been found. Although dispersal involves a risk to the dispersed offspring, the optimal strategy implies that a substantial fraction of the progeny should be dispersed.

1. INTRODUCTION

The effect of natural selection on the dispersal strategy of diploid organisms is investigated. We consider the problem of how an individual should divide its progeny into dispersed and non-dispersed descendants, where the survival probability of a dispersed offspring is lower than that of an offspring which remains near the parent. In other words, assuming that for the descendants, dispersal is more risky than staying at home, we are looking for the parent's optimal strategy of progeny division; optimal in the sense that the type with this strategy has a selective advantage over other types, having different strategies.

In a previous paper (Motro, 1982a), we have studied haploid populations. In various models we have shown the existence of a single optimal dispersal strategy which is selected for in the population. This evolutionary optimal rate of dispersal has been shown to depend both on the ecological structure of the population and on the relative survival probability of the dispersed offspring. In the simplest case of a panmictic haploid population which occupies all its potential habitats, the optimal rate of dispersal was found to be $1/(2 - \beta)$, where β is the probability of a dispersed offspring to withstand the risks of dispersal.

The present work deals with diploid populations, in which the probability of an offspring's migration is determined by the genotype of the parent. In a later paper (Motro, 1982b) diploid populations in which this probability is determined by the offspring's genotype will be discussed.

* Present address: Department of Genetics, The Hebrew University, Jerusalem 91904, Israel.

412

We consider here diploid populations with several possible mating systems: random mating; mixed selfing and random mating; and vegetative reproduction combined with sexual reproduction. It is shown that in both the model of random mating and in the model of mixed selfing and random mating, natural selection operates to establish the same optimal rate of dispersal, independently of the mating system (but depending, as expected, on the survival probability of the dispersed offspring). Moreover, this rate is identical to the optimal rate of dispersal arising in the simple haploid model (Motro, 1982a). A lower optimal rate of dispersal, however, is obtained in the case in which the dispersed descendants are sexually produced, while those non-dispersed are produced by vegetative reproduction.

2. Diploid Population with Random Mating (the Simple Diploid Model)

In this section we investigate the optimal dispersal strategy in a randomly mating diploid population. The assumptions of this model are as follows:

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

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

(3) A fraction $1 - \alpha$ $(0 \leqslant \alpha \leqslant 1)$ of the progeny remains near the parent, whereas a fraction α is scattered away. The number α, the dispersal rate, is genetically determined (by a single locus).

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

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

(6) The successor of a living site is chosen at random from among all the young individuals at that place, which are either the non-dispersed descendants of the former occupant, or the immigrating descendants of other previous generation individuals.

(7) Due to loss of energy and other risks involved in dispersal, the probability of replacing an old individual is assumed to be smaller for a dispersed offspring than for a non-dispersed one. Thus, the probability that a dispersed descendant withstands the risks of dispersal, and finally reaches the state of competition on a living site, is only a fraction β $(0 < \beta \leqslant 1)$ of that probability for a descendant which stays at home. The smaller β is, the more stringent the environmental conditions endured by the dispersed descendants.

It should be noted that except for diploidy, the above assumptions are the same as those of the simple haploid model (Motro, 1982a).

In order to investigate selection on the rate of dispersal, we consider the locus which determines the dispersal rate α to have two alleles A and B, so that the population can consist of three genotypes AA, AB, and BB, with dispersal 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 the expected number of immigrating descendants per living site is $\lambda = \mu\beta(\alpha_1 u + \alpha_2 v + \alpha_3 w)$, where $1 - \beta$ is the proportion lost during dispersal. Assuming random mating (pollen or sperm are uniformly scattered over the living area of the population), the expected number of AA's among the foreign descendants is $\lambda_1 = \mu\beta(\alpha_1 pu + \frac{1}{2}\alpha_2 pv)$, the expected number of AB's is $\lambda_2 = \mu\beta(\alpha_1 qu + \frac{1}{2}\alpha_2 v + \alpha_3 pw)$ and that of BB is $\lambda_3 = \mu\beta(\frac{1}{2}\alpha_2 qv + \alpha_3 qw)$, 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 seeds per living site)

$$P_{11} = \frac{\mu(1 - \alpha_1)p + \lambda_1}{\mu(1 - \alpha_1) + \lambda}, \qquad P_{12} = \frac{\mu(1 - \alpha_1)q + \lambda_2}{\mu(1 - \alpha_1) + \lambda},$$

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

$$P_{21} = \frac{\frac{1}{2}\mu(1 - \alpha_2)p + \lambda_1}{\mu(1 - \alpha_2) + \lambda}, \qquad P_{22} = \frac{\frac{1}{2}\mu(1 - \alpha_2) + \lambda_2}{\mu(1 - \alpha_2) + \lambda},$$

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

$$P_{31} = \frac{\lambda_1}{\mu(1 - \alpha_3) + \lambda}, \qquad P_{32} = \frac{\mu(1 - \alpha_3)p + \lambda_2}{\mu(1 - \alpha_3) + \lambda},$$

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

We proceed to investigate the conditions for the stability of the monomorphic equilibria $(u, v, w) = (1, 0, 0)$ and $(u, v, w) = (0, 0, 1)$.

