2

Classifications of Selection–Migration Structures and Conditions for a Protected Polymorphism

SAMUEL KARLIN

Department of Mathematics
Stanford University
Stanford, California 94305

INTRODUCTION

The idea that levels and forms of genetic variability can be related to temporal and spatial patterns of environmental heterogeneity is a widely promulgated theme in evolutionary biology. Recent reviews pertaining to genetic polymorphisms under conditions of variable selection and migration are given by Hedrick *et al.* (1976) and Felsenstein (1976), which include numerous references to experimental, field, and theoretical studies.

Three classes of migration patterns have been predominantly studied in theoretical population genetics:

a. The island model (Wright, 1943) consists of an array of islands exchanging genes uniformly. Equivalently, the island model involves N "equidistant" islands that share a common migrant pool drawn equally from all demes.

The Levene population subdivision structure (1953) is a direct generalization of Wright's model that allows for variable deme (island) sizes. Deakin (1966) introduced a homing or sessile tendency so that some individuals would remain in their deme of birth rather than enter the migrant pool. He assumed that a fixed proportion of the population is sessile while the remainder of the population acts according to the Levene model.

b. The stepping-stone model and, more generally, isolation-by-distance migration patterns assume that the rates of migration between demes depend on the distances between them. Isolation by distance based on a one, two, or even higher dimensional layout (strata defined by physical position, social or behavioral characteristics) of the population has been investigated by Malécot (1948, 1951, 1959, 1967), Jain and Bradshaw (1966), Kimura and Weiss (1964), Maruyama (1970), among others. This class of models generally involves *no* differential selection within or between localities. In the context of environmental selection gradients, some cline stepping-stone models have been extensively investigated (e.g., Slatkin, 1973; Nagylaki, 1974, 1975, 1976*b*, 1978, 1979; Nagylaki and Lucier, 1980; Fleming, 1975; Karlin and Richter-Dyn, 1976).

c. Migration matrix models are designed to deal with general migration patterns (e.g., Malécot, 1951, 1959; Bodmer and Cavalli-Sforza, 1968; Carmelli and Cavalli-Sforza, 1976; Smith, 1969). Most authors have limited their attention to linear pressures, i.e., mutation and/or migration from an external fixed population, but having no mating or natural selection differences operating.

In both classes of migration structures (b) and (c), computations have been mainly directed to evaluating the correlation of gene frequencies over space and the changes of these with time.

This work is part of a continuing series of theoretical studies that seek to understand the effects of different types of spatially and temporally varying selection regimes coupled with migration patterns on the existence and nature of polymorphism (Karlin, 1976, 1977*a,b*; Karlin and Richter-Dyn, 1976; Karlin and Campbell, 1978, 1979, 1980). In this chapter we establish the conditions for the existence of a protected polymorphism (protection means that none of the alleles become extinct even when initially rare) for a hierarchy of migration patterns. These results will permit qualitative comparisons of the influence of different structures of migration exchange in contributing to the maintenance of polymorphisms.

In this review we describe a series of hybrid migration structures composed from canonical, e.g., Levene, Deakin, stepping-stone, circulant migration patterns that entail one or several clusters of demes. Deme clusters can reflect the background terrain, geographical relationships, geological, climatic, or other ecological and environmental factors, and also behavioral, social, or exogenous genetic-environmental characteristics. Moreover, by introducing suitable fictitious deme arrays we can simulate the effects of seasonal variation in selection by a spatial selection gradient. The seasons often induce cyclic variation.

Some of the models are partly motivated by observations from insect populations that divide into demes or groups of demes, depending on the spacing of the plants on which they feed. Natural groupings of demes can also be associated with arrays of islands, an archipelago, tributaries of a river, inlets along a coast, a range of hills, spacing of flora, or mountain–valley–canyon topography.

The partitioning of demes into clusters often distinguishes local population interactions against far movements. For example, with respect to plant dispersal we can contrast the nearby seed droppings with the long migrations mediated by vectors (insects, mammals).

A three-tiered clustering of some human populations may arise from the family-tribe, nation, and race structures. Other criteria for groupings may relate to social economic status, life-styles, religion and customs, and educational levels.

Conditions for clustering may be based on aspects of the environment such as degree and kind of salinity, food availability, moistness, exposure, etc. The modeling of migration should reflect various levels of clustering and associated with the clustering is a related pattern of selection.

We will investigate typically the following questions: To what extent is the maintenance of polymorphism facilitated by the nature of hierarchical determinations of deme clustering? What are the consequences associated with asymmetries in population exchanges? What are the relative influences of migration rates between and within clusters of demes? Also, how do we compare spatial versus temporal variations in selection and migration parameters?

The text is arranged as follows. The migration patterns on which we focus are described in Sections 2–4. In Section 2 we review the formulation of the Levene and Deakin migration models and their extensions that allow variable (habitat-dependent) rates of homing, several stages of migration in each life cycle, and different characteristic deme sizes. The nature of clinal flow, i.e., migration exchanges per generation limited to neighboring demes whose rates can vary with respect to positions and/or differ in reciprocal directions, is described. A number of relevant circulant migration patterns are set forth. A final class of basic migration forms involving directional migration via a distinguished (major) deme dispersing to or receiving from "subordinate" demes is detailed. The process of delayed germination in plant species with seed pools can be modeled by such a migration scheme.

Sections 3 and 4 delineate more-complex migration structures encompassing clusters of several demes each. A population is assumed to naturally divide into clusters with each cluster consisting of a number of demes where the migration contrasts refer to intra- and interdeme cluster movements. For example, a "star" migration form is developed where demes along each ray communicate only through a central deme. The combined effects accruing from temporal and spatial variation can be studied expeditiously by regarding the aggregate population as consisting of a multicluster deme formation. Other relevant hybrid migration structures, such as Kronecker products and generalized circulant migration systems, are also elaborated. For all these cases we ascertain the conditions for a protected polymorphism and discern their dependence on the model parameters.

The analytic apparatus used in ascertaining protection for the general multideme migration–selection model is reviewed at the close of Section 1. Sections 7–10 present conditions for a protected polymorphism appropriate for the models of Sections 2–4.

It is of interest to contrast migration structures as to their degrees of mixing and isolation. Two such notions were introduced in Karlin (1976). Several additional concepts and their analyses are set forth in Section 5. A number of means of comparing selection heterogeneity are introduced and some robust results interpreted in Section 6. Specifically, we address the issue of the relationship between spatial or temporal selection "heterogeneity" and the existence of a protected polymorphism.

In Section 11 we compare the opportunities for protection with migration once per season versus once per generation for a multideme population subject to seasonal selection variation. The conditions for protection in a multideme seed pool process are delineated in Section 13. A number of relations of deme size distributions and allele protection are developed in Section 14. Some models of multiple migration stages per generation are investigated in Section 15. We set forth in Section 16 a number of results pertaining to the existence of protection attendant to the addition or deletion of demes. In this vein, we examine the effects with respect to protection of the unification or the separation of different parts of a population range. It is also of interest to ascertain the similarities and contrasts in the equilibrium gene frequency patterns that accrue from an enlarged neutral zone where in other respects the selection migration structure is unchanged.

The discussion of Section 17 summarizes in qualitative terms some of the implications and contrasts of the quantitative results of the previous sections. Mathematical proofs and analyses are relegated to Appendices A–F. The reader not concerned with the technical developments henceforth may best concentrate on Sections 1–4 to understand the spirit of the formulations and motivations on the various migration structures, and then skip to Section 17 for the qualitative summary and discussion of the results.

1. GENERAL CONCEPTS, MOTIVATIONS, AND BASIC FORMULATION OF THE MODEL

Classic examples of visible polymorphisms significantly correlated with environmental parameters include the phenomenon of industrial melanism in the *Biston betularia* moth, and shell color and banding pattern in populations of land snails of the genus *Cepaea* (e.g., see Cain and Sheppard, 1952; Ford, 1975; Jones *et al.*, 1977). A selective agent to some extent acting in both these examples is differential predation. In recent years a large number of surveys of allozymic variation have been reported (e.g., Powell, 1975; Nevo, 1978; Brown, 1979). Included among these are several clines discerned despite the fact that associations between the gene frequencies and the components of the habitat are quite ambiguous. Studies pertaining to linear associations between allele frequencies and spatial environmental variation include Dobzhansky (1943, 1956), Koehn (1969), Powell (1971), Merritt (1972), Bryant (1974), McDonald and Ayala (1974), Mitton and Koehn (1975), Soule (1976), Endler (1977), and Clarke (1979); see also Hedrick *et al.* (1976) for further citations. Some cases of correlations of gene frequencies with seasonal variations are also reviewed in these references.

The concept of a hybrid demic structure represents a partitioning of sets of demes where the migration among the demes of a cluster can be of a simple mode, e.g., Levene, Deakin, stepping stone, isolation by distance, circulant, while the exchange pattern between clusters may correspond to another basic structure. For example, the generalized multiuniform migration form (Section 3, Part VII) prescribes a Deakin model for the demes of each cluster (where the parameters can vary from cluster to cluster), while the migrations between clusters conform to a Levene pattern. Multiuniform (with added homing) may be appropriate in describing many insect pest movements that locally manifest a Deakin migration pattern, which is supplemented by occasional long-range migration. As applied to human populations, it would correspond to a primary tendency to remain in one's own village followed by a secondary tendency to settle in a different village of one's own culture and a tertiary tendency to move to another culture (country) (cf. Carmelli and Cavalli-Sforza, 1976).

A case of the star migration mode (Section 3, part VIII) precluding direct migration between arms of the star entails a species associated with river valleys at a fork in a river. Transient parasites on salmon and other fish, which mature together and then spawn up different streams, would also experience this migration structure. The star migration model also describes migration among tributaries of a central lake, or among canyons accessible to each other through a central region. In particular, star migration forms might be appropriate for organisms living in irrigation water or terraced hillsides where lateral migration is within a ditch at a given level and centripetal.

The mixed block migration structure (Section 4, part IX) may be appropriate for multivoltine insects.

The Kronecker product migration structures (Section 3, part XI) may be appropriate for some insect populations (e.g., butterflies) that identify with their larval food plant and are most likely to lay eggs on the same type of plant. If some supermigration mechanism transports them to another habitat region, they will probably seek out ovipositional sites in accordance with the biotype preferences that would have been manifested in their original habitat region.

Circulating clusters of populations may be mediated by natural currents (the Gulf Stream) or innate (possibly genetically controlled) movements (e.g., bird migrations); planktonic masses are subjected to travel cycles. The mats of *Sargassum* weed carried along by currents have some animal populations (e.g., crabs) that live on them. The movements can be interspersed with sessile phases (caused by attachment to a shore), and these effects on migration are incorporated in the migration matrix structure of Section 4, part X.

The phenomenon of seed pools involving groupings of plants can be modeled by a migration matrix of the structure (4.28) where the elements are suitably replaced by blocks of matrices. The isolation-by-distance circulant block matrix of Section 4, part XIII can be interpreted in terms of population areas situated around a central lake with distance (in circular units) indexing the migration rates.

The Concept of a Protected Polymorphism

In any evolving population genetic system the property of persistence of an allele A, even when initially rare, is commonly called protection of the A-allele or *A-protection* (Prout, 1968; Christiansen, 1974). If all alleles are protected, then a *protected polymorphism* is said to exist. It should be realized that with a protected polymorphism there may be several stable equilibrium states or oscillatory behavior strictly among polymorphic states or even unpredictable dynamics, although these latter contingencies are uncommon. The evolutionary development of the population in this situation depends sensitively on the initial composition of the population.

In the presence of only two possible alleles A and a, the protection of A is equivalent to the instability of the fixation state corresponding to allele a. Accordingly, a *protected polymorphism* occurs if the fixation of both allele A and allele a is unstable.

In the case of many alleles, say $A_1, A_2, \ldots, A_r$, even after checking that each fixation state of $A_2, A_3, \ldots, A_r$ is unstable, it would be necessary to eliminate the existence of stable states (or cyclic or ergodic behavior) involving any combinations among the alleles $A_2, \ldots, A_r$ before A_1-protection is assured with respect to all internal initial conditions. This procedure entails a formidable if not prohibitive task. Accordingly, the methodology for verifying the existence of a protected polymorphism in multiallele (and a fortiori in multilocus situations) is limited. Nevertheless, the analysis for the case allowing only two alternative alleles may be suggestive for more general situations as well as having independent interest.

Formulation of the Model

A multideme population model involves three principal components: the selection regime, the migration pattern, and the population structure.

(i) *Selection Regimes*

In the genetics context, a multideme population is partitioned into N habitats and/or separate breeding units, $\mathcal{P}_1, \mathcal{P}_2, \ldots, \mathcal{P}_N$, that are subject to local selection forces and migration among them. The changes in the population composition of a trait expressed by two possible *types* labeled A and a are observed over discrete successive generations. We assume here that the deme sizes are large so that sampling effects can be ignored. The transformation of gene frequency accountable to the *local* selection forces in deme $\mathcal{P}_i$ is characterized by a relation $x' = f_i(x)$ such that if x is the A-frequency in $\mathcal{P}_i$ at the start of a generation, then after the action of mating and selection the resulting A-frequency prior to migration is x'. For many relevant cases, $f_i(x)$ (defined for $0 \le x \le 1$) is a nonlinear smooth function obeying the boundary conditions

$$f_i(0) = 0, \qquad f_i(1) = 1 \tag{1.1}$$

It is unnecessary to spell out the mating system or the specific fitness scheme operating in each deme. In our general formulation, fitness can equally well represent a number of components of reproductivity, including fertility, viability, segregation distortion, and others. The consequences of mating and selection are for our purposes implicitly incorporated in the local selection functions $f_i(x)$.

One example of $f_i(x)$ that we will pursue at length arises from the classical diploid one-locus, two-allele viability model and has the form

$$f_i(x) = \frac{v_i x^2 + x(1 - x)}{v_i x^2 + w_i(1 - x)^2 + 2x(1 - x)} \tag{1.2}$$

when the viability parameters of the genotypes are

$$\begin{array}{ccc} AA & Aa & aa \\ v_i & 1 & w_i \end{array} \tag{1.2a}$$

The case of a dominant trait has $v_i = 1$ for all i, and the case of additive allelic effects corresponds to $v_i = 1 + \delta_i$, $w_i = 1 - \delta_i$, $|\delta_i| \leq 1$. Multiplicative allelic effects are characterized by the parameter relationship $v_i w_i = 1$ for all i.

