*Heredity* (1976), **37** (1), 59-67

# DISPERSION-SELECTION BALANCE IN LOCALISED PLANT POPULATIONS*

THOMAS NAGYLAKI
*Department of Biophysics and Theoretical Biology, The University of Chicago,
920 East 58th Street, Chicago, Illinois 60637*

Received 29.xi.75

## SUMMARY

Two single-locus deterministic models are constructed for the maintenance of genetic variability in localised plant populations. In the first model, it is supposed that self-pollination is complete, heterozygotes are absent, and only seeds disperse. Then the ploidy is arbitrary. In the second, it is assumed that the plants are diploid, cross-pollination is total, and only pollen disperse. Explicit conditions for a protected polymorphism are derived for each model in the diallelic two-niche case. These conditions are simplified, displayed graphically, and discussed extensively for directional selection for different alleles in the two niches. If the amount of seed dispersal is divided by two, the criteria for a protected polymorphism in the self-pollinating scheme become identical to the criteria in the cross-pollinating situation with no multiplicative dominance. The restrictions that must be placed on the fitnesses for a protected polymorphism always become more stringent as the amount of dispersion increases. If the dispersion rate is not very close to zero and the selection coefficients are very small, the protection conditions reduce to overdominance for the mean fitnesses in the habitat. Unless there is complete dominance, protection always exists with fixed fitnesses for sufficiently low non-zero dispersal. For any amount of dispersion, there is always protection in the second model if, in each niche, the fitness of the deleterious homozygote is less than that of the heterozygote.

## 1. INTRODUCTION

THERE has been much interest recently in the maintenance of genetic variability by the joint action of migration and selection. Considerable progress has been made in deriving conditions for the existence of clines and in relating the equilibrium gene frequency in the cline to the migration and selection patterns, and some results concerning uniqueness and stability have been proved (Slatkin, 1973; Fleming, 1975; Karlin and Dyn, 1976; Nagylaki, 1975*a*, *b*, 1976). Simultaneously, multiniche migration-selection models were formulated generally, and conditions for a protected polymorphism were given (Bulmer, 1972; Christiansen, 1974, 1975; Karlin, 1976).

In this paper, we shall study the maintenance of genetic diversity in localised populations of annual plants. Most work on clines employs continuous-time, continuous-space models because they are analytically more tractable than the corresponding discrete schemes. Although the continuous-time description is probably reasonably accurate for many, perhaps most, populations with overlapping generations (Nagylaki and Crow, 1974; Cornette, 1975), it is clearly inappropriate for annual plants in the presence of substantial selection. Furthermore, the assumption of continuous local dispersal underlying the treatment of clines is not well

---

* Supported by the National Science Foundation (Grant No. DEB76-01550).

suited to plant populations occupying a small area and having considerable dispersion of seeds or pollen.

We shall construct two single-locus deterministic models with discrete non-overlapping generations, taking into account the reproductive and dispersal mechanisms of plants. In the first, we suppose that self-pollination is complete. Then only seeds will disperse, and heterozygotes will be rapidly eliminated unless there is strong selection in their favour. Since stable polymorphism is guaranteed in that case, we shall study the effect of dispersion on genetic diversity by assuming that only homozygotes are present. The ploidy is clearly arbitrary. In the second model, we posit that the plants are diploid, cross-pollination is total, and only pollen disperse. We assume that at each location a certain proportion of the seeds in the first scheme and pollen in the second come from the immediate neighbourhood, while the rest come at random from the entire population. This is probably a reasonable simplification for small habitat size.

In his discussion of the Levene model (Levene, 1953), Dempster (1955) distinguished two modes of selection in subdivided populations. In the first mode, employed by Levene (1953) and now usually called " soft selection ", the proportion of adults in each niche is fixed. As observed by Dempster (1955), this should be a good approximation if the population is regulated within each niche. If it is total population size that is controlled, Dempster pointed out that it is better to suppose that the fraction of zygotes in each niche is prescribed, and the fraction of adults is proportional to the mean fitness in the niche, a scheme now commonly termed " hard selection ". Since plants compete for resources locally, it is plain that we should hypothesise soft selection.