We start with the point $(u, v, w) = (0, 0, 1)$ (i.e., allele B is the only

TABLE 1

The Simple Diploid Model

	Site AA	Site AB	Site BB
Frequency	u	v	w
Mean progeny size	μ	μ	μ
Fraction of progeny dispersed	α_1	α_2	α_3
Expected number remaining near parent	$\mu(1-\alpha_1)$	$\mu(1-\alpha_2)$	$\mu(1-\alpha_3)$
Expected number of AA's among immigrants	$\lambda_1 = \mu\beta(\alpha_1 pu + \tfrac{1}{2}\alpha_2 pv)$	$\lambda_1 = \mu\beta(\alpha_1 pu + \tfrac{1}{2}\alpha_2 pv)$	$\lambda_1 = \mu\beta(\alpha_1 pu + \tfrac{1}{2}\alpha_2 pv)$
Expected number of AB's among immigrants	$\lambda_2 = \mu\beta(\alpha_1 qu + \tfrac{1}{2}\alpha_2 v + \alpha_3 pw)$	$\lambda_2 = \mu\beta(\alpha_1 qu + \tfrac{1}{2}\alpha_2 v + \alpha_3 pw)$	$\lambda_2 = \mu\beta(\alpha_1 qu + \tfrac{1}{2}\alpha_2 v + \alpha_3 pw)$
Expected number of BB's among immigrants	$\lambda_3 = \mu\beta(\tfrac{1}{2}\alpha_2 qv + \alpha_3 qw)$	$\lambda_3 = \mu\beta(\tfrac{1}{2}\alpha_2 qv + \alpha_3 qw)$	$\lambda_3 = \mu\beta(\tfrac{1}{2}\alpha_2 qv + \alpha_3 qw)$
Expected total number of immigrants per site	$\lambda = \mu\beta(\alpha_1 u + \alpha_2 v + \alpha_3 w)$	$\lambda = \mu\beta(\alpha_1 u + \alpha_2 v + \alpha_3 w)$	$\lambda = \mu\beta(\alpha_1 u + \alpha_2 v + \alpha_3 w)$
Expected number of AA's among competing young	$\mu(1-\alpha_1)p + \lambda_1$	$\tfrac{1}{2}\mu(1-\alpha_2)p + \lambda_1$	λ_1
Expected number of AB's among competing young	$\mu(1-\alpha_1)q + \lambda_2$	$\tfrac{1}{2}\mu(1-\alpha_2) + \lambda_2$	$\mu(1-\alpha_3)p + \lambda_2$
Expected number of BB's among competing young	λ_3	$\tfrac{1}{2}\mu(1-\alpha_2)q + \lambda_3$	$\mu(1-\alpha_3)q + \lambda_3$
Expected total number of competing young per site	$\mu(1-\alpha_1) + \lambda$	$\mu(1-\alpha_2) + \lambda$	$\mu(1-\alpha_3) + \lambda$

existing allele). The detailed analysis of the case $\alpha_2 \neq \alpha_3$ can be found in Appendix 1. The results are graphically summarized in Fig. 1.

For the complete dominance case $(\alpha_2 = \alpha_3)$, the analysis can be found in Appendix 2, and the results are summarized in Fig. 2.

Set $\alpha^* = 1/(2 - \beta)$. With the above results, we have proved

PROPOSITION. *Each* $\alpha_3 \neq \alpha^* = 1/(2 - \beta)$ *determines an inteval* I *(containing α^* on its interior and having α_3 as an open-end bound), such that if $\alpha_2 \in I$, then $(0, 0, 1)$ is unstable, and if $\alpha_2 \notin \bar{I}$ ($\bar{I}$ is the closure of I), then $(0, 0, 1)$ is stable.*

$$I = (1 - \alpha_3 + \beta\alpha_3, \alpha_3) \qquad if \quad \alpha_3 > \alpha^*$$
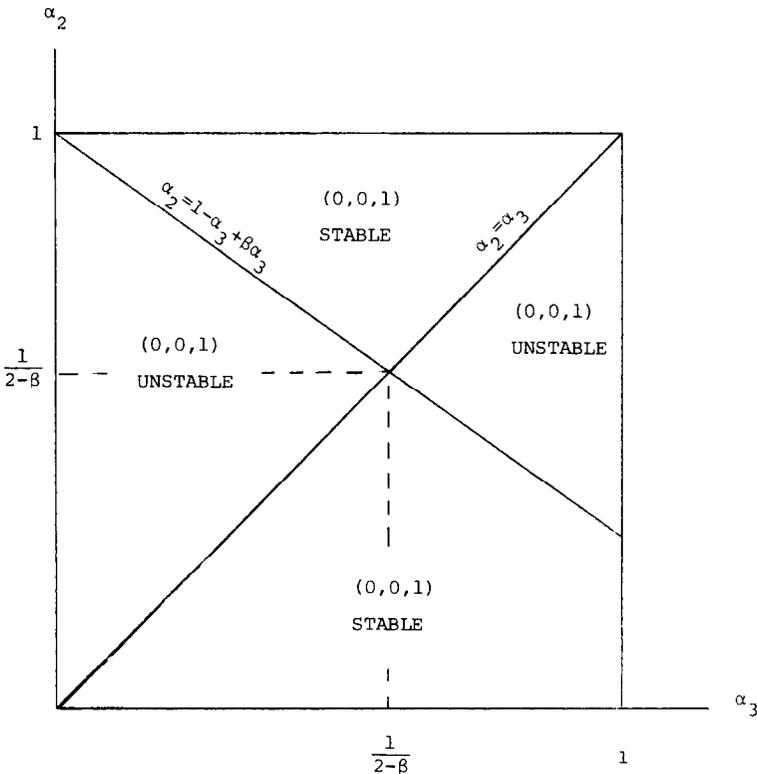$$= (\alpha_3, 1 - \alpha_3 + \beta\alpha_3) \qquad if \quad \alpha_3 < \alpha^*.$$

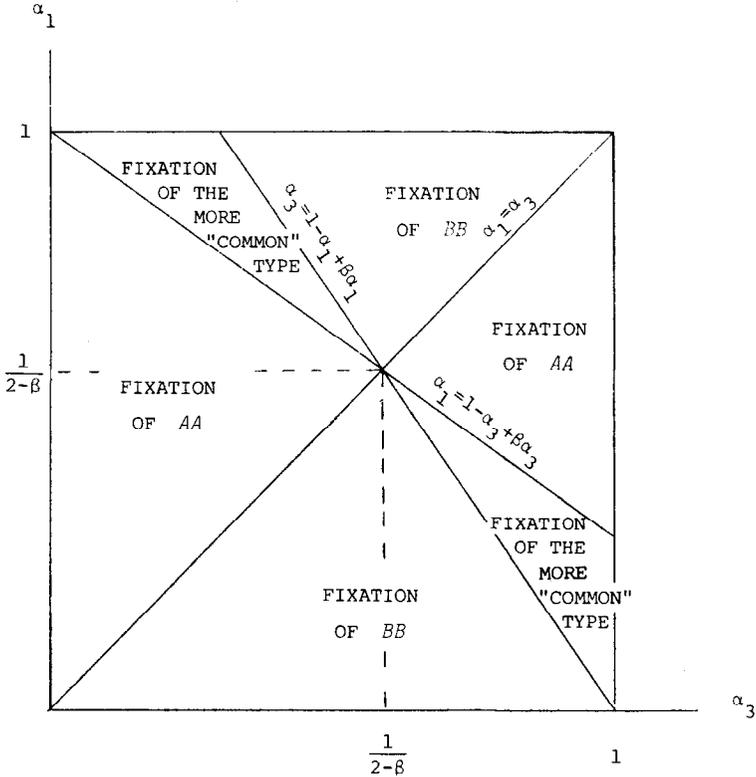FIG. 1. The simple diploid model, no dominance. Stability analysis of the monomorphic equilibrium $(u, v, w) = (0, 0, 1)$.