In the corresponding haploid situation we should take $f_i(x) = v_i x/[v_i x + w_i(1 - x)]$. Parenthetically, multiplicative allelic viability effects for the standard diploid model are equivalent to the case of haploid selection just cited. Other determinations for $f_i(x)$ can be generated by superimposing forms of frequency-dependent selection or selection induced on a single locus when part of a multilocus system.

The environmental or geographical selection gradient is characterized by *the complete array* $\mathbf{f}(\mathbf{x}) = \{f_1(x_1), \ldots, f_N(x_N)\}$. The extent of environmental heterogeneity is reflected in the differences among the components of $\mathbf{f}(\mathbf{x})$.

When all local selection functions are of the form (1.2), the selection regime is equivalent to the fitness parameter array $\{(v_1, w_1), (v_2, w_2), \ldots, (v_N, w_N)\}$. Four global selection patterns studied at length are as follows.

A Selection Regime Involving Local Directed Selection in All Demes. This depicts a situation when in each deme either allele A or allele a is advantageous. Equivalently, if migration ceases, then a mosaic of pure populations would emerge with allele A or a established in its natural habitat (i.e., at those demes where allele A or a is advantageous, respectively). Where the same allele is not favored throughout, then for some levels of migration a globally stable polymorphism may be achieved. Definitely, under small migration flux, a unique polymorphic globally stable state is attained. However, with a more substantial gene flow, the effects of selection and migration blend in a complex fashion and the evolutionary outcomes are less predictable. We refer to the underlying selection pattern described above as a *mosaic pattern of directional selection.* Where the selection strength is correlated with some environmental parameter over a population range (e.g., temperature, water availability, background coloration), a mosaic of directed selection patterns may be appropriate. A case in point involving generally one to three loci is dorsal coloration in lizards adapting to background colors.

A Global Selection Pattern with Local Overdominance Manifested throughout the Range. In this circumstance, the heterozygote is advantageous in each deme and the strength of its advantage can vary spatially and/or temporally. It can be surmised that for this geographical selection regime a global unique stable polymorphism exists for any migration structure. The validity of this principle is corroborated for several common migration patterns in Karlin and Campbell (1979).

Underdominant Local Selection Forces throughout the Population Range. This reflects a situation where the heterozygote is deleterious compared to both homozygotes. The degree of heterozygote disadvantage may vary from locality to locality. In such a model of N habitats, entailing very slight migration flow connecting the separate demes, 2^N different stable polymorphisms can coexist where in each deme one of the two allelic types predominates. Usually, with moderate or substantial gene flow and some degree of underdominance expressed in each locality, the possibilities of polymorphism are significantly reduced (see Karlin and McGregor, 1972*b*). There are many writings that ascribe the distribution of plant allelomorphs for certain traits to microgeographical adaptations exhibiting patches of different homozygous genotypes consonant to a regime of underdominant selection effects (Hamrick and Allard, 1972), with circumstances reflecting underdominance throughout (heterozygote inferiority) that may be associated with the prevalence of hybrids between species.

Mixed Underdominant–Overdominant Regime. This natural selection regime has each local selection function expressing either overdominance or underdominance. It is of interest to discern the equilibrium gene frequency patterns in the presence of such a mixed underdominant–overdominant regime.

Gillespie and Langley (1976) emphasized a selection regime of a mosaic of directional selection effects engendered by additive allelic contributions to fitness as a model to explain biochemical allelic diversity.

(They concentrate mostly on temporal rather than spatial selection variation.) Although such a model may be germane to some situations, the biochemical properties of heterozygotes are usually not *exactly* intermediate not only for multimeric enzymes but for monomeric enzymes. Cases of nonintermediacy of biochemical properties are known for heat stability and specific activity of esterase-5. A discussion of this matter is presented in Berger (1976). Berger further advances a number of cases where the heterozygote compared with homozygotes maintains a higher level of catalytic activity and/or increased efficiency in conserving metabolic energy under suitable conditions of temperature, chemical-electrical, or environmental backgrounds.

The detailed expression for $f_i(x)$ is relevant with regard to the problem of polymorphic protection only through its values near 0 and 1. Actually, only the derivative values $f_i'(0)$ and $f_i'(1)$ matter and these are assumed to be positive.

Throughout this chapter we will concentrate on selection regimes involving variable local viability effects as in (1.2). The selection structure can then be described by the array of parameters

$$\mathbf{v} = (v_1, v_2, \ldots, v_N) \quad \text{and} \quad \mathbf{w} = (w_1, w_2, \ldots, w_N) \tag{1.2b}$$

where the v_i and w_i are selection values at deme $\mathcal{P}_i$ [see (1.2a)]. In this formulation the normalization of constant fitness value 1 for heterozygotes over all demes is made. One advantage of this assumption is that it allows a consistent symmetric formulation of protection for both alleles A and a. However, there is also motivation for choosing the normalization that assigns equal absolute viabilities to the *common* homozygote. This ensues from the perspective that a mutant type would be introduced into an equilibrium population, where at equilibrium the wild type would be equally viable in all habitats. Otherwise, selection would act on migration parameters favoring migration to the fittest habitat.

Under the normalization that the homozygous aa individuals have equal absolute viabilities in all habitats, the relative viabilities

$$AA\colon (v_1, v_2, \ldots, v_N); \qquad Aa\colon (1, 1, \ldots, 1); \qquad aa\colon (w_1, w_2, \ldots, w_N)$$

correspond to the absolute viability

$$AA\colon \left(\frac{v_1}{w_1}, \frac{v_2}{w_2}, \ldots, \frac{v_N}{w_N}\right); \qquad Aa\colon \left(\frac{1}{w_1}, \frac{1}{w_2}, \ldots, \frac{1}{w_N}\right);$$
$$aa\colon (1, 1, \ldots, 1)$$

For the soft selection model [see subsection (v) later] the nature of the normalization does not alter conditions of a protected polymorphism. But for the hard selection model the nature of the normalization can be decisive.

(ii) Local Relative Population Sizes

We assume that the individual demes have a characteristic population size at a specified stage. Various possibilities have been proposed of which we indicate three.

a. The relative number of adults at deme i of the total population is c_i ($c_i > 0$, $\sum_{i=1}^{N} c_i = 1$) constant over successive generations (the soft selection case, see below). This assumption reflects a self-regulating mechanism such that at the adult stage of each generation the demes confer a constant relative contribution to the total mating pool. The c_i may also be construed as a measure of "interdemic selection" not significantly affected by the local genetic selection forces.

b. The relative size c_i reflects the proportion of the entire adult population located in deme $\mathcal{P}_i$ after migration (the hard selection case).

c. For a model with multiple mating areas (where mating and possibly reproduction take place) which can be coincident or distinguished from the deme sites, we could also stipulate an "inter-mating area selection" maintaining a set of constant relative juvenile numbers (or gamete population sizes) per generation. The relative mating area sizes can be correlated with physical area characteristics, local environmental variations, etc. The existence of differential fertility effects at the mating areas and/or degrees of sexual or assortative mating selection may be involved.

(iii) Hard and Soft Selection

In a multideme population there are two principal complementary models relating the interaction between selection and local population size, those of *hard* and *soft* selection. This distinction was emphasized by Wallace (1968, 1975); see also Dempster (1955) in the single-deme context and for the multideme situation, Christiansen (1975), Sved (1976).

For *soft selection,* the proportion of adults in each niche is fixed. As observed by Dempster, this can be a reasonable approximation when population is regulated within each niche (deme). When it is total population size that is controlled, Dempster suggests prescribing the fraction of zygotes in each deme. Then when the fraction of adults is proportional to the mean fitness in the deme, the underlying scheme is termed *hard selection.*

The distinction of hard versus soft selection pertains to individual fitness attributes. Accordingly, with hard selection independent of the genotypes of other individuals, the individual's genotype in the population determines the fitness expression, while soft selection implies that the deme population size is "constant" and accordingly the capability of an individual surviving and reproducing is subject to the limitation imposed by the deme "resources."

Soft selection postulates that each deme contributes a constant proportion of the mating pool for each generation and that this is independent of the genotypic composition of the habitat. The hard selection formulation postulates that a constant proportion of zygotes is present in each habitat in each generation before selection, but selection subsequently modifies this proportion. Thus, under soft selection the local viability selection does not change the relative proportions of the deme populations in passing from the offspring to the adult stage. This is the most commonly applied model where preceding migration each subpopulation carries a constant characteristic fraction of adult individuals in every generation. In contrast, hard selection prescribes only that after mating each local population includes a characteristic fraction of the total population, independent of the generation time.

One consequence of hard selection is that the local population sizes change due to differential birth and death rates of different genotypes. In some cases it may be relevant to formulate mixed versions of the effects of hard and soft selection.

In formal terms, with the operation of hard selection at deme $\mathcal{P}_i$ we postulate the existence of $W_i(x)$, a function of the A-allele frequency, x_i, such that $c_i W_i(x_i)$ measures the relative population size resulting from the effects of local differential selection.

For the choice of (1.2) a common determination has $W_i(x) =$ the mean fitness function in $\mathcal{P}_i$, viz., $W_i(x) = v_i x^2 + w_i(1 - x)^2 + 2x(1 - x)$.

Because viabilities preceding migration are absolute under hard selection but relative under soft selection, these models offer one manner of contrasting *relative versus absolute viabilities*. The normalization of viability parameters inherent to relative viabilities (constant deme sizes) prescribes a form of frequency-dependent absolute viabilities. Therefore, soft selection can be characterized as *frequency dependent*, and contrastingly for hard selection as *frequency independent*.

Because the local deme sizes are regulated preceding migration under soft selection, but no constraints on the population size exist until after migration under hard selection, the models are also characterized as *local versus global population size regulation*, respectively. This phenomenon is also referred to as *local versus global competition* because population size regulation must entail deaths of excess individuals, although these deaths are not correlated with genotype. The total population size is regulated to be constant after migration under both models.

Another interpretation considers population size regulation as a form of selection because it involves deaths, as mentioned above. In this perspective the same initial absolute viabilities are manifested at birth under both models, but genotype-independent mortality occurs before migration, say on juveniles, under soft selection but not until after migration, say on adults, under hard selection. This suggests the dichotomy of *juvenile versus adult selection*.

Table I summarizes the foregoing discussion (cf. Karlin and Campbell, 1981).

(iv) Migration Structure

The elements of a forward migration matrix $\mathrm{F} = \| \mu_{ij} \|$ measure the probability of an individual from locality i to migrate to j. The parameters of F do not reflect the actual immigration rates, which are further influenced by the differences in deme sizes, possible changes due to local selection forces, and other genetic and ecological factors.

The transformation relations for the gene frequency arrays

$$\mathbf{x} = (x_1, x_2, \ldots, x_N) \quad \text{and} \quad \mathbf{x}' = (x_1', x_2', \ldots, x_N')$$

where x_i denotes the current A-allele frequency in deme $\mathcal{P}_i$ and x_i' the corresponding frequency in the next generation requires the concept of the backward migration matrix

$$M = \| m_{ij} \|_{i,j=1}^{N} \tag{1.3}$$

where $m_{ij} =$ the fraction in the ith deme originating from the jth deme at the start of a given generation. The specification of m_{ij} takes account of the population structure expressed by variable deme size, the individual

TABLE I. Contrasts and Interpretations of Soft versus Hard Selection

Soft selection	Hard selection
Frequency dependent	Frequency independent
Relative viabilities	Absolute viabilities
Local population regulation	Global population regulation
Viability selection on juveniles	Viability selection on adults

migration propensities, and the influence of environmental selection variation on these factors [see (1.6) below]. The backward migration matrix commonly corresponds to the manner in which data are collected. In fact, mark–release–recapture experiments attempt to estimate a row of the backward migration matrix.

(v) The Transformation Equations of the Frequency States

We indicate first the calculation of the backward migration matrix. Following Christiansen (1974), the local differential selection effects convert the relative subpopulation sizes into

$$\begin{aligned} c_i^* &= c_i && \text{(soft selection)} \\ c_i^* &= \frac{c_i W_i(x_i)}{\sum_{k=1}^{N} c_k W_k(x_k)} && \text{(hard selection)}, \qquad i = 1, 2, \ldots, N \end{aligned} \tag{1.4}$$

where $W_i(x)$ usually designates the local mean fitness functions.

We concentrate on the model where the genetic forces in each generation are ordered according to

$$\text{mating and selection} \xrightarrow{\text{(followed by)}} \text{migration} \tag{1.5}$$

Migration here occurs at the adult stage, but prior to mating in the next generation. An elementary calculation provides

$$m_{ij} = \frac{c_j^* \mu_{ji}}{\sum_{k=1}^{N} c_k^* \mu_{ki}}, \qquad i = 1, \ldots, N \tag{1.6}$$

In more succinct notation, the backward migration is constructed from the forward migration matrix as the matrix product [diag$(c_1, \ldots, c_N)$ stands for the diagonal matrix with entries c_i on the diagonal]:

$$M = B\mathrm{F}'C^* \qquad (\mathrm{F}' = \text{the transpose matrix to F}) \tag{1.7}$$

where

$$C^* = \operatorname{diag}(c_1^*, c_2^*, \ldots, c_N^*) \quad \text{and} \quad B = \operatorname{diag}\left(\frac{1}{b_1}, \frac{1}{b_2}, \ldots, \frac{1}{b_N}\right)$$

with

$$b_i = \hat{c}_i = \sum_{k=1}^{N} c_k^* \mu_{ki}$$

Thus, M arises from F′ by pre- and postmultiplication with suitable positive diagonal matrices. It is important to emphasize that for hard selection the backward migration matrix depends on the specific genetic composition of the population at hand, $c_i^* = c_i^*(\mathbf{x})$, while under soft selection $M = \| m_{ij} \|$ is independent of the specific gene frequency configuration at hand.