Instead of finding equilibria and investigating their stability, Levene (1953) sought conditions required for the maintenance of polymorphism. If, no matter what the initial conditions are, the population cannot become monomorphic, we shall say there is a " protected polymorphism " (Prout, 1968). In general, a protected polymorphism is neither necessary nor sufficient for the existence of a stable polymorphic equilibrium. For instance, on the one hand, there may be a (locally) stable polymorphic equilibrium, but selection may remove a rare allele from the population. On the other hand, polymorphism may be maintained by a stable limit cycle. We shall derive sufficient conditions for a protected polymorphism for the diallelic two-niche case. Mathematically, the two-niche models are modifications of those of Deakin (1966) and Maynard Smith (1966, 1970).

The models developed in this paper were motivated by recent studies of intrapopulation differentiation in some species of annual plants (Linhart, 1972, 1973, 1974; Linhart and Baker, 1973; Keeler, 1975). The predominantly self-pollinating species *Veronica peregrina* L. (Scrophulariaceae) and *Boisduvalia glabella* Walp. (Onagraceae) and the primarily outcrossing species *Downingia concolor* Green (Companulaceae) grow in small vernal pools. The pools are always less than 10 m in diameter, and are sometimes much smaller, but typically contain thousands of plants. Plants in the central region of the pool enjoy a larger and less variable amount of moisture than those in the peripheral area. Winter temperatures fluctuate less at the centre, under water, than at the periphery, in the open air, where water and surface soil can freeze overnight. The population densities near the centre are high, and competition is mainly intraspecific. Near the periphery, the population densities are much lower, and competition is chiefly against various grasses. The environmental difference between the centre and periphery is reflected in the different characteristics of the progeny of plants from those regions when grown under uniform greenhouse conditions. Plants from the periphery produce more, but smaller, seeds than those from the centre. This may be advantageous in increasing dispersion, raising the probability of survival, and permitting more genotypes to test the rather variable environment (Linhart, 1974). Progeny of peripheral plants are taller than those of the central ones, perhaps allowing them to compete more successfully with the taller grasses. Progeny of plants from a cultivated field, where the amount of dispersion is very high, show no statistically significant differentiation (Linhart, 1974).

The self-pollinating scheme in Sec. 2 is a rough conceptual model for *V. peregrina* and *B. glabella*, and the cross-pollinating model in Sec. 3 mimics *D. concolor*. The two niches may be identified with the centre and periphery. The population sizes are probably large enough to justify neglecting random drift. No numerical comparisons are intended: the traits discussed above are undoubtedly too complicated genetically for our simple models.

## 2. SELF-POLLINATION

Let $p_i(\mathbf{x}, t)$ be the frequency of the allele $A_i$ immediately after fertilisation at location $\mathbf{x}$ in generation $t$. Since we assume that, due to past complete self-pollination, heterozygotes have been eliminated, $p_i$ is also the frequency of homozygous seeds carrying $A_i$. We suppose that at each location a fraction $\beta_1 (0 \leqq \beta_1 \leqq 1)$ of the seeds originate locally, while a proportion $\beta_2 (= 1-\beta_1)$ come at random from the entire population. Let the $N$ plants in the habitat be distributed with density $\rho(\mathbf{x})$. Then the frequency of $A_i$ in seeds in generation $t$ reads

$$\bar{p}_i(t) = N^{-1} \int p_i(\mathbf{x}, t)\rho(\mathbf{x}) d^2x, \tag{1}$$

where $d^2x$ is the element of area. Therefore, the frequency of $A_i$ at $\mathbf{x}$ just after dispersion of seeds is

$$P_i(\mathbf{x}, t) = \beta_1 p_i(\mathbf{x}, t) + \beta_2 \bar{p}_i(t). \tag{2}$$

If $w_i(\mathbf{x})$ represents the seed-to-adult viability of homozygous plants carrying $A_i$, our basic equation is

$$p_i(\mathbf{x}, t+1) = w_i(\mathbf{x}) P_i(\mathbf{x}, t)/\bar{w}(\mathbf{x}, t), \tag{3}$$

where the mean fitness at $\mathbf{x}$ is given by

$$\bar{w}(\mathbf{x}, t) = \sum_i w_i(\mathbf{x}, t) P_i(\mathbf{x}, t). \tag{4}$$

Obviously, as long as all plants are homozygous, the ploidy is irrelevant.