FIG. 2. The simple diploid model with dominance. On the line $\alpha_1 = 1 - \alpha_3 + \beta\alpha_3$, except for the point $(1/(2-\beta), 1/(2-\beta))$, $\bar{u} = 0$. On the line $\alpha_3 = 1 - \alpha_1 + \beta\alpha_1$, except for the point $(1/(2-\beta), 1/(2-\beta))$, $\bar{u} = 1$.

If $\alpha_2 = \alpha_3$, then if $\alpha_1 \in I$, $(0, 0, 1)$ is unstable, and if $a_1 \notin \bar{I}$, $(0, 0, 1)$ is stable. If $\alpha_3 = \alpha^*$, then I is an empty set.

On account of symmetry, the above results are also valid for the other monomorphic equilibrium point $(u, v, w) = (1, 0, 0)$, provided α_1 and α_3 are interchanged.

Let us define: α_i $(i = 1, 2)$ is "*closer*" to α^* than α_3, if $\alpha_i \in I$. α_i is "*further*" from α^* than α_3, if $\alpha_i \notin \bar{I}$. (Note that here, "closer" implies $|\alpha_i - \alpha^*| < |\alpha_3 - \alpha^*|$. The reverse is not necessarily true: Let $\alpha^* < \alpha_3$. Then each α_i in $(2\alpha^* - \alpha_3, \ 1 - \alpha_3 + \beta\alpha_3]$ satisfies $|\alpha_i - \alpha^*| < |\alpha_3 - \alpha^*|$, and $\alpha_i \notin I$.) Thus, the results of our proposition can be put as follows:

(1)   In the case of a completely dominant allele, if the rate of dispersal of the recessive type is "closer" to α^* than that of the dominant type, then the monomorphic equilibrium of the recessive type is stable, whereas that of the dominant is unstable.

If the rate of dispersal of the recessive type is "further" from α^* than that of the dominant type, the monomorphic equilibrium of the dominant type is stable, and that of the recessive is unstable.

(2)   If one of the homozygotes has a rate of dispersal which is "closer" to α^* than α_2 (which is the rate of dispersal 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.

(3)   If the α of both homozygotes are "closer" to α^* than the rate of dispersal of the heterozygote, both monomorphic equilibria are stable.

(4)   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 in the population (a protected polymorphism) is achieved.

Hence the type with the strategy $\alpha^* = 1/(2 - \beta)$ (i.e., which disperses a fraction $1/(2 - \beta)$ of its progeny) has a selective advantage over all types having other strategies: A population consisting of α^*-type individuals is stable against the appearance of any possible mutant, whereas the mutant having α^* as the rate of dispersal will be established in every population having any α different from the optimal value α^*. (In fact, for the dominance case we obtained even stronger results—a global fixation of the α^*-type.)

Surprisingly the same value $\alpha^* = 1/(2 - \beta)$ is also the optimal rate of dispersal in the simple haploid model (Motro, 1982a).

3. MIXED SELFING AND RANDOM MATING

Selfing—either autogamy, in which the stamens pollinate the stigmas of the same flower, or geitonogamy, in which pollination takes place between different flowers of the same plant—is a widespread occurrence in the plant kingdom. These two forms of selfing have the same genetic effect.

In this section we investigate the effect of selfing on the rate of dispersal. We make the same assumptions as in the simple diploid model, except that here a proportion t $(0 \leqslant t \leqslant 1)$ of the progeny of each individual is produced by selfing and $1 - t$ by random xenogamy. Thus, the transition probabilities of the simple diploid model (Section 2) change into

$$P_{11} = \frac{\mu(1-\alpha_1)[(1-t)\,p+t]+\lambda_1}{\mu(1-\alpha_1)+\lambda}, \qquad P_{12} = \frac{\mu(1-\alpha_1)(1-t)\,q+\lambda_2}{\mu(1-\alpha_1)+\lambda}$$

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

$$P_{21} = \frac{\frac{1}{2}\mu(1-\alpha_2)[(1-t)\,p+\frac{1}{2}t]+\lambda_1}{\mu(1-\alpha_2)+\lambda}, \qquad P_{22} = \frac{\frac{1}{2}\mu(1-\alpha_2)+\lambda_2}{\mu(1-\alpha_2)+\lambda}$$

$$P_{23} = \frac{\frac{1}{2}\mu(1-\alpha_2)[(1-t)\,q+\frac{1}{2}t]+\lambda_3}{\mu(1-\alpha_2)+\lambda}$$

$$P_{31} = \frac{\lambda_1}{\mu(1-\alpha_3)+\lambda}, \qquad P_{32} = \frac{\mu(1-\alpha_3)(1-t)\,p+\lambda_2}{\mu(1-\alpha_3)+\lambda}$$

$$P_{33} = \frac{\mu(1-\alpha_3)[(1-t)\,q+t]+\lambda_3}{\mu(1-\alpha_3)+\lambda},$$

where

$$\lambda = \mu\beta(\alpha_1 u + \alpha_2 v + \alpha_3 w)$$

$$\lambda_1 = \mu\beta\{\alpha_1[(1-t)\,p+t]\,u + \tfrac{1}{2}\alpha_2[(1-t)\,p+\tfrac{1}{2}t]\,v\}$$

$$\lambda_2 = \mu\beta[\alpha_1(1-t)\,qu + \tfrac{1}{2}\alpha_2 v + \alpha_3(1-t)\,pw]$$

$$\lambda_3 = \mu\beta\{\tfrac{1}{2}\alpha_2[(1-t)\,q+\tfrac{1}{2}t]\,v + \alpha_3[(1-t)\,q+t]\,w\}.$$

The analysis of the stability of the monomorphic equilibria is carried out in Appendix 3. It turns out that, for every proportion t $(0 \leqslant t \leqslant 1)$ of selfing, the monomorphic equilibrium of the homozygote which has $\alpha^* = 1/(2-\beta)$ as the rate of dispersal is stable against the appearance of any possible mutant having $\alpha \neq \alpha^*$.