When all demes are of equal size and $\mathrm{F} = \| \mu_{ij} \|$ is symmetric (as in the homogeneous stepping-stone model), then for soft selection $M = \mathrm{F}$ so that the backward and forward matrices coincide in this case. The coefficients μ_{ij} may then be interpreted as the per generation proportion of population exchange between demes $\mathcal{P}_i$ and $\mathcal{P}_j$.

Let x_i denote the frequency of allele A in deme $\mathcal{P}_i$ at the start of a generation and x_i' the frequency for the next generation. The standard global transformation equations connecting $\mathbf{x} = (x_1, \ldots, x_N)$ to $\mathbf{x}' = (x_1', \ldots, x_N')$ over two successive generations are given by

$$x_i' = \sum_{j=1}^{N} m_{ij} f_j(x_j), \qquad i = 1, 2, \ldots, N \tag{1.8}$$

where $f_j(x_j) = x_j^*$ is the local transformation of allele frequencies due to selection. [For definiteness, the form of f_j is given in (1.2).]

The deme sizes after migration can be calculated directly. The ith deme contributes a fraction $\mu_{ij} c_i^*$ of genes to deme j. It follows that the relative size of the jth deme following migration is given by $\hat{c}_j = \sum_{i=1}^{N} \mu_{ij} c_i^*$, $j = 1, 2, \ldots, N$, or in vector notation $\hat{\mathbf{c}} = \mathrm{F}'\mathbf{c}^*$ where F′ denotes the transpose matrix of F.

For helpful reference, the occurrence of these processes during the life history is shown in Table II. Note that selection occurs twice during

TABLE II. The Selection–Migration Process per Generation

		Census stage		Premigration		Postmigration	Next generation
Deme size	c_i	mating reproduction selection	c_i^*	(migration)	$\hat{c}_i$	genotype- independent mortality	c_i
A-Allele frequency	x_i		x_i^*		x_i'		x_i'

the generation cycle. Preceding migration it may be dependent on genotype and genotype frequencies. Following migration it is independent of both genotype frequencies and is sometimes referred to as *population regulation* to underscore this fact.

Another formulation would reverse the order of selection and migration, viz.,

$$\text{migration} \xrightarrow{\text{(followed by)}} \text{selection and mating} \qquad (1.9)$$

For the model of (1.9) the offspring (infant) migrates rather than the adult population (e.g., as in seed or larvae movement) and subsequently differential viability is in force. Where migration and selection operate in the order as in (1.9), the transformation equations replacing (1.8) take the form

$$x_i' = f_i\left(\sum_{j=1}^{N} m_{ij}x_j\right), \qquad i = 1, 2, \ldots, N \qquad (1.10)$$

We can write (1.10) in the form (provided f is strictly monotone)

$$y_i' = \sum_{j=1}^{N} m_{ij}f_j(y_j) \qquad \text{with } f_j(y_j) = x_j \qquad (1.11)$$

reducing to that of (1.8) in the variables $\{y_i\}$. It follows from these considerations that the qualitative nature of the equilibrium possibilities does not depend on the timing of the selection, mating, and migration operations.

From another perspective, selection generally has two major components reflecting fertility and viability effects. Therefore, for some natural populations, neither model (1.5) nor model (1.9) is appropriate. Viability selection is likely to take place before migration, while fertility selection may take place after migration. Thus, a mixed model involving possibly two stages of migration or some selection prior to and some selection after migration may be more germane.

We illustrate briefly the ingredients of such a two-stage model involving separate multiple mating areas and deme (habitat) sites. Thus, as before, the population is most of the time distributed into separate demes $\mathcal{P} = (\mathcal{P}_1, \mathcal{P}_2, \ldots, \mathcal{P}_n)$ at which local viability selection may operate. There are r areas $\mathcal{M} = (\mathcal{M}_1, \ldots, \mathcal{M}_r)$ where mating and reproduction take place. In the extended model there are two significant stages of migration: movement of adults from demes to mating areas, and after mating and reproduction, dispersal of offspring from the mating areas to the deme sites.

The migration matrix $F = \| \gamma_{ij} \|_{i=1,j=1}^{n,\ r}$ summarizes the forward migration rates of adults from deme sites to mating areas. The matrix $\Delta = \| \delta_{ij} \|_{i=1,j=1}^{r,\ n}$ represents the forward migration matrix corresponding to dispersal from $\mathcal{M}$ to $\mathcal{P}$. Assuming the adult population sizes at the deme sites are prescribed by $\mathbf{c} = (c_1, c_2, \ldots, c_n)$, then $\lambda_i = \sum_{k=1}^{n} c_k\gamma_{ki}$, $i = 1, 2, \ldots, r$, indicate the relative population sizes in the mating areas.

There are two backward migration matrices $L = \| l_{ij} \| = \| c_j\gamma_{ji}/\lambda_i \|$ where l_{ij} is the fraction of adults in $\mathcal{M}_i$ originating from $\mathcal{P}_j$ and

$$M = \| m_{ij} \| = \left\| \frac{\lambda_j\delta_{ji}}{\sum_{k=1}^{r} \lambda_k\delta_{ki}} \right\|$$

where m_{ij} is the fraction of young individuals in $\mathcal{P}_i$ deriving from the jth mating area $\mathcal{M}_j$. The relative population numbers at the habitat sites corresponding to the juvenile stage (i.e., before selection) are

$$\tilde{c}_i = \sum_{k=1}^{r} \lambda_k\delta_{ki}$$

A discussion of some conditions for a protected polymorphism in this two-stage model occurs in Karlin and Kenett (1977) (see also Strobeck, 1974).

(vi) Classes of Migration Forms

Migration and population structure influence the occurrence and nature of a protected polymorphism in markedly different ways. We will delineate classes of possible natural migration forms that reflect environmental and ecological profiles, systematic and fluctuating temporal effects, behavioral and physiological attributes, and population structure parameters.

Our second objective is to ascertain the conditions for a protected polymorphism or allele protection for a variety of reasonable situations and offer comparisons and contrasts between the various migration forms. We seek in particular to assess the influence of (i) variable homing rates; (ii) the level and form of clustering over multideme populations; (iii) the role of the distribution of population sizes; (iv) the extent and nature of migration distance; (v) seasonal effects; and (vi) other hierarchical characteristics. It is hoped that several of the hybrid migration structures of Tables III and IV may provide insights for evaluating the empirical adequacy of some field population genetics studies. The results we provide may aid in interpreting the observed gene frequency distribution with respect to possible migration-selection mechanisms, and in deciphering the relative role of mating pattern, multigene interactions, correlated environmental influences, residual perturbations, and related factors.

We describe in Table III several canonical migration forms. Various extensions are indicated in Table IV of hybrid compositions of canonical migration forms. Their detailed formulations and discussions are set forth in Sections 2–4. The conditions for protection for these models and some of their interpretations and implications are developed in Sections 5–13.

(vii) General Conditions for a Protected Polymorphism

A-protection (protection of allele A) in the general selection migration model of (1.8) holds in the presence of the following analytic condition:

The spectral radius of the product matrix MD, written $\rho(MD)$, must exceed 1 (i.e., the dominant eigenvalue of MD is greater than unity):

$$\rho(MD) > 1 \tag{1.12}$$

(Bulmer, 1972; see also Karlin, 1976), where M is the backward migration matrix and $D = \mathrm{diag}(d_1, d_2, \dots, d_N)$ is a diagonal matrix with values $d_i = f_i'(0)$, $i = 1, 2, \dots, N$, down the diagonal. If

$$\rho(MD) < 1 \tag{1.13}$$

holds, then allele A goes extinct when its initial frequency is low. Therefore, apart from the possibility that $\rho(MD) = 1$, the necessary and sufficient condition for A-protection is the inequality (1.12). It should be noted that the explicit calculation of $\rho(MD)$ is generally a prohibitive task and tractable only for special migration patterns. In a similar manner, protection of the a-allele is assured by the inequality $\rho(M\bar{D}) > 1$ where $\bar{D} \doteq \mathrm{diag}(\bar{d}_1, \bar{d}_2, \dots, \bar{d}_N)$ and now $\bar{d}_i = f_i'(1)$.

TABLE III. Some Canonical Migration Forms of n-Demes $\{\mathcal{P}_1, \mathcal{P}_2, \dots, \mathcal{P}_n\}$

	Backward migration form		Characteristics
Island model (Section 2, part I)	$m_{ij} = 1/n$ (independent of i and j)		The population is redistributed every generation from a common pool equally to all demes. All demes carry approximately equal population numbers
Levene model (Section 2, part I)	$m_{ij} = c_j$	Rank-1 matrix: $M = \|e_i c_j\| = C$, $e_i \equiv 1$	Deme $\mathcal{P}_j$ receives the same proportion c_j of the total gametic pool in each generation
Deakin model (Section 2, part II)	$m_{ii} = 1 - \alpha + \alpha c_i$ $m_{ij} = \alpha c_j,\ i \neq j$	$M = (1 - \alpha) I + \alpha C$	A homogeneous homing rate $1 - \alpha$ superimposed on a Levene model; α can be interpreted as an innate sessile tendency
Variable-homing-rate model (Section 2, part III) [see also (2.9)–(2.13) for other formulations of the variable-homing and population structure factors]	$m_{ii} = 1 - \alpha_i + \alpha_i c_i$ $m_{ij} = \alpha_i c_j$	$M = \Delta + R$, Δ = diagonal, R is of rank 1, $R = \|\alpha_i c_j\|$	The sessile tendency is dependent on deme site
Stepping stone (Section 2, part IV)	General form $m_{ii} = r_i$ $m_{i,i+1} = p_i$ $m_{i,i-1} = q_i$ otherwise, $m_{ij} = 0$	Homogenous case $r_i = 1 - 2m$ $p_i = q_i = m$ (at boundary demes $r = 1 - m$, p or $q = m$)	Migration only possible to neighboring demes. Stepping stone can be construed as the extreme case of isolation-by-distance migration
Circulant (Section 2, part V)	$m_{ij} = a_{i-j}$ (interpret $a_{-k} = a_{n-k}$)		(i) Migration mediated by wind or water current; (ii) corresponds also to temporal variation in selection intensities
Directional migration with a distinguished deme; major/subordinate deme structure (includes models of age-structured populations) (Section 2, part VI)	See (2.22) and (2.23)		The configuration of demes resembles a mainland with islands or a forest and trees spreading out from the forest. This form also models seed pool processes

TABLE IV. Hybrid Multicluster–Multideme Population Structures

	Backward migration form	Characteristics
Generalized multiuniform migration flow (Section 3, part VII)	m clusters of n demes in each cluster (e.g., Deakin migration within each cluster and Levene migration between clusters)	Clusters—nations; demes—tribes or societies
Generalized star migration pattern (Section 3, part VIII)	Clusters of demes connected through a central deme (e.g., stepping-stone connecting clusters, migration patterns of general form within clusters)	Tributaries of a lake; canyons connected through a central valley
Temporal and spatial variation intermeshed; (Section 4, parts IX, X)	A directional circulant migration form superimposed on a general n-deme migration matrix. Can entail differential cluster homing tendencies	Allows treatment of seasonal variation in selection intensity in a multideme context
Kronecker product (Section 4, part XI)	For example, $M = M_1 \otimes M_2$	The demes are delineated by classes of independent characteristics
Circulant cluster (Section 4, parts X, XII, XIII)		A general circulant matrix superimposed on clusters of demes reflecting also geographical properties of the population range
Cluster seed load model (Section 4, part XIV)		Pattern of directional flow with distinguished environmental state superimposed on a multideme (plant) population

Recall under soft selection that $C = C^*$ and

$$\hat{C} = \operatorname{diag}\left[\sum_{k=1}^{N} \mu_{ki} c_k\right] = \operatorname{diag}[\mathrm{F}'\mathbf{c}]$$

so that

$$B = \hat{C}^{-1} = \operatorname{diag}[(\mathrm{F}'\mathbf{c})^{-1}] = \operatorname{diag}\left[\frac{1}{\sum_{k=1}^{N} \mu_{ki} c_k}\right]$$

The backward migration under soft selection is therefore [see (1.7)]

$$M_s = (\operatorname{diag}[\mathrm{F}'\mathbf{c}]^{-1})\mathrm{F}'C \tag{1.14}$$

which is, in particular, independent of the population frequency vector **x**.

Under hard selection with $W_i(x_i)$ as in (1.4), $W_i(x) = v_i x^2 + 2x(1 - x) + w_i(1 - x)^2$ so that $C^* = \operatorname{diag}\{c_i[x_i^2 v_i + 2x_i(1 - x_i) + w_i(1 - x_i)^2]\}$, which for **x** sufficiently small is well approximated by $C^* = C \operatorname{diag}[\mathbf{w}] = CD^{-1}$, where D is defined to be the diagonal matrix $(d_1, \ldots, d_N)$, $d_i = w_i^{-1}$. The backward migration matrix under hard selection relevant for **x** near **0** becomes

$$(\operatorname{diag}[\mathrm{F}'C\mathbf{d}^{-1}]^{-1})\mathrm{F}'CD^{-1} \tag{1.15}$$

If the change of the A-allele frequency vector over successive generations is given by $\mathbf{x}' \approx MD\mathbf{x}$ when **x** is sufficiently small (i.e., when allele A is sufficiently rare), then the criterion that **x** increases (that the A allele spreads) is that

$$\rho(MD) > 1 \tag{1.16}$$

If we define $D_{\mathrm{H}} = (\operatorname{diag}[M_s\mathbf{d}^{-1}]^{-1})$ (i.e., $d_{ii}^{(\mathrm{H})} = [\sum_{j=1}^{N} m_{ij}^{(s)}(1/d_j)]^{-1}$) (the subscript H serves to refer to hard selection), then the conditions for hard and soft protection may be displayed concisely as

$$\begin{aligned} &\rho(M_s D_{\mathrm{H}}) > 1 \qquad \text{(hard protection)} \\ &\rho(M_s D) > 1 \qquad \text{(soft protection)} \end{aligned} \tag{1.17}$$

We established in Karlin (1976) as a sufficient condition for A-protection, applicable to any selection–migration system, the inequality

$$\prod_{i=1}^{N} d_i^{\xi_i} > 1 \tag{1.18}$$

where $\boldsymbol{\xi} = (\xi_1, \xi_2, \ldots, \xi_N)$ is the unique left eigenvector corresponding to the eigenvalue 1 for the matrix M, normalized such that $\sum_{i=1}^{N} \xi_i = 1$.