To study the protection of polymorphism, we linearise (3) near $p_j = 1$ to obtain

$$p_i(\mathbf{x}, t+1) = w_i(\mathbf{x}) P_i(\mathbf{x}, t)/w_j(\mathbf{x}). \tag{5}$$

We specialise to two alleles, $A_1$ and $A_2$, with frequencies $p(\mathbf{x}, t)$ and $q = 1-p$, and two niches, $R_1$ and $R_2$. The regions $R_1$ and $R_2$ of the habitat may be in patches, but each has the same fitnesses throughout. Let $\alpha_1 (0 < \alpha_1 < 1)$ and $\alpha_2 (= 1 - \alpha_1)$ be the proportions of plants in $R_1$ and $R_2$. Then (1) reduces to

$$\bar{p}(t) = \alpha_1 p^{(1)}(t) + \alpha_2 p^{(2)}(t), \tag{6}$$

where $p^{(i)}$ is the frequency of $A_1$ in $R_i$. We may choose the $A_1$ homozygote to have fitness 1 everywhere. The $A_2$ homozygote has fitness $u$ in $R_1$ and $v$ in $R_2$. Let the two-component column vector $\mathbf{p}(t)$ designate the frequency of $A_1$, the components corresponding to $R_1$ and $R_2$, respectively. Rewriting (5) in the neighbourhood of $\mathbf{p} = \mathbf{0}$, we find with the aid of (6)

$$\mathbf{p}(t+1) = \boldsymbol{B}\mathbf{p}(t), \tag{7}$$

where

$$\boldsymbol{B} = \begin{pmatrix} u^{-1}(1-\alpha_2\beta_2) & u^{-1}\alpha_2\beta_2 \\ v^{-1}\alpha_1\beta_2 & v^{-1}(1-\alpha_1\beta_2) \end{pmatrix} \tag{8}$$

The two eigenvalues of $\mathbf{B}$ differ in absolute value. Let us call them $\lambda_1$ and $\lambda_2$, with corresponding eigenvectors $\mathbf{V}_1$ and $\mathbf{V}_2$. We choose $|\lambda_1| > |\lambda_2|$. It is easy to see that $\lambda_1$ and $\lambda_2$ are real, $\lambda_1 > 0$, and the components of $\mathbf{V}_1$ have the same sign, while those of $\mathbf{V}_2$ have the opposite sign. To prevent $A_1$ from disappearing, we wish to make $\mathbf{p} = \mathbf{0}$ unstable, and hence require $\lambda_1 > 1$. To conclude that the local instability of $\mathbf{p} = \mathbf{0}$ protects $A_1$, we must rule out two possibilities. First, since time is discrete, in principle, $\mathbf{p}(t)$ may converge to $\mathbf{0}$ from points not close to the origin. For instance, we might have sequences $\mathbf{p}(2t)$ and $\mathbf{p}(2t+1)$ with $\mathbf{p}(2t)$ not close to $\mathbf{0}$ but $\mathbf{p}(2t+1) \to \mathbf{0}$ as $t \to \infty$. If this happened, however, the sequence $\mathbf{p}(2t)$ would have a point of accumulation in the interior from which the population would move to $\mathbf{p} = \mathbf{0}$ in a single step. But with positive fitnesses (5) shows that this is impossible. Second, if $|\lambda_2| < 1$, it is reasonable to appeal to small perturbations to dismiss the possibility that the population may start on the unique curve (parallel to $\mathbf{V}_2$ as $\mathbf{p} \to \mathbf{0}$) from which it would converge to $\mathbf{p} = \mathbf{0}$. This does not imply, however, that it could not repeatedly approach the origin from a direction tending toward $\mathbf{V}_2$, and thereby converge to $\mathbf{p} = \mathbf{0}$. Since $p^{(1)} \geqq 0$ and $p^{(2)} \geqq 0$, such a possibility is ruled out by the fact that the components of $\mathbf{V}_2$ have the opposite sign.