The fact that we get the same optimal rate of dispersal for every mixture of selfing and random mating may seem surprising at first. Nevertheless, we have already shown that for the case of completely random mating (the simple diploid model) and for complete selfing in the limit situation (which is equivalent to the simple haploid model), we get the same optimal rate $\alpha^* = 1/(2-\beta)$. Therefore it is not surprising that, at least from the point of view of stability against mutations, selfing, in any proportion, does not affect the optimal rate of dispersal.

4. Mixed Vegetative and Sexual Reproduction

The combination of sexual and vegetative reproduction is quite a common phenomenon among plants and animals. In plants exhibiting both sexual and

vegetative reproduction, the dispersed descendants are usually from the seeds produced sexually, while descendants which remain near the parent plant are vegetatively produced (in the form of bulblets, cormlets, rhizomes, etc.) and are genetically identical to the parent plant. In many sessile animals, such as sponges, sea anemones, marine hydras, and corals, the dispersed larvae are, usually, sexually produced, while vegetative descendants are produced by budding and remain close to the parent.

In this section we develop a model similar to the simple diploid model (Section 2), except that here, $1 - \alpha$ is the fraction of the reproductive investment used in producing vegetative descendants (including the investment in producing the parent's own regeneration organs for the next season) and α is the fraction invested in sexual reproduction. The progeny produced vegetatively remain near the parent, whereas those produced sexually are uniformly dispersed over the entire population range.
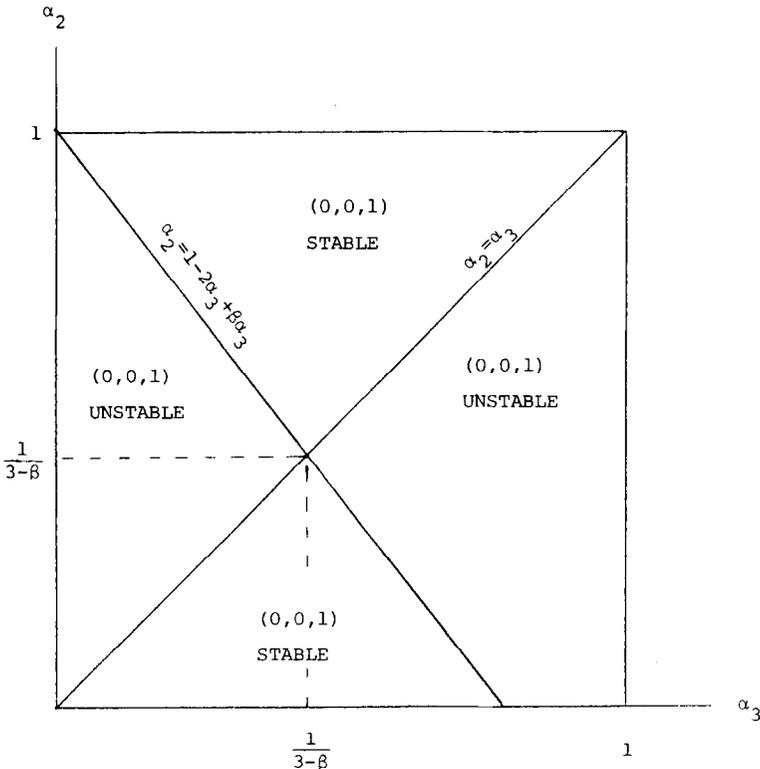

FIG. 3. The mixed vegetative and sexual reproduction model, no dominance. Stability analysis of the monomorphic equilibrium $(u, v, w) = (0, 0, 1)$.

Assuming a large number of seeds per living site, the transition probabilities P_{ij} are

$$P_{11} = \frac{\mu(1 - \alpha_1) + \lambda_1}{\mu(1 - \alpha_1) + \lambda}, \quad P_{12} = \frac{\lambda_2}{\mu(1 - \alpha_1) + \lambda}, \quad P_{13} = \frac{\lambda_3}{\mu(1 - \alpha_1) + \lambda}$$

$$P_{21} = \frac{\lambda_1}{\mu(1 - \alpha_2) + \lambda}, \quad P_{22} = \frac{\mu(1 - \alpha_2) + \lambda_2}{\mu(1 - \alpha_2) + \lambda}, \quad P_{23} = \frac{\lambda_3}{\mu(1 - \alpha_2) + \lambda}$$