When M admits the representation

$$M = E_1 K E_2 \tag{1.19a}$$

where E_1 and E_2 are positive diagonal matrices, and K is positive definite, then (1.18) can be replaced by the inequality

$$\sum_{i=1}^{N} \xi_i d_i > 1 \tag{1.19b}$$

and then A-protection prevails. Of course, (1.18) implies (1.19b).

The sufficient condition (1.18) for protection presents a *generalized geometric mean criterion* that applies for *any* migration scheme while the condition (1.19b) is easier to achieve but the form of (1.19a) is valid only if the extent of migration flow per generation is not excessive. The caveat should be added that the verifications of (1.18) and (1.19b) provide only sufficient conditions for protection.

With the foregoing facts in mind, in comparing selection regimes and/or migration patterns with respect to the opportunities for polymorphism (or A-protection) it is easier for qualitative purposes to compare the function

$$G(\mathbf{d}, \boldsymbol{\xi}) = \prod_{i=1}^{N} d_i^{\xi_i} \quad \text{and} \quad A(\mathbf{d}, \boldsymbol{\xi}) = \sum_{i=1}^{N} d_i \xi_i \tag{1.20}$$

which are largely accessible, whereas verifying the precise spectral radius condition (1.12) or (1.13) is often prohibitive. The complexity of migration in dealing with (1.20) is summarized by the left eigenvector $\boldsymbol{\xi} = (\xi_1, \ldots, \xi_N)$ of the backward migration matrix, and the effects of selection are expressed by the parameters d_i, $i = 1, 2, \ldots, N$.

2. SOME BASIC CLASSES OF MIGRATION STRUCTURES

We highlight in this and the following two sections mostly new classes of useful migration matrices with some that have been studied before. For each model the precise conditions for the existence of a protected polymorphism are ascertained (Sections 5–13 and Appendices C and D). We later set forth some comparisons and interpretations of the results. Theoretical insights derived by the study of classes of migration–selection population structures and their attendant stable equilibrium configurations may also be used as a simulation control to evaluate more complex interactions and consequences of multidemic dynamics.

I. The Levene Population Subdivision Model

The Wright island model (1943) depicts a situation where the population is divided into N equal-sized units each of which contributes equally to and receives equally from a panmictic mating pool. The local populations are genetically identical following migration and mating. The Levene migration structure (1953) generalizes the island model by assigning different sizes (specified as c_i) to the islands so that they do not contribute equally to the mating pool, but such that the genetic compositions of all demes are the same immediately following migration and mating. It has been suggested that the foregoing setup may be appropriate for a species whose numbers are regulated within each of the separate demes, but not on the whole population. For this model, under the stipulation of soft selection, we have

$$m_{ij} = \mu_{ij} = c_j, \qquad i, j = 1, 2, \ldots, N \tag{2.1}$$

The Levene subdivision model is essentially characterized by three main features: (a) Numerous microhabitats are available for the population; (b) mating occurs at random across the local habitat structure; and (c) the output from each site is locally set. Some classes of organisms that possibly fit this life-style include the polychaetes (marine worms), which are principally sessile but in mating engage in swarming maneuvers and then mostly settle back to available habitats. A number of fish populations (e.g., the American eel and herring) breed together in spawning areas and then disperse back to habitats located up various streams, somewhat reminiscent of the foregoing population structure. Other cases approximating the Levene subdivision model may include seabird populations that nest in large rookeries.

Some discussion of the inherent limitations in the Levene model is found in Karlin and Kenett (1977). It should be realized that the Levene structure constitutes the most homogeneous environment of a whole hierarchy of heterogeneous environmental selection–migration patterns (on this concept see Karlin, 1976).

II. A Homogeneous Homing Model

The Levene model was generalized by Deakin (1966) who assumed that only a proportion α of the individuals are inclined to disperse and these are relocated (as adults) according to (2.1). The remaining fraction

$1 - \alpha$ contribute progeny directly in their home (parental) habitat. Equivalently, an individual stays put with probability $1 - \alpha$ while a fraction α of the total population seek to migrate. Let $\mathbf{a} = (a_1, \ldots, a_N)$ be the vector of premigration deme sizes. Of those that migrate, let c_j, $\mathbf{c} = (c_1, \ldots, c_N)$, be the proportion that immigrate to $\mathcal{P}_j$ where the birthplace of the individual does not influence the choice of where the migrant settles. (Model III below considers variable homing rates dependent on the origin and destination of the deme sites involved.) These prescriptions are formally summarized by the forward migration matrix

$$\begin{aligned} \mu_{ii} &= \frac{(1-\alpha)a_i + \alpha a_i c_i}{a_i} = 1 - \alpha + \alpha c_i \\ \mu_{ij} &= \alpha c_j, \qquad i \neq j \end{aligned} \tag{2.2}$$

In compact notation, the forward migration matrix becomes $F = (1 - \alpha)I + \alpha C$ (where I is the identity matrix) with $C = \| e_i c_j \|$ $(e_i \equiv 1)$ a rank-one matrix whose common row vector indicates the relative deme sizes after migration without homing. We transform to the backward migration form following the recipe of (1.6)–(1.7) yielding

$$M = \Gamma^{-1} F' \hat{C} \qquad (F' = \text{transpose of } F) \tag{2.3}$$

with $\hat{C} = \operatorname{diag}(c_1, c_2, \ldots, c_N)$, and where Γ equals the diagonal matrix exhibiting the values $\gamma_i = (1 - \alpha) + \alpha c_i$, $i = 1, 2, \ldots, N$, down the diagonal. Clearly, $M = \Gamma^{-1} F' \hat{C} = (1 - \alpha)I + \alpha C = F$. Thus, when superimposing uniform homing tendencies on the Levene subdivision structure, the backward and forward migration matrices coincide. [There is some mechanism that brings the premigration sizes back to $\mathbf{a} = (a_1, a_2, \ldots, a_N)$ which can differ from $\mathbf{c}$ but in the foregoing model this does not affect the form of the forward and backward migration matrices.]

In the event that pre- and postmigration population sizes are not the same, homing rates can be imposed meaningfully in terms of either the forward or the backward migration prescription. Accordingly, uniform homing in the forward migration matrix can be interpreted as reflecting territorial behavior such that the sessile proportion of the population is a given fraction of the juveniles independent of the habitat. In this circumstance, selection acts in the same way on those who remain in the habitat and those who migrate.

There exist in some formulations theoretical and practical reasons for adding homing to the backward rather than to the forward migration matrix. It is clear that any forward migration matrix with homing can be transformed into a backward migration matrix with homing (not necessarily uniform).

An interpretation of (uniform) homing superimposed on a backward migration matrix is that at mating season a proportion $(1 - \alpha)$ of the mating sites in each niche are already occupied. For example, there are situations where the mating population size is limited by the number of mating sites (e.g., nesting). Possibly, a territorial behavior permits one (or a few) juveniles to remain in the mating site of their birth while the others are compelled to mature in distant environs. After mating, those that matured elsewhere randomly return seeking nesting sites that have been vacated due to predation or other causes. Thus, in this context uniform homing reflects an equal degree of mortality in all niches. A departure from the assumption of a constant homing rate may be used to reflect different amounts of mortality perhaps due to natural cycles in predation, artificial harvesting of predators, or effects on predation by man.

III. A Nonhomogeneous Homing Pattern

We now introduce an extension of (2.2) that allows the rate of homing to differ over the respective demes. The parallel rationale to (2.2) leads to

$$\mu_{ii} = 1 - \alpha_i + \alpha_i c_i, \qquad \mu_{ij} = \alpha_i c_j, \qquad i \neq j \tag{2.4}$$

The backward migration matrix is then

$$\begin{aligned} m_{ij} &= \frac{\alpha_j c_j}{\gamma_i}, \qquad i \neq j, \qquad \text{with } \gamma_i = 1 - \alpha_i + \sum_{k=1}^{N} \alpha_k c_k \\ m_{ii} &= \frac{1 - \alpha_i + \alpha_i c_i}{\gamma_i}, \qquad i = 1, 2, \ldots, N \end{aligned} \tag{2.5}$$

Thus, $M = \| m_{ij} \|$ has the form $= \Delta + R$, where $\Delta = \operatorname{diag}(\delta_1, \delta_2, \ldots, \delta_N)$ is a diagonal matrix, $\delta_i = (1 - \alpha_i)/\gamma_i$, $i = 1, 2, \ldots, N$, and R is a matrix of rank one, $R = \| r_i s_j \|$ having explicitly $r_i = 1/\gamma_i$ and $s_j = c_j \alpha_j$, $j = 1, 2, \ldots, N$. We will see that the interaction of migration and selection forces are more recondite in the presence of a *nonuniform* than a uniform homing rate.

The migration behavior in some bird populations may have a nonuniform error rate in homing. Another example is the homing propensities among salmon and similar fish populations. In certain primate troops, generally small numbers of young stay in the group while the others relocate or establish new groupings. The nonhomogeneous homing pattern described in this paragraph may approximate the migration dynamics for such cases.

A Further Extension

Suppose that at deme $\mathcal{P}_i$ ($i = 1, 2, \ldots, N$) the a priori probability of an individual not migrating is $1 - \alpha_i$. Let the relative sizes of the adult population at the deme locations be described by $(c_1, c_2, \ldots, c_N)$. Consider the behavior pattern such that those that migrate congregate in a single mating area whose progeny disperse back to the deme sites $(\mathcal{P}_1, \mathcal{P}_2, \ldots, \mathcal{P}_N)$ by the mixing distribution $(\delta_1, \delta_2, \ldots, \delta_N)$, $\delta_i > 0$, $\sum_{i=1}^{N} \delta_i = 1$, where (2.4) and (2.5) reflect the special relation $c_i = \delta_i$. In this context the forward migration rates are summarized by the matrix $F = \| \mu_{ij} \|$ and are calculated as follows: The fraction of adult individuals in $\mathcal{P}_i$ that do not move is $(1 - \alpha_i)$. Of those that breed at the common mating area, a proportion δ_j of their offspring locate at deme $\mathcal{P}_j$. The conjunction of these contingencies leads to the formula

$$\begin{aligned} \mu_{ii} &= \frac{[(1-\alpha_i) + \alpha_i\delta_i]c_i}{c_i} = 1 - \alpha_i + \alpha_i\delta_i \\ \mu_{ij} &= \alpha_i\delta_j, \qquad j \neq i \end{aligned} \qquad (2.6)$$

This forward migration matrix has the representation

$$F = \Delta + R \qquad \text{where } \Delta = \operatorname{diag}(1-\alpha_1, 1-\alpha_2, \ldots, 1-\alpha_N) \qquad (2.7)$$

while $R = \| s_i r_j \|$ is rank one with $s_i = \alpha_i$, $r_j = \delta_j$. It is convenient to write

$$F = \Delta + AUB = A(\tilde{\Delta} + U)B \qquad (2.8)$$

composed from the factors $A = \operatorname{diag}(\alpha_1, \ldots, \alpha_N)$, $B = \operatorname{diag}(\delta_1, \ldots, \delta_N)$, $U = \| e_i e_j \|$, $e_i \equiv 1$, and $\tilde{\Delta} = A^{-1}\Delta B^{-1}$. Following (1.7), the backward migration matrix associated with (2.8) has the expression

$$M = \Gamma^{-1}F'C$$

$$C = \operatorname{diag}(c_1, \ldots, c_N) \quad \text{and} \quad \Gamma = \operatorname{diag}(\gamma_1, \ldots, \gamma_N) \qquad (2.9)$$

where

$$\gamma_k = \sum_{j=1}^{N} c_j\mu_{jk}, \qquad k = 1, \ldots, N$$

In the particular case of (2.6), M reduces to

$$M = \Gamma^{-1}[\Delta C + BUAC] = \| m_{ij} \| \qquad (2.10)$$

such that

$$\begin{aligned} m_{ii} &= \frac{(1-\alpha_i)c_i + \delta_i\alpha_i c_i}{\gamma_i}, \qquad i = 1, 2, \ldots, N \\ m_{ij} &= \frac{\delta_i\alpha_j c_j}{\gamma_i}, \qquad i \neq j \end{aligned} \qquad (2.11)$$

$$\gamma_i = (1-\alpha_i)c_i + \delta_i \sum_{j=1}^{N} \alpha_j c_j \qquad (2.12)$$

For the case with $\delta_i = c_i$, $i = 1, \ldots, N$, then

$$m_{ii} = \frac{1 - \alpha_i + \alpha_i c_i}{\tilde{\gamma}_i}, \qquad m_{ij} = \frac{\alpha_j c_j}{\tilde{\gamma}_i}, \qquad i \neq j \qquad (2.13)$$

and

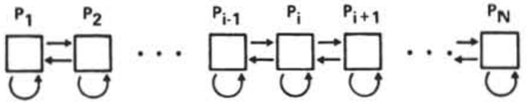
$$\tilde{\gamma}_i = 1 - \alpha_i + \sum_{k=1}^{N} c_k\alpha_k$$

Further interpretations and relevance of the variable-homing-rate models stem from the following considerations. Environments have different carrying capacities at various times of the year reflecting both a change in the nutrients available and changes in the nutrient requirements of organisms as they pass through different phases of their life cycle. In this regard consider butterflies, which have several larval stages and which may consume different food plants. If we postulate that larvae are fairly immobile, that selection operates primarily on larvae (i.e., adult morphs do not differ significantly with respect to predation), and that adults migrate, then we have the standard order of forces and events: migration → mating → selection order.