From (8) we deduce that for the sufficient condition for protection of $A_1$, $\lambda_1 > 1$, we must require that

$$u^{-1}(1-\alpha_2\beta_2) + v^{-1}(1-\alpha_1\beta_2) > \min\,[2,\ 1 + u^{-1}v^{-1}\beta_1]. \tag{9}$$

Examining (5) near $\mathbf{q} = \mathbf{0}$, we find, as expected by symmetry, that $A_2$ will be protected if (9) holds with the replacement $(u, v) \to (u^{-1}, v^{-1})$. Then we have a protected polymorphism. To model environmental diversity, we suppose $A_1$ is advantageous in $R_1$ and deleterious in $R_2$: $0 < u < 1$ and $v > 1$. For protection of $A_1$, we derive from (9) the sufficient condition

$$u < F(v), \tag{10a}$$

and to protect $A_2$ it suffices to have either

$$v \geqq y, \quad \text{or} \quad 1 < v < y \quad \text{and} \quad u > f(v), \tag{10b}$$

where $y = (1-\alpha_1\beta_2)^{-1} \geqq 1$,

$$f(v) = \frac{1-v(1-\alpha_1\beta_2)}{1-\alpha_2\beta_2-\beta_1 v}, \quad F(v) = [f(v^{-1})]^{-1}. \tag{11}$$

The region of protected polymorphism, (10), is the shaded area in fig. 1. Note that $F(\infty) = 1-\alpha_2\beta_2$.

By direct calculation, we can prove that

$$\frac{\partial f}{\partial\beta_2} > 0, \quad \text{which implies} \quad \frac{\partial F}{\partial\beta_2} < 0. \tag{12}$$

Thus, the shaded region in fig. 1 shrinks as $\beta_2$ increases, *i.e.* the sufficient conditions for a protected polymorphism become more stringent as the amount of dispersion increases.

As $\beta_2 \to 0$, $y \to 1$ and $F(v) \to 1$, so that the shaded region approaches $u < 1$, $v > 1$. Therefore, for sufficiently small non-zero dispersion, a protected polymorphism always exists.

If selection is weak, we may write $u = 1-s$, $v = 1+\sigma$, and approximate $f(v) \approx 1 - \dfrac{\alpha_2\sigma}{\alpha_1} \approx F(v)$. Hence, there is no protected polymorphism for weak selection.

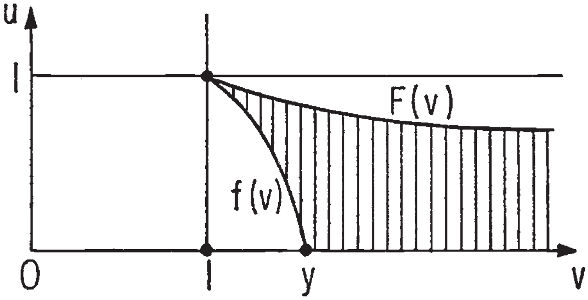

FIG. 1.—Region of protected polymorphism (shaded) for self-pollination.

## 3. CROSS-POLLINATION

Let $p_i(\mathbf{x}, t)$ designate the frequency of $A_i$ in the gametic output of plants at $\mathbf{x}$ in generation $t$. The frequency of $A_i$ in gametes in the entire population is $\tilde{p}_i(t)$, given by (1). Hence the frequency of $A_i$ in pollen immediately after dispersion, $P_i(\mathbf{x}, t)$, is given by (2). Assuming only pollen disperse, the (ordered) frequency of $A_iA_j$ seeds at $\mathbf{x}$ reads

$$\tfrac{1}{2}[p_i(\mathbf{x}, t)P_j(\mathbf{x}, t) + p_j(\mathbf{x}, t)P_i(\mathbf{x}, t)].$$

If $w_{ij}(\mathbf{x})$ denotes the seed-to-adult viability of $A_iA_j$ plants, the allelic frequencies satisfy

$$p_i(\mathbf{x}, t+1) = \tfrac{1}{2}[\bar{w}(\mathbf{x}, t)]^{-1} \sum_j w_{ij}(\mathbf{x})[p_i(\mathbf{x}, t)P_j(\mathbf{x}, t) + p_j(\mathbf{x}, t)P_i(\mathbf{x}, t)], \tag{13}$$

where

$$\bar{w}(\mathbf{x}, t) = \tfrac{1}{2} \sum_{ij} w_{ij}(\mathbf{x})[p_i(\mathbf{x}, t)P_j(\mathbf{x}, t) + p_j(\mathbf{x}, t)P_i(\mathbf{x}, t)] \tag{14}$$

is the mean fitness at $\mathbf{x}$.