$$P_{31} = \frac{\lambda_1}{\mu(1 - \alpha_3) + \lambda}, \quad P_{32} = \frac{\lambda_2}{\mu(1 - \alpha_3) + \lambda}, \quad P_{33} = \frac{\mu(1 - \alpha_3) + \lambda_3}{\mu(1 - \alpha_3) + \lambda}$$
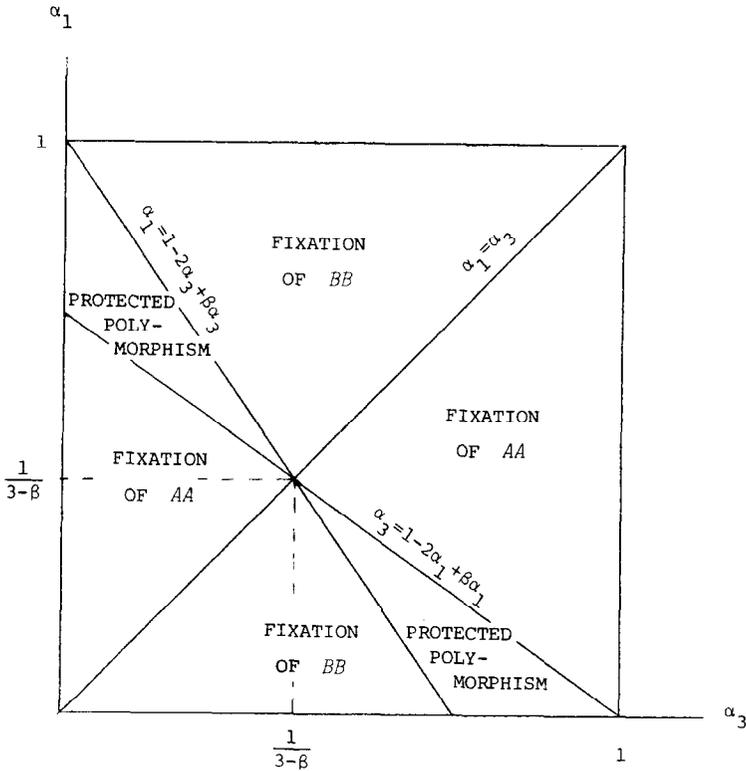

FIG. 4. The mixed vegetative and sexual reproduction model with dominance. On the line $\alpha_1 = 1 - 2\alpha_3 + \beta\alpha_3$, except for the point $(1/(3 - \beta), 1/(3 - \beta))$, $\bar{u} = 0$. On the line $\alpha_3 = 1 - 2\alpha_1 + \beta\alpha_1$, except for the point $(1/(3 - \beta), 1/(3 - \beta))$, $\bar{u} = 1$.

where

$$\lambda = \mu\beta(\alpha_1 u + \alpha_2 v + \alpha_3 w)$$
$$\lambda_1 = \mu\beta(\alpha_1 pu + \tfrac{1}{2}\alpha_2 pv)$$
$$\lambda_2 = \mu\beta(\alpha_1 qu + \tfrac{1}{2}\alpha_2 v + \alpha_3 pw)$$
$$\lambda_3 = \mu\beta(\tfrac{1}{2}\alpha_2 qv + \alpha_3 qw).$$

Again, we investigate the stability of $(u, v, w) = (0, 0, 1)$ and $(u, v, w) = (1, 0, 0)$. The analysis is in Appendix 4 (for the case without dominance) and in Appendix 5 (for the complete dominance case). The results are presented in Figs. 3 and 4, and we conclude that the optimal ratio of dispersal is $1/(3 - \beta)$, a ratio which is smaller than the α^* obtained in the simple diploid model.

Remark. This model does not take into account other advantages of sexual reproduction over vegetative propagation, which probably prevail in nature (see, e.g., Williams, 1975). It is expected that these advantages, which are difficult to analyze quantitatively, will act to decrease the investment in vegetative reproduction to a smaller amount than the fraction $1 - 1/(3 - \beta)$ obtained in this model.

5. Discussion

In this work we were concerned with the strategy of progeny dispersal. We examined the genetics of the division of the progeny into those which remain near the parent and those which are dispersed, where the survival probability of a dispersed descendant is smaller than that of an offspring which stays at home. In each of the diploid models studied here (which differ from each other by the mating system of the population), a single optimal strategy of progeny division was found to exist. Here, "optimal" means that the type with such a division strategy has a selective advantage over other types. In each case, the optimal strategy implies that a substantial fraction of the progeny will be dispersed, a fraction which is an increasing function of the survival probability of the dispersed descendants.

Interestingly, we obtained exactly the same value for the optimal rate of dispersal in the diploid model of complete random mating and in the model of mixed selfing and random mating. Moreover, this value is also identical with the optimal rate of dispersal arrived at in the simple haploid model, treated in a previous paper (Motro, 1982a).

We also treated a model in which the dispersed descendants are produced

by random mating, while those non-dispersed are produced vegetatively, thus genetically identical to the parent. As expected, the optimal rate of dispersal in this model is smaller than that of the models previously discussed.

APPENDIX 1:   STABILITY ANALYSIS OF THE MONOMORPHIC EQUILIBRIUM—THE SIMPLE DIPLOID MODEL

We investigate here the conditions for the stability of the monomorphic equilibrium point $(u, v, w) = (0, 0, 1)$, for the general case $\alpha_2 \neq \alpha_3$. We apply the local stability analysis technique, and consider the eigenvalues of the matrix

$$\begin{bmatrix} \dfrac{\partial p'}{\partial p}\Big|_{\substack{p=0 \\ v=0}} & \dfrac{\partial p'}{\partial v}\Big|_{\substack{p=0 \\ v=0}} \\[2em] \dfrac{\partial v'}{\partial p}\Big|_{\substack{p=0 \\ v=0}} & \dfrac{\partial v'}{\partial v}\Big|_{\substack{p=0 \\ v=0}} \end{bmatrix}$$

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

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

Hence

$$\frac{\partial p'}{\partial p}\bigg|_{\substack{p=0 \\ v=0}} = \frac{\tfrac{1}{2}(1 - \alpha_1)}{1 - \alpha_1 + \beta\alpha_3} + \frac{\tfrac{1}{2}(1 - \alpha_3) + \tfrac{1}{2}\beta(\alpha_1 + \alpha_3)}{1 - \alpha_3 + \beta\alpha_3}$$

$$\frac{\partial p'}{\partial v}\bigg|_{\substack{p=0 \\ v=0}} = \frac{-\tfrac{1}{4}(1 - \alpha_1)}{1 - \alpha_1 + \beta\alpha_3} + \frac{\tfrac{1}{4}(1 - \alpha_2)}{1 - \alpha_2 + \beta\alpha_3} + \frac{\tfrac{1}{4}\beta(\alpha_2 - \alpha_1)}{1 - \alpha_3 + \beta\alpha_3}$$

$$\frac{\partial v'}{\partial p}\bigg|_{\substack{p=0 \\ v=0}} = \frac{1 - \alpha_1}{1 - \alpha_1 + \beta\alpha_3} + \frac{1 - \alpha_3 + \beta(\alpha_1 + \alpha_3)}{1 - \alpha_3 + \beta\alpha_3}$$

$$\frac{\partial v'}{\partial v}\bigg|_{\substack{p=0 \\ v=0}} = \frac{-\tfrac{1}{2}(1 - \alpha_1)}{1 - \alpha_1 + \beta\alpha_3} + \frac{\tfrac{1}{2}(1 - \alpha_2)}{1 - \alpha_2 + \beta\alpha_3} + \frac{\tfrac{1}{2}\beta(\alpha_2 - \alpha_1)}{1 - \alpha_3 + \beta\alpha_3}.$$