If we assume that migration is random but that each area receives a fraction of the total population proportional to the number of plants suitable for egg-laying, afterwards selection acts and the relative premigration deme sizes are proportional to, e.g., the number of sites suitable for diapausing. Accordingly, we have a modified Levene migration pattern. Let $\{c_i\}$, $\sum_{i=1}^{N} c_i = 1$ be the proportion of premigrant adults in each habitat and $\{\delta_i\}$, $\sum_{i=1}^{N} \delta_i = 1$ the proportion of larval egg sites in each habitat. Then the forward migration matrix is $\| \delta_j e_i \|$, $e_i \equiv 1$, and the backward migration matrix is $\| e_i c_j \|$.

IV. Homogeneous and Nonhomogeneous Linear Stepping-Stone Migration Model

The demes can be arranged in a linear order where per generation migration reaches only to neighboring demes:



Population structures entailing small migration flow per generation abound in nature. An example is the case of many grasses and plant populations (thistles, milkweeds) distributed in discrete patches along a shoreline, through a narrow valley, etc. Stepping-stone migration modes may reasonably approximate the population movement among relatively sessile organisms. Ehrlich *et al.* (1974) cite many examples of animal and plant populations where gene flow is considerably localized.

The classical homogeneous stepping-stone migration mode with N demes has a common forward and backward migration matrix of the form

$$M = \left\| \begin{matrix} 1-m & m & 0 & \cdots & & 0 \\ m & 1-2m & m & & & 0 \\ \cdot & \cdot & \cdot & & & \cdot \\ \cdot & & \cdot & \cdot & & \cdot \\ \cdot & & & \cdot & \cdot & \cdot \\ & & & m & 1-2m & m \\ 0 & & & 0 & m & 1-m \end{matrix} \right\| \qquad (2.14)$$

where each deme exchanges a fraction m of its population with each of its neighboring demes provided the relative deme sizes are the same.

The stepping-stone model is an extreme case among migration patterns based on the principle of *isolation by distance* where the degree of migration diminishes with the "distance" from the parental deme. The stepping-stone model for migration including two- and higher dimensional versions and continuous formulations has been widely used in the study of geographical genetic models *without selection*. Isolation by distance of one- or higher dimensional migration forms is intrinsically associated with, e.g., seed and pollen dispersal in plant populations, travels in certain rodent species, mobility in snails.

For an isolation-by-distance migration pattern, the geographical arrangement among demes determines the nature and magnitude of population movement. The analysis of the stepping-stone mode provides bounds on the effects of such (ordered) selection–migration systems.

If the relative deme sizes are summarized by the vector $\mathbf{c} = (c_1, c_2, \ldots, c_N)$, $c_i > 0$, $\sum c_i = 1$, then the backward migration matrix attached to (2.14) [following the computation of (1.7)] is

$$M = \left\| \begin{matrix} \dfrac{c_1(1-m)}{\gamma_1} & \dfrac{mc_2}{\gamma_1} & 0 & \cdots & 0 \\ \dfrac{c_1 m}{\gamma_2} & \dfrac{(1-2m)c_2}{\gamma_2} & \dfrac{mc_3}{\gamma_2} & & 0 \\ \cdot & & & \cdot & \\ \cdot & & & & \cdot \\ \cdot & & & & \\ 0 & 0 & & \dfrac{mc_{N-1}}{\gamma_N} & \dfrac{(1-m)c_N}{\gamma_N} \end{matrix} \right\| \qquad (2.15)$$

where

$$\gamma_i = mc_{i-1} + (1-2m)c_i + mc_{i+1}, \qquad 2 \le i \le N-1 \qquad (2.16)$$
$$\gamma_1 = (1-m)c_1 + mc_2, \qquad \gamma_N = mc_{N-1} + (1-m)c_N$$

Where the migration flow between neighboring demes can also vary or differ in reciprocal directions, the backward migration matrix attains the general tridiagonal form

$$M = \left\| \begin{matrix} r_1 & p_1 & 0 & 0 & \cdot & \cdot & 0 \\ q_2 & r_2 & p_2 & 0 & \cdot & \cdot & 0 \\ 0 & q_3 & r_3 & p_3 & \cdot & \cdot & 0 \\ \cdot & & \cdot & \cdot & & & \\ \cdot & & & \cdot & \cdot & \cdot & \\ \cdot & & & & q_{N-1} & r_{N-1} & p_{N-1} \\ 0 & \cdot & \cdot & \cdot & 0 & q_N & r_N \end{matrix} \right\| \qquad (2.17)$$

where $r_i \ge 0$, $q_i > 0$, $p_i > 0$, $r_i + q_i + p_i = 1$, $i = 1, 2, \ldots, N$.

Clines. The term *cline* refers to the gradual transition over space of the frequency of an allele (or phenotypic characteristic). Clines are widespread in nature and have been studied both experimentally and theoretically (see Endler, 1973, and the review by Felsenstein, 1976). It is generally assumed that the changes in allele frequencies parallel changes in selection coefficients and migration is slight in order to maintain this agreement. It is often meaningful to make assumptions on the geographical selection gradient regime in addition to the nature of the migration pattern. For example, a relevant case exhibits the selection parameters as a monotone sequence (increasing or decreasing) when indexed by the demes. A complement to the concept of a monotone selection gradient is provided by symmetric selection regimes that are monotone bidirectionally from their center. These might describe viabilities as one passes from one margin of a habitat through the center to the other margin. For example, some alleles may adapt a species to a particular environment and the fitness of such alleles can be expected to decrease as the margin of a habitat is approached. Other alleles endow individuals with the competitive qualities of a generalist rather than a specialist and these alleles should manifest enhanced viabilities toward the margins of habitats where there are no specialist alleles adapted to the particular environmental conditions.

V. Circulant Migration Patterns

Circulant migration comprises a mathematical grouping of what superficially appear to be distinct phenomena biologically. At one end is temporal variation. This is actually a single-deme phenomenon appropriate to, e.g., multivoltine insects that systematically experience a sequence of environments over subsequent generations each year. The temporal change can be simulated by "migration" of an array of demes, each moving en masse into new environments.

At the other end is the standard circular stepping-stone model. This is a special form of isolation-by-distance models for a geographical circular arrangement of demes. It is neither necessary that migration be symmetric with respect to direction (thus allowing migration mediated by ocean currents) nor that migration decreases with distance. The exact constraints on migration are most easily described in terms of the migration matrix.

If the demes occur in a circular fashion rather than linearly as they would around the base of a central mountain or along (or near) the shores of a lake, then the homogeneous stepping-stone migration mode assumes the forward migration matrix expression

$$\mu_{i,i+1} = \mu_{i,i-1} = m, \qquad \mu_{i,i} = 1 - 2m, \qquad i = 1, 2, \ldots, N \qquad (2.18)$$

(with the convention to interpret $N + 1 = 1$ and $0 = N$).

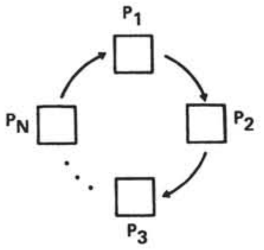
A circulant isolation-by-distance migration matrix possesses the representation

$$M = \begin{Vmatrix} a_0 & a_1 & a_2 & \cdots & a_n \\ a_n & a_0 & a_1 & & \\ \cdot & \cdot & \cdot & & \cdot \\ \cdot & \cdot & \cdot & & \cdot \\ \cdot & \cdot & \cdot & & \cdot \\ a_1 & a_n & a_{n-1} & \cdots & a_0 \end{Vmatrix} \qquad \begin{array}{l} \text{i.e., } m_{ij} = a_{|i-j|} \text{ and} \\ \quad a_j \geq 0, \quad \sum a_j = 1 \end{array} \qquad (2.19)$$

and for the case of (2.18) $a_0 = 1 - 2m$, $a_1 = a_n = m$. A particularly relevant specialization of (2.19) has

$$a_1 = 1, \qquad a_i = 0, \qquad i \neq 0 \qquad (2.20)$$

which corresponds to a unidirectional migration flow as described by



(2.21)

perhaps mediated by underlying currents (e.g., wind, water, chemical, electrical).

Another more important perspective concerning the migration flow (2.21) corresponds to that of a single-population habitat subjected to *seasonal temporal variation in selection intensities*. Thus, consonant to (2.20) [or (2.21)], a single population starting in $\mathcal{P}_1$ in the first generation is acted upon by the selection associated with $\mathcal{P}_1$ and in the next generation the offspring population is subjected to the selection forces inherent to the habitat $\mathcal{P}_2$, and continuing in this way the Nth generation progeny is subject to the selection effects of $\mathcal{P}_N$. In subsequent generations the selection forces repeat cyclically in the order of the selection regime $(f_1, f_2, \ldots, f_N)$. In summary, the spatial migration–selection pattern of (2.20) entailing *N demes engenders a population dynamics equivalent to that of a single population subject to a fluctuating seasonal selection pattern*. The above example depicts the simplest version of the proposition that the consequences of temporal selection variation are mostly subsumed as a subclass of special form among the class of all spatial migration–selection structures. We amplify more on this theme in Section 4, part IX.

VI. Directional Migration Pattern with a Distinguished Deme

In a subdivided population all of the demes may not be of equal importance. Rather there may be one or a few major demes and several subordinate demes. One manifestation of such a dichotomy is the single-island model of Wright, which contrasts a stable mainland population with an island population linked by limited migration. The model of Levene (1953) generalizes the multiple-island model of Wright (1951) in which each island receives an equal immigrant fraction from every island by assigning different relative importance to the different islands, but this represents a continuum of deme significance rather than a dichotomy. We focus here on models involving a single major (distinguished) deme.

The two models that we consider here entail a linear array of demes connected by unidirectional stepping-stone migration concurrent with movement from the distinguished deme, which either receives immigrants from all or some of the demes or disperses emigrants to all or some of the demes. These models are suggestive of a physical array consisting of a major island and several smaller islands extending alone a line. Other physical settings include a forest with nearby clusters of trees and shrubs, a stream flowing into (or out of) a lake, and a major city with satellite towns along the main highway. The unidirectional migration could be mediated by wind or water currents, a population density gradient, or the flight patterns of insect vectors.

The distinguished immigrant deme model is also appropriate for studying age-structured populations. A familiar example is the Leslie matrix employed in demographic studies that specifies age-specific birth and death rates. The problem of protection of an allele with different survival probabilities in different age classes can be identified with the problem of growth or extinction of an age-structured population; temporal variation in selection intensities can be identified with temporal variation in birth and death rates.

Consider a backward migration matrix of the form

$$M = \begin{Vmatrix} r_1 & p_1 & 0 & 0 & \cdots & 0 \\ q_2 & r_2 & p_2 & 0 & \cdots & 0 \\ q_3 & 0 & r_3 & p_3 & & \\ \cdot & & \cdot & \cdot & \cdot & \\ \cdot & & & & \cdot & \\ q_{N-1} & & & & & p_{N-1} \\ q_N & 0 & 0 & \cdots & & r_N \end{Vmatrix} \qquad \begin{matrix} r_i + q_i + p_i = 1, & q_i > 0, \\ p_i > 0, & i = 1, \ldots, N-1 \end{matrix} \qquad (2.22)$$

The first deme is distinguished (e.g., as a mainland habitat, a major city). Every other deme in each generation receives a proportion of its inhabitants from the central deme and the remaining from the neighboring deme to the right.

Thus, the migration flow is principally directed toward deme 1, while deme 1 disperses its population to all the demes. Where $q_2 = q_3 = \cdots = q_{N-1} = 0$, $q_N > 0$, the migration flow is primarily in a circular direction.

Where the migration propensity is in the other direction, away from the mainland, (2.22) is replaced by

$$M = \begin{Vmatrix} a_1 & a_2 & a_3 & a_4 & & a_{N-1} & a_N \\ b_2 & c_2 & d_2 & 0 & & 0 & 0 \\ 0 & b_3 & c_3 & d_3 & & 0 & 0 \\ & & \cdot & & \cdot & & \\ & & & \cdot & & \cdot & \\ 0 & 0 & 0 & 0 & & b_N & c_N \end{Vmatrix} \qquad \begin{matrix} a_i \geq 0, & \sum a_i = 1, \\ b_i + c_i + d_i = 1, & \text{and} \\ b_i > 0, & i = 2, 3, \ldots, N \end{matrix} \qquad (2.23)$$

A process of facultative seed dormancy or germination can be encompassed by the migration scheme (2.23); cf. Templeton and Levin (1979). The identifications are as follows. We assume that a plant produces seeds yearly that can lie dormant up to N years. In each generation a seed already dormant k years has a probability p_k of germinating and $1 - p_k$ of continued dormancy. Environment 1 (deme condition $\mathcal{P}_1$) of (2.23) refers to a live plant state and deme k ($k = 2, \ldots, N$) signifies a dormant state of k–1 years' duration. The change of state over successive generations conforms to the migration matrix (2.23) where $r_i = 0$ and the distinguished deme represents the live plant state. The environmental selection regime can reflect viability and/or fertility selection in state $\mathcal{P}_1$, and zygotic selection under the dormant conditions $\mathcal{P}_2, \ldots, \mathcal{P}_N$. A probably more relevant prescription may have the selection intensities fluctuating randomly in time (Karlin and Campbell, 1980).

3. SOME HYBRID MIGRATION PATTERNS INVOLVING CLUSTERS OF SEVERAL DEMES EACH

VII. Population Subdivision Models Having Different Rates of Migration within and between Natural Groupings of Demes

We may interpret this category of migration patterns as a conglomerate of interrelated Wright island models. The totality of demes divide intrinsically into clusters of demes such that the migration pattern in each cluster entails a separate Levene (or Deakin) migration mode coupled to some degree of exchange between clusters.