To investigate protection, we linearise (13) near $p_k = 1$ to obtain

$$p_i(\mathbf{x}, t+1) = \tfrac{1}{2}[w_{kk}(\mathbf{x})]^{-1} w_{ik}(\mathbf{x})[p_i(\mathbf{x}, t) + P_i(\mathbf{x}, t)]. \tag{15}$$

Specialising to the diallelic two-niche case as in Sec. 2, we choose the general fitness pattern

$$\begin{array}{cccc} & A_1A_1 & A_1A_2 & A_2A_2 \\ R_1 & u_1^{-1} & 1 & u_2^{-1} \\ R_2 & v_1^{-1} & 1 & v_2^{-1} \end{array} \tag{16}$$

The use of inverses slightly simplifies the algebra. Passing to the two-component notation as in Sec. 2 and employing (6) and (16), near $\mathbf{p} = \mathbf{0}$ we may reduce (15) to

$$p(t+1) = Cp(t), \tag{17}$$

with

$$C = \begin{pmatrix} u_2(1-\frac{1}{2}\alpha_2\beta_2) & \frac{1}{2}u_2\alpha_2\beta_2 \\ \frac{1}{2}v_2\alpha_1\beta_2 & v_2(1-\frac{1}{2}\alpha_1\beta_2) \end{pmatrix}. \tag{18}$$

Observe that $\mathbf{C}$ has the same form as $\mathbf{B}$ in (8) except that the fitnesses have been redefined and $\beta_2$ has been replaced by $\frac{1}{2}\beta_2$. Since only pollen disperse, the latter substitution is not surprising. The discussion following (8) applies unaltered here, so a sufficient condition for protection of $A_1$ is that

$$u_i(1-\tfrac{1}{2}\alpha_2\beta_2) + v_i(1-\tfrac{1}{2}\alpha_1\beta_2) > \min\,[2,\ 1 + u_iv_i(1-\tfrac{1}{2}\beta_2)] \tag{19}$$

for $i = 2$. If (19) holds with $i = 1$, $A_2$ cannot be lost, so (19) with $i = 1, 2$ is a sufficient condition for a protected polymorphism.

Since we are interested in the maintenance of genetic variability by environmental diversity, we shall assume there is directional selection favouring $A_1$ in $R_1$ and $A_2$ in $R_2$: $0 < u_1 \leqq 1 \leqq u_2$ and $0 < v_2 \leqq 1 \leqq v_1$. Then from (19) we deduce that $A_1$ is protected if

$$u_2 > g(v_2), \tag{20a}$$

and $A_2$ cannot be lost if either

$$v_1 \geqq z, \quad \text{or} \quad 1 \leqq v \leqq z \quad \text{and} \quad u_1 > g(v_1), \tag{20b}$$

where $z = (1-\frac{1}{2}\alpha_1\beta_2)^{-1}$, $1 \leqq z < 2$, and

$$g(v) = \frac{1 - v(1-\frac{1}{2}\alpha_1\beta_2)}{1 - \frac{1}{2}\alpha_2\beta_2 - v(1-\frac{1}{2}\beta_2)}. \tag{21}$$

Notice that if $\beta_2$ is replaced by $\frac{1}{2}\beta_2$ in $y$ and $f(v)$, we obtain $z$ and $g(v)$. The sufficient condition (20) for a protected polymorphism corresponds to the shaded regions in fig. 2. In fig. 2, $g(0) = (1-\frac{1}{2}\alpha_2\beta_2)^{-1}$ and $1 \leqq g(0) < 2$.

Due to the above simple connection between $f$ and $g$, (12) implies

$$\frac{\partial g}{\partial \beta_2} > 0,$$

so that the shaded area in fig. 2 shrinks as $\beta_2$ increases, and the polymorphism conditions become more restrictive with greater dispersion.