The eigenvalues of the above matrix are $x_1 = 0$ and

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

$$\text{Sign}(1 - x_2) = \text{sign} \left\{ \frac{\frac{1}{2}\beta(\alpha_3 - \alpha_2)(1 - \alpha_3 + \beta\alpha_3 - \alpha_2)}{(1 - \alpha_2 + \beta\alpha_3)(1 - \alpha_3 + \beta\alpha_3)} \right\}$$

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

If $x_2 < 1$, i.e., if $(\alpha_3 - \alpha_2)(1 - \alpha_3 + \beta\alpha_3 - \alpha_2) > 0$, then $(u, v, w) = (0, 0, 1)$ is stable.

If $x_2 > 1$, i.e., if $(\alpha_3 - \alpha_2)(1 - \alpha_3 + \beta\alpha_3 - \alpha_2) < 0$, then $(u, v, w) = (0, 0, 1)$ is unstable.

The results are graphically summarized in Fig. 1.

APPENDIX 2: ANALYSIS OF THE COMPLETE DOMINANCE CASE—THE SIMPLE DIPLOID MODEL

For $\alpha_2 = \alpha_3$ (i.e., complete dominance of B over A), the largest eigenvalue x_2 (of Appendix 1) is equal to 1, and so we shall look into $\Delta p = p' - p$:

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

$$= \frac{\frac{1}{2}\mu(1 - \alpha_1)q + \lambda_1 + \frac{1}{2}\lambda_2 - \lambda p}{\mu(1 - \alpha_1) + \lambda}u$$

$$+ \frac{\frac{1}{2}\mu(1 - \alpha_2)(\frac{1}{2} - p) + \lambda_1 + \frac{1}{2}\lambda_2 - \lambda p}{\mu(1 - \alpha_2) + \lambda}v$$

$$+ \frac{-\frac{1}{2}\mu(1 - \alpha_3)p + \lambda_1 + \frac{1}{2}\lambda_2 - \lambda p}{\mu(1 - \alpha_3) + \lambda}w,$$

where

$$\lambda_1 + \tfrac{1}{2}\lambda_2 - \lambda p = \mu\beta[\tfrac{1}{2}\alpha_1 qu + \tfrac{1}{2}\alpha_2(\tfrac{1}{2} - p)v - \tfrac{1}{2}\alpha_3 pw].$$

Denoting

$$\pi = \frac{u}{\mu(1 - \alpha_1) + \lambda} + \frac{v}{\mu(1 - \alpha_2) + \lambda} + \frac{w}{\mu(1 - \alpha_3) + \lambda},$$

we get

$$\Delta p = \tfrac{1}{2}\mu qu \left[\frac{1 - \alpha_1}{\mu(1 - \alpha_1) + \lambda} + \beta\alpha_1\pi \right]$$

$$+ \tfrac{1}{2}\mu(\tfrac{1}{2} - p)v \left[\frac{1 - \alpha_2}{\mu(1 - \alpha_2) + \lambda} + \beta\alpha_2\pi \right]$$

$$- \tfrac{1}{2}\mu pw \left[\frac{1 - \alpha_3}{\mu(1 - \alpha_3) + \lambda} + \beta\alpha_3\pi \right].$$

Since $\frac{1}{2}(\frac{1}{2} - p)v = \frac{1}{2}pw - \frac{1}{2}qu$, it follows that

$$\Delta p = \frac{1}{2}\mu qu \left[\frac{1 - \alpha_1}{\mu(1 - \alpha_1) + \lambda} + \beta\alpha_1\pi - \frac{1 - \alpha_2}{\mu(1 - \alpha_2) + \lambda} - \beta\alpha_2\pi \right]$$

$$+ \frac{1}{2}\mu pw \left[\frac{1 - \alpha_2}{\mu(1 - \alpha_2) + \lambda} + \beta\alpha_2\pi - \frac{1 - \alpha_3}{\mu(1 - \alpha_3) + \lambda} - \beta\alpha_3\pi \right].$$

If $\alpha_2 = \alpha_3$, the second term in the right-hand side of our equation vanishes. Also, in this case,

$$\lambda = \mu\beta[\alpha_1 u + \alpha_3(1 - u)] \quad \text{and} \quad \pi = \frac{u}{\mu(1 - \alpha_1) + \lambda} + \frac{1 - u}{\mu(1 - \alpha_3) + \lambda}.$$

Hence (if $\alpha_2 = \alpha_3$),

$$\Delta p = \frac{-\frac{1}{2}\mu^2\beta qu(\alpha_3 - \alpha_1)}{[\mu(1 - \alpha_1) + \lambda][\mu(1 - \alpha_3) + \lambda]} [1 - \alpha_3 + \beta\alpha_3 - \alpha_1 - \beta(\alpha_3 - \alpha_1)u].$$

Setting

$$\tilde{u} = \frac{1 - \alpha_3 + \beta\alpha_3 - \alpha_1}{\beta(\alpha_3 - \alpha_1)},$$

we get (if $u \neq 0$)

$$\text{sign}(\Delta p) = \text{sign}[(\alpha_3 - \alpha_1)^2 (u - \tilde{u})] = \text{sign}(u - \tilde{u}).$$

Thus, if $\tilde{u} \leqslant 0$, then $\Delta p > 0$ for every p $(0 < p < 1)$, which entails a global fixation of AA.

If $\tilde{u} \geqslant 1$, then $\Delta p < 0$ for every p $(0 < p < 1)$, and we obtain a global fixation of BB.