In its simplest version, the complete population comprises m clusters (groupings) with each cluster consisting of n demes aggregating to $N = m \times n$ demes. We list the demes starting with those in group 1, followed by the demes of group 2, and so on. In this notation, the kth cluster $\mathscr{C}_k$ is comprised of the demes

$$\mathscr{C}_k = \{\mathscr{P}_{(k-1)n+1}, \mathscr{P}_{(k-1)n+2}, \ldots, \mathscr{P}_{kn}\}, \qquad k = 1, 2, \ldots, m$$

The forward migration matrix has the form

$$\Gamma = \| \mu_{ij} \| = \begin{array}{ll||cccc|cccc|c|ccc||}
 & \mathscr{P}_1 & a & \beta_1 & \cdots & \beta_1 & \beta_2 & \beta_2 & \cdots & \beta_2 & \cdots & \beta_2 & \cdots & \beta_2 \\
 & \mathscr{P}_2 & \beta_1 & a & & \beta_1 & \beta_2 & \beta_2 & & \beta_2 & & & & \\
\mathscr{C}_1 & \vdots & \vdots & \vdots & & & \vdots & \vdots & & \vdots & & \vdots & & \vdots \\
 & \mathscr{P}_n & \beta_1 & \beta_1 & & a & \beta_2 & \beta_2 & & \beta_2 & \cdots & \beta_2 & \cdots & \beta_2 \\
\hline
 & \mathscr{P}_{n+1} & \beta_2 & \beta_2 & \cdots & \beta_2 & a & \beta_1 & \cdots & \beta_1 & \cdots & \beta_2 & \cdots & \beta_2 \\
\mathscr{C}_2 & \vdots & \vdots & \vdots & & \vdots & \vdots & & \ddots & \vdots & & \vdots & & \vdots \\
 & \mathscr{P}_{2n} & \beta_2 & \beta_2 & \cdots & \beta_2 & \beta_1 & \beta_1 & \cdots & a & \cdots & \beta_2 & & \beta_2 \\
\hline
 & \vdots & \vdots & & & \vdots & \vdots & & & & & \vdots & & \\
\hline
 & \mathscr{P}_{(m-1)n+1} & \beta_2 & \beta_2 & \cdots & \beta_2 & & & & & & & & \\
\mathscr{C}_n & \vdots & \vdots & \vdots & & \vdots & & & & & & & & \\
 & \mathscr{P}_{mn} & \beta_2 & \beta_2 & \cdots & \beta_2 & & & & & & & &
\end{array} \tag{3.1}$$

signifying that the probability of an individual not migrating is a while his migration propensity to another deme of the same cluster is β_1 and to a deme of a different cluster β_2. Of course, the parameters are constrained to satisfy $a + (n - 1)\beta_1 + (m - 1)n\beta_2 = 1$, which merely states that the migration of each individual per generation must terminate in some deme. Carmelli and Cavalli-Sforza (1976) refer to the structure (3.1) as a "multi-uniform" pattern.

The expression (3.1) may be more succinctly represented in the Kronecker product form

$$\Gamma = (a - \beta_1)I_m \otimes I_n + (\beta_1 - \beta_2)I_m \otimes U_n + \beta_2 U_m \otimes U_n \tag{3.2}$$

where I_r is the identity matrix of order r and $U_r = \| e_i e_j \|$ is the rank-one matrix of size $r \times r$ having $e_i \equiv 1$ so that U displays all ones and $A \otimes B$ denotes the Kronecker product of the matrices A and B. (See Appendix A concerning the concepts and operations of Kronecker products.)

A selection regime carrying the same selection forces for each deme of a cluster but entailing divergent selection regimes between clusters concurs with the inherent symmetry of the migration pattern of (3.1). The demes within a cluster can be construed as arising from Wahlund-type population subdivision that maintains the same local selection forces. The diagonal matrix D featured in (1.12), which summarizes the selection effects corresponding to A-protection, decomposes to the form

$$\bar{D} = D \otimes I_n, \qquad D = \operatorname{diag}(d_1, d_2, \ldots, d_m) \tag{3.3}$$

where d_k is the relevant selection factor for the demes of cluster $\mathscr{C}_k$.

The backward migration matrix corresponding to variable intercluster deme sizes, but having a common deme size within a cluster, is established as follows. Suppose

$$c_k, \qquad k = 1, 2, \ldots, m \tag{3.4}$$

is the relative adult population size of each respective deme in the cluster $\mathscr{C}_k = \{\mathscr{P}_{(k-1)n+1}, \mathscr{P}_{(k-1)n+2}, \ldots, \mathscr{P}_{kn}\}$. Of course, $n \sum_{i=1}^{m} c_i = 1$ as there are n demes per cluster. Assume the forward migration matrix is (3.1). Following the recipe of (1.7), the backward migration matrix has the form

$$M = \begin{array}{l||cccc|ccc|c|ccc||}
\mathcal{P}_1 & \frac{ac_1}{\gamma_1} & \frac{\beta_1 c_1}{\gamma_1} & \cdots & \frac{\beta_1 c_1}{\gamma_1} & \frac{\beta_2 c_2}{\gamma_1} & \cdots & \frac{\beta_2 c_2}{\gamma_1} & \cdots & \frac{\beta_2 c_m}{\gamma_1} & \cdots & \frac{\beta_2 c_m}{\gamma_1} \\
\mathcal{P}_2 & \vdots & \ddots & & \vdots & \vdots & & \vdots & & \vdots & & \vdots \\
\vdots & & & \ddots & & & & & & & & \\
\mathcal{P}_n & \frac{\beta_1 c_1}{\gamma_1} & & \cdots & \frac{ac_1}{\gamma_1} & \frac{\beta_2 c_2}{\gamma_1} & \cdots & \frac{\beta_2 c_2}{\gamma_1} & & \frac{\beta_2 c_m}{\gamma_1} & \cdots & \frac{\beta_2 c_m}{\gamma_1} \\
\hline
\mathcal{P}_{n+1} & \frac{\beta_2 c_2}{\gamma_2} & & \cdots & \frac{\beta_2 c_1}{\gamma_2} & \frac{ac_2}{\gamma_2} & \cdots & \frac{\beta_1 c_2}{\gamma_2} & \cdots & \frac{\beta_2 c_m}{\gamma_2} & \cdots & \frac{\beta_2 c_m}{\gamma_2} \\
\vdots & \vdots & & & \vdots & \vdots & & \vdots & & \vdots & & \vdots \\
\mathcal{P}_{2n} & \frac{\beta_2 c_1}{\gamma_2} & & \cdots & \frac{\beta_2 c_1}{\gamma_2} & \frac{\beta_1 c_2}{\gamma_2} & \cdots & \frac{ac_2}{\gamma_2} & & \frac{\beta_2 c_m}{\gamma_2} & \cdots & \frac{\beta_2 c_m}{\gamma_2} \\
\hline
 & & & \vdots & & & \vdots & & & & \vdots &
\end{array} \tag{3.5}$$

where

$$\gamma_i = ac_i + \beta_1(n-1)c_i + n\beta_2 \sum_{\substack{j=1 \\ j \neq i}}^{m} c_j \tag{3.6}$$

A Kronecker product representation of (3.5) is

$$M = \bar{E}\cdot[(a - \beta_1)I_m \otimes I_n + (\beta_1 - \beta_2)I_m \otimes U_n + \beta_2 U_m \otimes U_n]\cdot E \tag{3.7}$$

where

$$\bar{E} = \bar{C} \otimes I_n \quad \text{and} \quad E = C \otimes I_n \tag{3.8a}$$

$$C = \operatorname{diag}(c_1, c_2, \ldots, c_m) \tag{3.8b}$$

and

$$\bar{C} = \operatorname{diag}\left(\frac{1}{\gamma_1}, \frac{1}{\gamma_2}, \ldots, \frac{1}{\gamma_m}\right) \tag{3.8c}$$

By virtue of the properties inherent to Kronecker products in Appendix A, the expression (3.7) reduces to

$$M = (a - \beta_1)\bar{C}C \otimes I_n + (\beta_1 - \beta_2)\bar{C}C \otimes U_n + \beta_2\bar{C}U_mC \otimes U_n \tag{3.9}$$

This can be compactly written as

$$M = H \otimes F + R \otimes G \tag{3.10}$$

where $G = U_n$, $R = (\beta_1 - \beta_2)\bar{C}C + \beta_2\bar{C}U_mC$, $H = (a - \beta_1)\bar{C}C$, $F = I_n$ in the case at hand.

Some Nonhomogeneous Variants

The formulation of (3.1) can be substantially generalized while retaining its analytic tractability. Again, the population divides into m groups of n demes arranged as follows:

$$\overbrace{\mathcal{P}_1, \mathcal{P}_2, \ldots, \mathcal{P}_n}^{\mathcal{G}^{(1)}}, \overbrace{\mathcal{P}_{n+1}, \ldots, \mathcal{P}_{2n}}^{\mathcal{G}^{(2)}}, \ldots, \overbrace{\mathcal{P}_{(m-1)n+1}, \ldots, \mathcal{P}_{mn}}^{\mathcal{G}^{(m)}} \tag{3.11}$$

The forward migration rates are now prescribed in the manner. Within group $\mathcal{G}^{(k)}$:

The probability of no movement from deme $\mathcal{P}_i$ of $\mathcal{G}^{(k)}$ is a_k (that is, $\mu_{ii} = a_k$ for $i = (k-1)n + 1, \ldots, kn$), while the probability of migration from $\mathcal{P}_i$ to $\mathcal{P}_j$ representing two distinct demes of $\mathcal{G}^{(k)}$, $i \neq j$, is b_k, $k = 1, 2, \ldots, m$ (3.12a)

The a priori probability of migration from any deme $\mathcal{P}_i$ in $\mathcal{G}^{(k)}$ to a deme $\mathcal{P}_j$ in $\mathcal{G}^{(l)}$, $k \neq l$, is $u_k v_l$, $k, l = 1, 2, \ldots, m$ (3.12b)

where

$$\{u_1, u_2, \ldots, u_m\} \text{ and } \{v_1, v_2, \ldots, v_m\} \tag{3.13}$$

are specified positive sequences

The special case of (3.1) has $a_k = a$, $b_k = \beta_1$ independent of k and $u_k \equiv v_l \equiv \beta_2^{1/2}$ for all k and l. The parameters are nonnegative and obey the constraints

$$a_k + (n-1)b_k + nu_k \sum_{\substack{j=1 \\ j\neq k}}^{m} v_j = 1, \qquad k = 1, 2, \ldots, m \tag{3.14}$$

merely expressing the mutually exclusive possibilities of migration flow. The stipulation of (3.12) introduces a nonhomogeneity into the migration pattern between the deme clusters. Each cluster involves a different rate of homing and movement among the demes of its grouping. Moreover, the a priori probability of an individual of deme $\mathcal{P}_i \in \mathcal{G}^k$ migrating to $\mathcal{P}_j \in \mathcal{G}^l$ is a product of two factors determined by the antecedent and destination groups $\mathcal{G}^k$ and $\mathcal{G}^l$, respectively.

The forward migration matrix paraphrasing the derivation of (3.2) can be compactly summarized as

$$\Gamma = L \otimes I + K \otimes U + R \otimes U \tag{3.15}$$

where

$$\begin{aligned} L &= \operatorname{diag}(a_1 - b_1, a_2 - b_2, \ldots, a_m - b_m), \\ K &= \operatorname{diag}(b_1 - u_1v_1, b_2 - u_2v_2, \ldots, b_m - u_mv_m) \end{aligned} \tag{3.16}$$

and R is the rank-one matrix

$$R = \| u_iv_j \|_1^m \tag{3.17}$$

where as before $U = \| e_ie_j \|_1^n$, $e_i \equiv 1$, $i = 1, 2, \ldots, n$.

The backward migration matrix (under soft selection) involving variable relative deme sizes c_k for the demes of group $\mathcal{G}^{(k)}$ is calculated by analogy with (3.7) giving

$$M = \hat{E} \cdot \Gamma \cdot E \tag{3.18a}$$

where

$$E = C \otimes I_n, \qquad C = \operatorname{diag}(c_1, c_2, \ldots, c_m) \tag{3.18b}$$

and

$$\hat{E} = \hat{C} \otimes I_n, \qquad \hat{C} = \operatorname{diag}\left(\frac{1}{\hat{\gamma}_1}, \ldots, \frac{1}{\hat{\gamma}_m}\right) \tag{3.18c}$$

$$\hat{\gamma}_k = a_kc_k + (n-1)b_kc_k + nu_k \sum_{\substack{i=1 \\ i\neq k}}^{m} c_iv_i, \qquad k = 1, 2, \ldots, m$$

More general tractable parameterizations can be set forth leading to

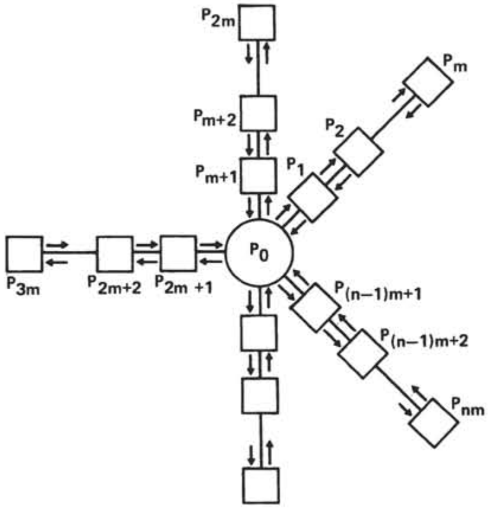
$$M = \frac{1}{r} \sum_{i=1}^{r} L_i \otimes F_i \tag{3.19}$$

where L_i (each of order $m \times m$) and F_i (each of order $n \times n$) are stochastic matrices so that $M\mathbf{e} \otimes \mathbf{e} = \mathbf{e} \otimes \mathbf{e}$ showing that M is stochastic. The migration form (3.18) plainly conforms to the structure of (3.19).

The structure of (3.15) with R of general form covers considerably more scope than the original model (3.1). However, the availability of an explicit formula for $\rho(MD)$ requires some degree of specialization, e.g., M as in (3.18).

VIII. The Star Migration Form

The population distribution entails a central deme and colonies extending along rays like spokes of a wheel:



The demes can be grouped in n collections each composed of m

demes

$$\overbrace{\mathcal{P}_1, \ldots, \mathcal{P}_m}^{\mathcal{G}^{(1)}}, \overbrace{\mathcal{P}_{m+1}, \ldots, \mathcal{P}_{2m}}^{\mathcal{G}^{(2)}}, \ldots, \overbrace{\mathcal{P}_{(n-1)m+1}, \ldots, \mathcal{P}_{nm}}^{\mathcal{G}^{(n)}}$$

apart from the distinguished central deme $\mathcal{P}_0$. Migration exchange occurs among the demes of a given grouping and with $\mathcal{P}_0$, but gene flow between groupings can only transpire via the central deme $\mathcal{P}_0$. The spokes may reflect tributaries feeding into a river or a large body of water. Corresponding geographical layouts may be ravines connected through a central area. The spread of an epidemic around a major city may also be modeled in this form.