As $\beta_2 \rightarrow 0$, $z \rightarrow 1$ and $g(v) \rightarrow 1$, so that the shaded region approaches $0 < u_1 < 1 < u_2$, $0 < v_2 < 1 < v_1$. Therefore, as long as we have heterozygote intermediacy, for sufficiently weak non-zero dispersion, there is a protected polymorphism.

For weak selection, we write $u_1 = 1 - s_1$, $u_2 = 1 + s_2$, $v_1 = 1 + \sigma_1$, $v_2 = 1 - \sigma_2$, and approximate $g(v_1) \approx 1 - \frac{\alpha_2 \sigma_1}{\alpha_1}$ and $g(v_2) \approx 1 + \frac{\alpha_2 \sigma_2}{\alpha_1}$. Then (20) reduces to $\alpha_1 s_1 - \alpha_2 \sigma_1 < 0$ and $\alpha_2 \sigma_2 - \alpha_1 s_2 < 0$, *i.e.* the requirement that the mean selection coefficient of each homozygote in the entire population be negative.

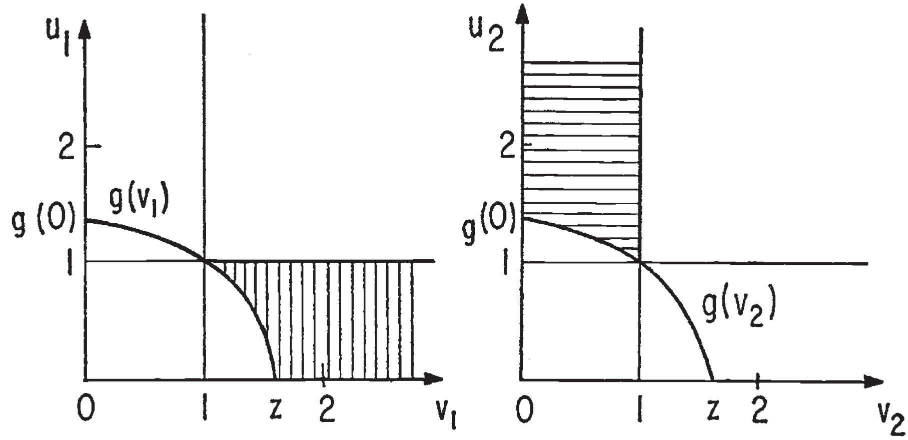

FIG. 2.—Region of protected polymorphism (shaded) for cross-pollination.

Therefore, the sufficient condition for a protected polymorphism becomes overdominance for the average fitnesses. If the degree of dominance is the same in the two niches, *i.e.*, $s_2/s_1 = \sigma_2/\sigma_1$, a protected polymorphism does not exist.

Fig. 2 informs us at a glance that there exists a protected polymorphism if $v_1 \geqq 2$ and $u_2 > 2$. This means that in each niche the fitness of the deleterious homozygote must be less than $\frac{1}{2}$. The intuitive reason for this asymmetric condition lies in the nature of protection. Near $\mathbf{p} = \mathbf{0}$, $A_1A_1$ is neglected, and the only way to prevent $A_2$ from being fixed is to make $A_2A_2$ very unfit in $R_1$, corresponding to $u_2 > 2$. Similarly for $v_1 \geqq 2$.

If there is no multiplicative dominance (*i.e.* genotypic fitnesses are expressible as products of allelic factors), we have $u_2^{-1} = u_1 \equiv u$ and $v_2^{-1} = v_1 \equiv v$. From (20) and fig. 2 we readily discover that the region of protected polymorphism looks just like the one in fig. 1, but the lower curve is $u = g(v)$ and the upper one is $u = G(v) \equiv [g(v^{-1})]^{-1}$. Note that $G(\infty) = 1 - \frac{1}{2}\alpha_2\beta_2$. If we replace $\beta_2$ in the protection conditions for the self-pollinating population by $\frac{1}{2}\beta_2$, we obtain the conditions for cross-pollination with no multiplicative dominance. Thus, even though these two models are not identical, we obtain the correct protection criteria by halving the amount of dispersion, since only pollen disperse in the cross-pollinating scheme, and recalling that in the simplest panmictic models no multiplicative dominance is the same as haploidy (Nagylaki, 1975*c*).