If $0 < \tilde{u} < 1$, then $\Delta p > 0$ for $u > \tilde{u}$ and $0 < p < 1$, and $\Delta p < 0$ for $u < \tilde{u}$ and $0 < p < 1$. In this case it can be shown that there exists an unstable equilibrium $(\tilde{u}, 2\sqrt{\tilde{u}}(1 - \sqrt{\tilde{u}}), (1 - \sqrt{\tilde{u}})^2)$. Since the two monomorphic equilibria are stable, there is a fixation of the more "common" allele.

The results of the complete dominance case are graphically summarized in Fig. 2.

APPENDIX 3: STABILITY ANALYSIS OF THE MONOMORPHIC
EQUILIBRIUM—THE MIXED SELFING AND RANDOM MATING MODEL

Here,

$$\frac{\partial p'}{\partial p}\bigg|_{\substack{p=0 \\ v=0}} = \frac{\frac{1}{2}(1-\alpha_1)(1+t)}{1-\alpha_1+\beta\alpha_3} + \frac{\frac{1}{2}(1-\alpha_3)(1-t)+\frac{1}{2}\beta[\alpha_1(1+t)+\alpha_3(1-t)]}{1-\alpha_3+\beta\alpha_3}$$

$$\frac{\partial p'}{\partial v}\bigg|_{\substack{p=0 \\ v=0}} = \frac{-\frac{1}{4}(1-\alpha_1)(1+t)}{1-\alpha_1+\beta\alpha_3} + \frac{\frac{1}{4}(1-\alpha_2)(1+t)}{1-\alpha_2+\beta\alpha_3} + \frac{\frac{1}{4}\beta(\alpha_2-\alpha_1)(1+t)}{1-\alpha_3+\beta\alpha_3}$$

$$\frac{\partial v'}{\partial p}\bigg|_{\substack{p=0 \\ v=0}} = \frac{(1-\alpha_1)(1-t)}{1-\alpha_1+\beta\alpha_3} + \frac{[1-\alpha_3+\beta(\alpha_1+\alpha_3)](1-t)}{1-\alpha_3+\beta\alpha_3}$$

$$\frac{\partial v'}{\partial v}\bigg|_{\substack{p=0 \\ v=0}} = \frac{-\frac{1}{2}(1-\alpha_1)(1-t)}{1-\alpha_1+\beta\alpha_3} + \frac{\frac{1}{2}(1-\alpha_2)}{1-\alpha_2+\beta\alpha_3} + \frac{\frac{1}{2}\beta[\alpha_2-\alpha_1(1-t)]}{1-\alpha_3+\beta\alpha_3}.$$

By setting

$$g(\alpha) = \frac{1-\alpha}{1-\alpha+\beta\alpha_3} + \frac{\beta\alpha}{1-\alpha_3+\beta\alpha_3},$$

the derivatives at $p=0$, $v=0$ take the form

$$\frac{\partial p'}{\partial p} = \frac{1}{2}(1+t)\,g(\alpha_1) + \frac{1}{2}(1-t), \qquad \frac{\partial p'}{\partial v} = -\frac{1}{4}(1+t)[\,g(\alpha_2) - g(\alpha_1)]$$

$$\frac{\partial v'}{\partial p} = (1-t)\,g(\alpha_1) + (1-t), \qquad \frac{\partial v'}{\partial v} = -\frac{1}{2}(1-t)\,g(\alpha_1) + \frac{1}{2}g(\alpha_2).$$

The eigenvalues of the above matrix are the solutions of the equation (in which the derivatives are taken at $p=0$ and $v=0$)

$$x^2 - x\left(\frac{\partial p'}{\partial p} + \frac{\partial v'}{\partial v}\right) + \frac{\partial p'}{\partial p}\frac{\partial v'}{\partial v} - \frac{\partial p'}{\partial v}\frac{\partial v'}{\partial p} = 0. \tag{A3.1}$$

The parabola in the left-hand side of Eq. (A3.1) has a minimum at $x = x_m$, where

$$x_m = \frac{1}{2}\left(\frac{\partial p'}{\partial p} + \frac{\partial v'}{\partial v}\right) = \frac{1}{2}\left[tg(\alpha_1) + \frac{1}{2}g(\alpha_2) + \frac{1}{2}(1-t)\right] \geqslant 0$$

and the minimal value of the parabola is

$$\frac{\partial p'}{\partial p}\frac{\partial v'}{\partial v} - \frac{\partial p'}{\partial v}\frac{\partial v'}{\partial p} - \frac{1}{4}\left(\frac{\partial p'}{\partial p} + \frac{\partial v'}{\partial v}\right)^2$$

$$= \tfrac{1}{4}t[2(1-t)\,g(\alpha_1) - (1-t)\,g(\alpha_2) + (1+t)\,g(\alpha_1)\,g(\alpha_2)]$$

$$\quad - \tfrac{1}{4}[tg(\alpha_1) + \tfrac{1}{2}g(\alpha_2) + \tfrac{1}{2}(1-t)]^2$$

$$= -\tfrac{1}{4}[tg(\alpha_1) - \tfrac{1}{2}g(\alpha_2) - \tfrac{1}{2}(1-t)]^2 - \tfrac{1}{4}t(1-t)\,g(\alpha_2)[1 + g(\alpha_1)]$$

$$\leqslant 0.$$

Hence Eq. (A3.1) has real solutions.

We now show that if $\alpha_3 = 1/(2-\beta)$, then for any α_1 and α_2 (provided that not both are equal to α_3 simultaneously), both solutions of Eq. (A3.1) are smaller, in absolute value, than 1.