Where the population dispersal ebbs toward the extreme demes, the migration pattern approximates outward population radiation, and where a centripetal tendency predominates, a type of urbanization results (see Carmelli and Cavalli-Sforza, 1976).

It is useful to refer to the demes closest to the central deme as of unit distance. Those colonies of distance r will correspond to the rth deme along each spoke counting from the center. In order to represent the migration matrix associated with the star model in an expeditious form, it is useful to arrange the demes with the central deme first proceeding around the spokes for each distance inducing the order

$$\mathcal{P}_0, \mathcal{P}_1, \mathcal{P}_{m+1}, \ldots, \mathcal{P}_{m(n-1)+1}, \mathcal{P}_2, \mathcal{P}_{m+2}, \ldots, \mathcal{P}_{(n-1)m+2}, \mathcal{P}_3, \ldots \tag{3.20}$$

We will concentrate henceforth, unless stated otherwise, on the *symmetric* situation where the migration structure is identical for the demes in each ray. Concomitantly, we stipulate that the rates of migration into and out of $\mathcal{P}_0$ are equal for each spoke. In particular, for each $\mathcal{P}_i$ the migration rate from $\mathcal{P}_0$ to the demes $\mathcal{P}_i, \mathcal{P}_{m+i}, \ldots, \mathcal{P}_{km+i}, \ldots, \mathcal{P}_{(n-1)m+i}$ agree.

Let $B = \| b_{\lambda\mu} \|_{\lambda,\mu=1}^{m}$ be the forward migration matrix corresponding to the migration propensities along each spoke except for the immigration rates into and out of $\mathcal{P}_0$. By our symmetry assumption the matrix B applies to each grouping $\mathcal{G}^{(k)}$, $k = 1, 2, \ldots, n$. We denote by $b_{\lambda 0}$, $\lambda = 1, 2, \ldots, m$, the forward migration probabilities to the central deme from the demes along a single ray. Finally, we let a_k be the a priori probability of migration of an individual from deme $\mathcal{P}_0$ to a specific deme of "distance" k. Thus, conforming to the arrangement (3.20), the forward migration matrix Γ has the form

$$
\begin{array}{cc|c|cccc|cccc|c|cccc|}
 & & \multicolumn{14}{l}{\mathcal{P}_0\ \mathcal{P}_1\ \mathcal{P}_{m+1} \cdots \mathcal{P}_{(n-1)m+1}} \\
\hline
 & \mathcal{P}_0 & a_0 & a_1, & a_1, & \ldots, & a_1 & a_2, & a_2, & \ldots, & a_2 & \cdots & a_m, & a_m, & \ldots, & a_m \\
\hline
 & \mathcal{P}_1 & b_{10} & b_{11} & 0 & \ldots & 0 & b_{12} & 0 & \ldots & 0 & \cdots & b_{1m} & 0 & \ldots & 0 \\
\text{distance} & \mathcal{P}_{m+1} & b_{10} & \vdots & \ddots & & \vdots & \vdots & \ddots & & \vdots & & \vdots & \ddots & & \vdots \\
1 & \vdots & \vdots & & & & & & & & & & & & & \\
 & \mathcal{P}_{(n-1)m+1} & b_{10} & 0 & 0 & \ldots & b_{11} & 0 & 0 & \ldots & b_{12} & & 0 & 0 & \ldots & b_{1m} \\
\hline
 & \mathcal{P}_2 & b_{20} & b_{21} & 0 & \ldots & 0 & b_{22} & 0 & \ldots & 0 & \cdots & b_{2m} & 0 & \ldots & 0 \\
\text{distance} & \mathcal{P}_{m+2} & b_{20} & \vdots & \ddots & & \vdots & \vdots & \ddots & & \vdots & & \vdots & \ddots & & \vdots \\
2 & \vdots & \vdots & & & & & & & & & & & & & \\
 & \mathcal{P}_{(n-1)m+2} & b_{20} & 0 & 0 & \ldots & b_{21} & 0 & 0 & \ldots & b_{22} & & 0 & 0 & \ldots & b_{2m} \\
\hline
 & & \vdots & & & & & \vdots & & & & & & & & \\
\hline
 & \mathcal{P}_m & b_{m0} & b_{m1} & 0 & \ldots & 0 & b_{m2} & 0 & \ldots & 0 & & b_{mm} & 0 & \ldots & 0 \\
\text{distance} & \mathcal{P}_{2m} & b_{m0} & \vdots & \vdots & & \vdots & \vdots & \ddots & & \vdots & & \vdots & \vdots & \ddots & \vdots \\
m & \vdots & \vdots & & & & & & & & & & & & & \\
 & \mathcal{P}_{nm} & b_{bm0} & 0 & 0 & \ldots & b_{m1} & 0 & 0 & \ldots & b_{m2} & & 0 & 0 & \ldots & b_{mm} \\
\hline
\end{array}
\tag{3.21}
$$

The submatrix of Γ obtained by deleting the first row and column (the connections to the central deme) can be succinctly expressed as a Kronecker product

$$B \otimes I_m, \qquad B = \| b_{\lambda\mu} \|_1^m \tag{3.22}$$

Because of (3.22) we can represent Γ more compactly as

$$
\Gamma = \left\| \begin{array}{c|c}
a_0 & a_1, a_1, \ldots, a_1, a_2, \ldots, a_2, \ldots, a_m, \ldots, a_m \\
\hline
b_{10} & \\
\vdots & \\
b_{10} & \\
b_{20} & \\
\vdots & \\
b_{20} & B \otimes I_m \\
\vdots & \\
b_{m0} & \\
\vdots & \\
b_{m0} & \\
\end{array} \right\|
\tag{3.23}
$$

In order to preserve the underlying symmetry we postulate that the demes at a given "distance" from the center are of equal relative size. Explicitly, we postulate for relative deme sizes

$$c_i = c_{m+i} = c_{2m+i} = \ldots = c_{(n-1)m+i}, \qquad i = 1, 2, \ldots, m \tag{3.24}$$

With (3.24) in force the backward migration matrix M associated with Γ possesses the representation

$$
\begin{array}{r||c|c||}
 & \frac{a_0c_0}{\gamma_0}, & \overbrace{\frac{b_{10}c_1}{\gamma_0}, \ldots, \frac{b_{10}c_1}{\gamma_0}}^{n}, \overbrace{\frac{b_{20}c_2}{\gamma_0} \cdots \frac{b_{20}c_2}{\gamma_0}}^{n}, \ldots, \overbrace{\frac{b_{m0}c_m}{\gamma_0} \cdots \frac{b_{m0}c_m}{\gamma_0}}^{n} \\ \cline{3-3}
n\left\{\begin{array}{c} \\ \\ \\ \\ \\ \end{array}\right. & \begin{array}{c} \frac{a_1c_0}{\gamma_1} \\ \vdots \\ \frac{a_1c_0}{\gamma_1} \end{array} & \\
 & \vdots & K \\
n\left\{\begin{array}{c} \\ \\ \\ \\ \\ \end{array}\right. & \begin{array}{c} \frac{a_mc_0}{\gamma_m} \\ \vdots \\ \frac{a_mc_0}{\gamma_m} \end{array} &
\end{array}
\tag{3.25}
$$

where

$$
\begin{gathered}
K = (\bar{C} \otimes I_n)\cdot(D' \otimes I_n)\cdot(C \otimes I_n) = \bar{C}B'C \otimes I_n = \hat{L} \otimes I_n \\
C = \operatorname{diag}(c_1, c_2, \ldots, c_m), \qquad \bar{C} = \operatorname{diag}(\gamma_1^{-1}, \gamma_2^{-1}, \ldots, \gamma_m^{-1})
\end{gathered}
\tag{3.26}
$$

and

$$
\begin{aligned}
\gamma_k &= a_kc_0 + \sum_{j=1}^{m} c_jb_{jk}, \qquad k = 1, 2, \ldots, m \\
\gamma_0 &= a_0c_0 + n\sum_{j=1}^{m} c_jb_{j0}
\end{aligned}
\tag{3.27}
$$

In the later analysis we also stipulate that the local selection forces depend essentially on the "distance" from the center. "Equivalently," we assume

$$
\begin{aligned}
f_i(x) = f_{m+i}(x) = f_{2m+i}(x) = \ldots \\
= f_{(n-1)m+i}(x), \qquad i = 1, 2, \ldots, m
\end{aligned}
\tag{3.28}
$$

4. SOME ADDITIONAL HYBRID MIGRATION PATTERNS

IX. A Multideme Genetic Model Entailing Seasonal and Spatial Variation in Selection Intensities

Consider a geographical population occupying N demes and the associated *backward* migration matrix

$$M = \| m_{ij} \|_{i,j=1}^{N} \tag{4.1}$$

It is helpful to list the actual demes as $\mathcal{P}_1, \mathcal{P}_2, \ldots, \mathcal{P}_N$. Suppose the selection regime in generation t is characterized by the array of local selection functions

$$\mathbf{f}_t = \{f_{t,1}(x), \ldots, f_{t,N}(x)\} \tag{4.2a}$$

and there is a cyclic variation in selection intensities (for p seasons or multivoltine states) through the identity

$$\mathbf{f}_{t+p} = \mathbf{f}_t \qquad \text{for all } t = 1, 2, \ldots \tag{4.2b}$$

Thus, for $p = 2$ there exist alternate winter and summer selection expressions.

The consequences of seasonal variation in selection can be incorporated into the model by enlarging the spatial array to embrace more demes. Specifically, we extend the N deme composition to Np demes consisting of p groups of N demes:

$$\overbrace{\mathcal{D}_1, \ldots, \mathcal{D}_N}^{\mathcal{G}^{(1)}}, \overbrace{\mathcal{D}_{N+1}, \ldots, \mathcal{D}_{2N}}^{\mathcal{G}^{(2)}}, \ldots, \overbrace{\mathcal{D}_{N(p-1)+1}, \ldots, \mathcal{D}_{pN}}^{\mathcal{G}^{(p)}} \tag{4.3}$$

The demes of group $\mathcal{G}^{(1)}$ are the bona fide demes $\mathcal{P}_1, \ldots, \mathcal{P}_N$ but subject to the selection regime

$$\{f_{1,1}(x), \ldots, f_{1,N}(x)\}$$

Consonantly, the demes of $\mathcal{G}^{(2)}$ are physically the same $\mathcal{P}_1, \ldots, \mathcal{P}_N$ but are now acted on by the selection regime of

$$\{f_{2,1}(x), \ldots, f_{2,N}(x)\}$$

and generally those of group $\mathcal{G}^{(k)}$ are the original bona fide demes, but now they are subject to the selection forces of

$$\{f_{k,1}(x), \ldots, f_{k,N}(x)\}, \qquad k = 1, 2, \ldots, p$$

Thus, the temporal seasonal variation in the selection intensities is accommodated by passing in successive generations from a deme of $\mathcal{G}^{(1)}$ to $\mathcal{G}^{(2)}$ on to $\mathcal{G}^{(3)}$ and after p generations to $\mathcal{G}^{(p)}$ and afterwards repeating the order from $\mathcal{G}^{(1)}$ to $\mathcal{G}^{(p)}$, and so forth. The actual movement between demes in each generation is reflected by the migration rates following M.

In this extended framework, we can express the combined effects of the temporal (seasonal) and spatial selection variation in terms of a migration matrix of order $pN \times pN$ given by

$$\tilde{M} = \left\| \begin{array}{cccccc} 0 & 0 & 0 & \cdots & & M \\ M & 0 & 0 & \cdots & & 0 \\ 0 & M & 0 & \cdots & & 0 \\ 0 & 0 & M & & & \\ \vdots & & & & & \vdots \\ 0 & 0 & 0 & & M & 0 \end{array} \right\| \tag{4.4}$$

displaying a $p \times p$ block structure of Nth-order matrices. It is manifest that individuals of $\mathcal{G}^{(k)}$ pass to a deme of $\mathcal{G}^{(k+1)}$ where the migration pattern among the actual demes conforms to M, whereas the selection regimes embody the consequences of deterministic seasonal changes.

A direct generalization of (4.4) allows the migration propensities to change seasonally with the variation in the selection regime. In this view, we let $M^{(k)}$ be the backward migration matrix among the demes $\{\mathcal{P}_1, \ldots, \mathcal{P}_N\}$ in the kth season. The corresponding representation of (4.4) then becomes

$$\tilde{M} = \left\| \begin{array}{cccccc} 0 & 0 & 0 & \cdots & & M^{(p)} \\ M^{(1)} & 0 & 0 & & & 0 \\ 0 & M^{(2)} & 0 & & & 0 \\ 0 & 0 & M^{(3)} & & & \vdots \\ \vdots & & & & & \\ 0 & 0 & 0 & & M^{(p-1)} & 0 \end{array} \right\| \tag{4.5}$$

For some biological examples, see Dobzhansky *et al.* (1969), Scott and McClelland (1977), Gourley and Lawrence (1977).

X. A Cluster Homing and Population Subdivision Migration Pattern

Consider a population distributed into p clusters of demes as follows:

$$\overbrace{\mathcal{P}_1, \ldots, \mathcal{P}_{n_1},}^{\mathcal{G}^{(1)}} \quad \overbrace{\mathcal{P}_{n_1+1}, \ldots, \mathcal{P}_{n_1+n_2},}^{\mathcal{G}^{(2)}} \quad \ldots \quad \overbrace{\mathcal{P}_{\sum_{i=1}^{p-1} n_i + 1}, \ldots, \mathcal{P}_{\sum_{i=1}^{p} n_i}}^{\mathcal{G}^{(p)}} \tag{4.6}$$

such that group $\mathcal{G}^{(k)}$ consists of n_k demes. The migration flow proceeds directionally from $\mathcal{G}^{(1)} \to \mathcal{G}^{(2)} \to \mathcal{G}^{(3)} \to \ldots \to \mathcal{G}^{(p)} \to \mathcal{G}^{(1)}$ with exchanges among the demes also possible. Thus, we consider a general cyclic-type block migration pattern superimposing the option of staying in the same cluster.