If $v_1 = 1$ and $u_1 < 1$ fig. 2 shows that there is no protected polymorphism. The same holds if $u_2 = 1$ and $v_2 < 1$. This leads us to consider the interesting and important case of complete dominance.

A$_1$ *Recessive.* We choose $u_2 = v_2 = 1$, $u_1 \equiv u < 1$, and $v_1 \equiv v > 1$ in the fitness pattern (16). The sufficient conditions (20b) for protection of $A_2$ still apply, but we must find a replacement for (20a). From (18) we deduce easily the eigenvalues and eigenvectors $\lambda_1 = 1$, $\lambda_2 = 1 - \frac{1}{2}\beta_2$,

$$V_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \quad V_2 = \begin{pmatrix} \alpha_2 \\ -\alpha_1 \end{pmatrix}. \tag{22}$$

Since $\lambda_1 = 1$, to derive a condition for protection of $A_1$, we must approximate (13) near $\mathbf{p} = \mathbf{0}$ to second order. Our method was used in a similar context by Maynard Smith (1970) and Christiansen (1974). We define gene frequency components $\pi_i(t)$ along $\mathbf{V}_i$:

$$p(t) = \pi_1(t)V_1 + \pi_2(t)V_2, \tag{23}$$

and conclude from (22)

$$\pi_1(t) = \alpha_1 p^{(1)}(t) + \alpha_2 p^{(2)}(t), \tag{24a}$$

$$\pi_2(t) = p^{(1)}(t) - p^{(2)}(t). \tag{24b}$$

Observe that $\pi_1 = \bar{p} \geqq 0$, the frequency of $A_1$ in the entire population.

From the previous linearisation of (13), we know that near $\boldsymbol{\pi} = \mathbf{0}$ $\pi_2$ must satisfy

$$\pi_2(t+1) = \lambda_2 \pi_2(t) + O(|\,\boldsymbol{\pi}\,|^2), \tag{25}$$

where $O(|\,\boldsymbol{\pi}\,|^2)$ represents terms of at most the second order as $\boldsymbol{\pi} \to \mathbf{0}$, which need not be computed. Calculating to second order, from (13) we obtain

$$\pi_1(t+1) - \pi_1(t) = Q(\pi_1, \pi_2) + O(|\,\boldsymbol{\pi}\,|^3), \tag{26}$$

with

$$Q(\pi_1, \pi_2) = \alpha_1(u^{-1}-1)p^{(1)}(\beta_1 p^{(1)} + \beta_2 \bar{p}) + \alpha_2(v^{-1}-1)p^{(2)}(\beta_1 p^{(2)} + \beta_2 \bar{p}). \tag{27}$$

When $|\,\boldsymbol{\pi}\,|$ is very small, (25) shows that for $0 < \beta_2 \leqq 1$ $|\,\pi_2\,|$ is decreasing at the geometric rate $\lambda_2^t$. Since $\pi_1(t) \geqq 0$, we expect from (26) that a sufficient condition for the instability of $\boldsymbol{\pi} = \mathbf{0}$ is $Q(\pi_1, 0) > 0$. This statement can be proved rigorously. With $\pi_2 = 0$, (22) and (23) give $p^{(1)} = p^{(2)} = \bar{p} = \pi_1$. Then (27) informs us that a sufficient condition for protection of $A_1$ is

$$\alpha_1(u^{-1}-1) + \alpha_2(v^{-1}-1) > 0,$$

which is the same as

$$\alpha_1 u^{-1} + \alpha_2 v^{-1} > 1. \tag{28}$$

Equation (28) just requires that the mean fitness of $A_1A_1$ exceed 1, *i.e.* that $A_1A_1$, or equivalently $A_1$, be favoured in the habitat as a whole. Since (28) is independent of the amount of dispersion, we need not be surprised that it is identical to Prout's (1968) condition for the Levene (1953) model and Maynard Smith's (1970) for habitat selection (Deakin, 1966; Maynard Smith, 1966). We may rewrite (28) as

$$u<h(v)\equiv \alpha_1 v(v-\alpha_2)^{-1}. \tag{29}$$

The region of protected polymorphism corresponding to (20b) and (29) again looks like fig. 1, with the lower curve being $u = g(v)$ and the upper one $u = h(v)$. Note that $h(\infty) = \alpha_1$.