If $\alpha_3 = 1/(2-\beta)$, then $g(\alpha) \leqslant 1$ for every $\alpha \in [0, 1]$,. (The equality holds only for $\alpha = \alpha_3$.) In this case,

$$x_{\mathrm{m}} \leqslant \tfrac{1}{2}[t + \tfrac{1}{2} + \tfrac{1}{2}(1-t)] = \tfrac{1}{2}(1 + \tfrac{1}{2}t) < 1,$$

and so it is sufficient to check that the value of the parabola at $x = 1$ is positive. Indeed,

$$1 - tg(\alpha_1) - \tfrac{1}{2}g(\alpha_2) - \tfrac{1}{2}(1-t)$$

$$\quad + \tfrac{1}{4}t[2(1-t)\,g(\alpha_1) - (1-t)\,g(\alpha_2) + (1+t)\,g(\alpha_1)\,g(\alpha_2)]$$

$$\quad > 1 - t - \tfrac{1}{2} - \tfrac{1}{2}(1-t) + \tfrac{1}{4}t[2(1-t) - (1-t) + (1+t)] = 0.$$

APPENDIX 4: STABILITY ANALYSIS OF THE MONOMORPHIC EQUILIBRIUM—THE MIXED VEGETATIVE AND SEXUAL REPRODUCTION MODEL

Here,

$$\left.\frac{\partial p'}{\partial p}\right|_{\substack{p=0 \\ v=0}} = \frac{1-\alpha_1}{1-\alpha_1+\beta\alpha_3} + \frac{\tfrac{1}{2}\beta(\alpha_1+\alpha_3)}{1-\alpha_3+\beta\alpha_3}$$

$$\left.\frac{\partial p'}{\partial v}\right|_{\substack{p=0 \\ v=0}} = \frac{-\tfrac{1}{2}(1-\alpha_1)}{1-\alpha_1+\beta\alpha_3} + \frac{\tfrac{1}{2}(1-\alpha_2)}{1-\alpha_2+\beta\alpha_3} + \frac{\tfrac{1}{4}\beta(\alpha_2-\alpha_1)}{1-\alpha_3+\beta\alpha_3}$$

$$\frac{\partial v'}{\partial p}\bigg|_{\substack{p=0\\v=0}} = \frac{\beta(\alpha_1 + \alpha_3)}{1 - \alpha_3 + \beta\alpha_3}$$

$$\frac{\partial v'}{\partial v}\bigg|_{\substack{p=0\\v=0}} = \frac{1 - \alpha_2}{1 - \alpha_2 + \beta\alpha_3} + \frac{\frac{1}{2}\beta(\alpha_2 - \alpha_1)}{1 - \alpha_3 + \beta\alpha_3}.$$

The eigenvalues are

$$x_1 = \frac{1 - \alpha_1}{1 - \alpha_1 + \beta\alpha_3} \geqslant 0$$

and

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

If $\alpha_3 = 0$, then $x_1 = 1$ and $x_2 > 1$, thus implying non-stability of $(0, 0, 1)$. Otherwise, $x_1 < 1$ and thus $(0, 0, 1)$ is stable if $x_2 < 1$ and unstable if $x_2 > 1$.

$$\text{Sign}(1 - x_2) = \text{sign}\left\{\frac{\frac{1}{2}\beta(\alpha_3 - \alpha_2)(1 - 2\alpha_3 + \beta\alpha_3 - \alpha_2)}{(1 - \alpha_2 + \beta\alpha_3)(1 - \alpha_3 + \beta\alpha_3)}\right\}$$

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

The results (for $\alpha_2 \neq \alpha_3$) are summarized in Fig. 3.

APPENDIX 5:   ANALYSIS OF THE COMPLETE DOMINANCE CASE—
THE MIXED VEGETATIVE AND SEXUAL REPRODUCTION MODEL

For $\alpha_2 = \alpha_3$, $x_2 = 1$ and so we have to look into $\Delta p = p' - p$. Along the lines of the simple diploid model (Section 2 and Appendix 2), and using the same notation, we get

$$\Delta p = \mu q u \left[\frac{1 - \alpha_1}{\mu(1 - \alpha_1) + \lambda} + \frac{1}{2}\beta\alpha_1\pi - \frac{1 - \alpha_2}{\mu(1 - \alpha_2) + \lambda} - \frac{1}{2}\beta\alpha_2\pi\right]$$

$$+ \mu p w \left[\frac{1 - \alpha_2}{\mu(1 - \alpha_2) + \lambda} + \frac{1}{2}\beta\alpha_2\pi - \frac{1 - \alpha_3}{\mu(1 - \alpha_3) + \lambda} - \frac{1}{2}\beta\alpha_3\pi\right].$$

If $\alpha_2 = \alpha_3$, the second term in the right-hand side of the above equation vanishes. After some rearranging, we get

$$\Delta p = \frac{-\tfrac{1}{2}\beta\mu^2 q u(\alpha_3 - \alpha_1)}{[\mu(1 - \alpha_1) + \lambda][\mu(1 - \alpha_3) + \lambda]}$$
$$\times [1 - 2\alpha_3 + \beta\alpha_3 - \alpha_1 + (1 - \beta)(\alpha_3 - \alpha_1) u].$$

We set

$$\tilde{u} = \frac{1 - 2\alpha_3 + \beta\alpha_3 - \alpha_1}{(1 - \beta)(\alpha_1 - \alpha_3)}.$$

Thus, for $u \neq 0$,

$$\text{sign}(\Delta p) = \text{sign}[(\alpha_1 - \alpha_3)^2 (\tilde{u} - u)] = \text{sign}(\tilde{u} - u).$$

Thus, if $\tilde{u} \geqslant 1$, then $\Delta p > 0$ for every p $(0 < p < 1)$. This entails the global fixation of AA.

If $\tilde{u} \leqslant 0$, then $\Delta p < 0$ for every p $(0 < p < 1)$; thus, the global fixation of BB is obtained.

If $0 < \tilde{u} < 1$, then $\Delta p > 0$ for $u < \tilde{u}$ and $\Delta p < 0$ for $u > \tilde{u}$. In this case both monomorphic equilibria are unstable (a protected polymorphism).

The results of the complete dominance case are summarized in Fig. 4.

ACKNOWLEDGMENTS

REFERENCES

MOTRO, U. 1982a Optimal rates of dispersal: I. Haploid populations. *Theor. Pop. Biol.* **21**, 394–411.

MOTRO, U. 1982b Optimal rates of dispersal: III. Parent–offspring conflict. *Theor. Pop. Biol.*, in press.

WILLIAMS, G. C. 1975 "Sex and Evolution," Princeton Univ. Press, Princeton, N. J.