*Acknowledgement.*—I am very grateful to Prof. Kathleen Keeler for drawing to my attention and discussing with me the work on the vernal pool populations. Without her stimulus, the research reported above would not have been carried out. It is a pleasure to thank Profs. Charles Conley and Richard McGehee for very helpful communication concerning the mathematical analysis.

## 4. REFERENCES

BULMER, M. G. 1972. Multiple niche polymorphism. *Amer. Nat.*, *106*, 254-257.

CHRISTIANSEN, F. B. 1974. Sufficient condition for protected polymorphism in a subdivided population. *Amer. Nat.*, *108*, 157-166.

CHRISTIANSEN, F. B. 1975. Hard and soft selection in a subdivided population. *Amer. Nat.*, *109*, 11-16.

CORNETTE, J. L. 1975. Some basic elements of continuous selection models. *Theor. Pop. Biol.*, *8*, 301-313.

DEAKIN, M. A. B. 1966. Sufficient conditions for genetic polymorphism. *Amer. Nat.*, *100*, 690-692.

DEMPSTER, E. R. 1955. Maintenance of genetic heterogeneity. *Cold Spring Harbor Symp. Quant. Biol.*, *20*, 25-32.

FLEMING, W. H. 1975. A selection-migration model in population genetics. *J. Math. Biol.*, *2*, 219-233.

KARLIN, S. 1976. Population subdivision and selection-migration interaction. In *Proc. Int. Conf. Pop. Genet. Ecol.* (ed. S. Karlin and E. Nevo). Academic Press, New York.

KARLIN, S., AND DYN, N. 1976. Some theoretical analyses of migration-selection interaction in a cline: a generalized two-range environment. In *Proc. Int. Conf. Pop. Genet. Ecol.* (ed. S. Karlin and E. Nevo). Academic Press, New York.

KEELER, K. H. 1975. Plant adaptation: insect defense and enzyme variation. Thesis, University of California, Berkeley.

LEVENE, H. 1953. Genetic equilibrium when more than one ecological niche is available. *Amer. Nat.*, *87*, 331-333.

LINHART, Y. B. 1972. Differentiation within natural populations of California annual plants. Thesis, University of California, Berkeley.

LINHART, Y. B. 1973. Intra-population differentiation in adaptive strategies. *Genetics, s160.*

LINHART, Y. B. 1974. Intra-population differentiation in annual plants. I. *Veronica peregrina* L. raised under non-competitive conditions. *Evolution*, *28*, 232-243.

LINHART, Y. B., AND BAKER, I. 1973. Intra-population differentiation in response to flooding in a population of *Veronica peregrina* L. *Nature*, *242*, 275-276.

MAYNARD SMITH, J. 1966. Sympatric speciation. *Amer. Nat.*, *100*, 637-650.

MAYNARD SMITH, J. 1970. Genetic polymorphism in a varied environment. *Amer. Nat.*, *104*, 487-490.

NAGYLAKI, T. 1975*a*. Conditions for the existence of clines. *Genetics*, *80*, 595-615.

NAGYLAKI, T. 1975*b*. Clines with variable migration. *Genetics*, in press.

NAGYLAKI, T. 1975*c*. Polymorphisms in cyclically-varying environments. *Heredity*, *35*, 67-74.

NAGYLAKI, T. 1976. The geographical structure of populations. *Math. Assoc. Amer. Study in Mathematical Biology*, in press.

NAGYLAKI, T., AND CROW, J. F. 1974. Continuous selective models. *Theor. Pop. Biol.*, *5*, 257-283.

PROUT, T. 1968. Sufficient conditions for multiple niche polymorphism. *Amer. Nat.*, *102*, 493-496.

SLATKIN, M. 1973. Gene flow and selection in a cline. *Genetics*, *75*, 733-756.