Consider a backward migration matrix having specific block form

$$\tilde{M} = \left\| \begin{array}{ccccc} A_1 & 0 & 0 & & 0 \\ 0 & A_2 & 0 & & 0 \\ 0 & 0 & A_3 & & 0 \\ \vdots & \vdots & \vdots & \ddots & \\ 0 & 0 & 0 & \cdots & A_p \end{array} \right\| + \left\| \begin{array}{cccccc} 0 & 0 & 0 & \cdots & 0 & R_{1p} \\ R_{21} & 0 & 0 & & 0 & 0 \\ 0 & R_{32} & 0 & & 0 & 0 \\ \vdots & & \ddots & & \vdots & \\ 0 & 0 & 0 & \cdots & R_{p,p-1} & 0 \end{array} \right\| \tag{4.7}$$

where A_k is an $n_k \times n_k$ matrix of the form $E_k + \| a_i^{(k)} b_j^{(k)} \|_1^{n_k}$

$$E_k = \operatorname{diag}(e_1^{(k)}, \ldots, e_{n_k}^{(k)}), \qquad e_i^{(k)} > 0 \tag{4.8}$$

$$R_{k+1,k} = \| u_i^{(k)} v_j^{(k)} \|_{i=1,\, j=1}^{n_{k+1},\, n_k}, \qquad k = 1, \ldots, p$$

The representation specifies that over one generation immigrants into the block of demes $\mathcal{G}^{(k)}$ can only originate from $\mathcal{G}^{(k)}$ or $\mathcal{G}^{(k-1)}$. Under the stipulations of (4.8) we can ascertain explicit conditions (Section 12) guaranteeing a protected polymorphism and these results for (4.8) may be suggestive of more general cases.

XI. Kronecker Products of Migration Structures

Representations involving Kronecker products arise naturally in dealing with special hybrid forms of multideme populations where the demes segment into intrinsic symmetric groupings. In this perspective, we consider a backward migration matrix admitting the Kronecker product representation

$$M = M^{(1)} \otimes M^{(2)} \tag{4.9}$$

where $M^{(1)}$ is a $p \times p$ matrix and $M^{(2)}$ is a $q \times q$ matrix.

The underlying geographical distribution appropriate to (4.9) reflects a collection of $N = p \times q$ demes that naturally divide into p clusters each composed of q demes (or approximately q demes). To be consistent with the representation (4.9), the demes are labeled in the order

$$\overbrace{\mathcal{D}_1, \mathcal{D}_2, \ldots, \mathcal{D}_q}^{\mathcal{C}^{(1)}}, \overbrace{\mathcal{D}_{q+1}, \ldots, \mathcal{D}_{2q}}^{\mathcal{C}^{(2)}}, \ldots, \overbrace{\mathcal{D}_{(p-1)q+1}, \ldots, \mathcal{D}_{pq}}^{\mathcal{C}^{(p)}}$$

The migration parameters of $M^{(1)} = \| m_{ij}^{(1)} \|_1^p$ are the fraction of individuals per generation moving to cluster $\mathcal{C}^{(i)}$ from cluster $\mathcal{C}^{(j)}$. Equivalently, $m_{ij}^{(1)}$ is the fraction of individuals in all the demes of $\mathcal{C}^{(i)}$ whose parents lived among the demes of $\mathcal{C}^{(j)}$. The components of $M^{(2)} = \| m_{k,l}^{(2)} \|_{k,l=1}^q$ summarize the effects of population structure and migration flow among the demes of each specific cluster. It is tacitly postulated that the subpopulations of each two clusters relate such that the same pattern of migration propensities and sizes between corresponding demes are maintained. In particular, the (backward) migration coefficient between $\mathcal{D}_i$ and $\mathcal{D}_j$, $1 \leq i, j \leq q$, given that movement is confined from $\mathcal{C}^{(1)}$ to $\mathcal{C}^{(1)}$ coincides with the migration coefficient between $\mathcal{D}_{(k-1)q+i}$ and $\mathcal{D}_{(k-1)q+j}$ when movement occurs among the demes of cluster $\mathcal{C}^{(k)}$. The unconditional probabilities are $m_{11}^{(1)} m_{ij}^{(2)}$ as against $m_{kk}^{(1)} m_{ij}^{(2)}$.

Consonant with the structure (4.9) we will also stipulate that the local selection function in deme i of cluster $\mathcal{C}^{(k)}$ can be composed in the form $F_{ik}(x) = f_i[g_k(x)]$. In particular,

$$F'_{ik}(0) = f'_i(0) g'_k(0) = d_i^{(1)} d_k^{(2)} \tag{4.10}$$

Let $D^{(1)} = \operatorname{diag}[d_1^{(1)}, \ldots, d_q^{(1)}]$, $D^{(2)} = \operatorname{diag}[d_1^{(2)}, \ldots, d_p^{(2)}]$. The investigation of A-protection under the assumption of (4.10) requires the evaluation of the spectral radius

$$\rho[M^{(1)} D^{(1)} \otimes M^{(2)} D^{(2)}]$$

which reduces to

$$\rho[M^{(1)} D^{(1)} \otimes M^{(2)} D^{(2)}] = \rho[M^{(1)} D^{(1)}] \rho[M^{(2)} D^{(2)}] \tag{4.11}$$

(see Appendix A). Thus, the composite effects of the two levels in the population are embodied in the *product* of the separate effects of each level. It is interesting to observe that protection in this two-stratum migration model is certain if the protection mechanism is separately favorable with respect to within and between cluster migration–selection interaction, i.e., where

$$\rho[M^{(1)} D^{(1)}] > 1 \quad \text{and} \quad \rho[M^{(2)} D^{(2)}] > 1 \quad \text{hold} \tag{4.12}$$

Moreover, protection can still be achieved given at least one of the factors $\rho[M^{(1)} D^{(1)}]$ or $\rho[M^{(2)} D^{(2)}]$ is sufficiently large such that the *product* of (4.11) exceeds 1.

The model above can manifestly be extended to a population structure carrying any number of levels (say r), corresponding to natural groupings of clusters of demes. Levels may reflect different geographical, social, or ecological dimensions. The r-level version of the backward migration matrix is

$$M = M^{(1)} \otimes M^{(2)} \otimes \cdots \otimes M^{(r)} \tag{4.13}$$

Assuming the selection effects relevant to A-protection concomitant to (4.13) factor in the form

$$D = D^{(1)} \otimes D^{(2)} \otimes \cdots \otimes D^{(r)} \tag{4.14}$$

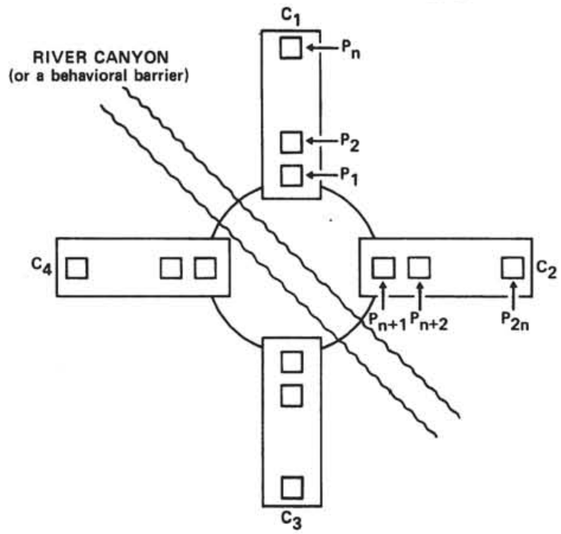
then the condition for A-protection becomes

$$\rho(MD) = \prod_{i=1}^{r} \rho[M^{(i)} D^{(i)}] > 1$$

We discuss other aspects of this model in Section 10.

XII. A Generalized Circulant Cluster Migration Pattern

It is instructive at first to deal with a 4-cluster population as depicted:



As usual, the demes within each cluster enjoy more opportunities for contacts because of physical proximity (or perhaps physiological–behavioral affinity). The diagram indicates that the migration propensities between deme clusters $\mathcal{C}_1$ and $\mathcal{C}_2$ are similar to those between $\mathcal{C}_3$ and $\mathcal{C}_4$. However, the population exchange potentialities between $\mathcal{C}_1$ and $\mathcal{C}_4$ can be quite different from those between $\mathcal{C}_1$ and $\mathcal{C}_2$ despite the circular arrangement. The relevant migration matrix reflecting these factors has the form of (4.19) below.

Each cluster $\mathcal{C}_i$, $i = 1, 2, 3, 4$, contains the same number of demes while the clusters exhibit a circular arrangement relative to one another. The appropriate listing is given by

$$\overbrace{\mathcal{P}_1, \mathcal{P}_2, \ldots, \mathcal{P}_n}^{\mathcal{C}_1}, \overbrace{\mathcal{P}_{n+1}, \ldots, \mathcal{P}_{2n}}^{\mathcal{C}_2}, \overbrace{\mathcal{P}_{2n+1}, \ldots, \mathcal{P}_{3n}}^{\mathcal{C}_3}, \overbrace{\mathcal{P}_{3n+1}, \ldots, \mathcal{P}_{4n}}^{\mathcal{C}_4} \tag{4.15}$$

and between clusters the demes

$$\mathcal{P}_i, \mathcal{P}_{n+i}, \mathcal{P}_{2n+i}, \quad \text{and} \quad \mathcal{P}_{3n+i} \tag{4.16}$$

correspond. The forward migration matrix appropriately reflecting the symmetries and intrinsic ordering relationships has the following structure. Let

$$A^{(0)} = \| a_{ij}^{(0)} \|_{i,j=1}^{n} \tag{4.17}$$

be the migration propensities with respect to the demes of $\mathcal{C}_1$. In view of the correspondence of (4.16), $A^{(0)}$ will also describe the forward migration rates among the demes of clusters $\mathcal{C}_2$, $\mathcal{C}_3$, and $\mathcal{C}_4$. Let

$$A^{(1)} = \| a_{ij}^{(1)} \|_{i,j=1}^{n} \tag{4.18}$$

delimit the forward migration probabilities between the demes of $\mathcal{C}_1$ and $\mathcal{C}_2$ and between those of $\mathcal{C}_3$ and $\mathcal{C}_4$ paralleling the correspondence (4.16). More specifically, the probability of migration from

$$\mathcal{P}_i \quad \text{to} \quad \mathcal{P}_{n+j}$$

and likewise from

$$\mathcal{P}_{n+i} \quad \text{to} \quad \mathcal{P}_j, \qquad \mathcal{P}_{2n+i} \quad \text{to} \quad \mathcal{P}_{3n+j}$$

and

$$\mathcal{P}_{3n+i} \quad \text{to} \quad \mathcal{P}_{2n+j}$$

coincide and are equal to $a_{ij}^{(1)}$. In a similar vein the elements of

$$A^{(2)} = \| a_{ij}^{(2)} \|_{i,j=1}^{n}$$

delineate the forward migration probabilities between the demes of $\{\mathcal{C}_1$ and $\mathcal{C}_3\}$ and $\{\mathcal{C}_2$ and $\mathcal{C}_4\}$. Thus, $a_{ij}^{(2)}$ equals the migration rate from $\mathcal{P}_i$ to $\mathcal{P}_{2n+j}$, from $\mathcal{P}_{n+i}$ to $\mathcal{P}_{3n+j}$, etc. Finally, $A^{(3)} = \| a_{ij}^{(3)} \|$ gives the migration probabilities between $\{\mathcal{C}_1$ and $\mathcal{C}_4\}$ and $\{\mathcal{C}_2$ and $\mathcal{C}_3\}$. The aggregate forward migration matrix has the block matrix representation

$$\Gamma = \left\| \begin{matrix} A^{(0)} & A^{(1)} & A^{(2)} & A^{(3)} \\ A^{(1)} & A^{(0)} & A^{(3)} & A^{(2)} \\ A^{(2)} & A^{(3)} & A^{(0)} & A^{(1)} \\ A^{(3)} & A^{(2)} & A^{(1)} & A^{(0)} \end{matrix} \right\| \tag{4.19}$$

Where $A^{(3)} = A^{(1)}$, the intercluster migration rates depend on the (circular) distance between clusters. In this circumstance, the set of migration rates between the demes of each pair of contiguous clusters $\{\mathcal{C}_i$ and $\mathcal{C}_{i+1}\}$ (interpret the subscript $5 = 1$) is summarized by $A^{(1)}$; the clusters, two units apart, namely $\{\mathcal{C}_i, \mathcal{C}_{i+2}\}$ has migration rates given by the migration matrix $\mathbf{A}^{(2)}$, and that between $\{\mathcal{C}_i, \mathcal{C}_{i+3}\}$ by the migration matrix $\mathbf{A}^{(3)}$.

Consistent with the structure of (4.19), we stipulate that the local selection functions satisfy

$$f_i(x) = f_{n+i}(x) = f_{2n+i}(x) = f_{3n+i}(x), \qquad i = 1, 2, \ldots, n \tag{4.20}$$

and the relative deme sizes obey the corresponding property

$$c_i = c_{n+i} = c_{2n+i} = c_{3n+i}, \qquad i = 1, 2, \ldots, n \tag{4.21}$$

In the presence of (4.19) and (4.21), the backward migration matrix has the form

$$M = \left\| \begin{matrix} M^{(0)} & M^{(1)} & M^{(2)} & M^{(3)} \\ M^{(1)} & M^{(0)} & M^{(3)} & M^{(2)} \\ M^{(2)} & M^{(3)} & M^{(0)} & M^{(1)} \\ M^{(3)} & M^{(2)} & M^{(1)} & M^{(0)} \end{matrix} \right\| \tag{4.22}$$

where

$$M^{(k)} = \| m_{ij}^{(k)} \|_{i,j=1}^{n}, \qquad m_{ij}^{(k)} = \frac{c_j a_{ji}^{(k)}}{\gamma_i}, \qquad i, j = 1, \ldots, n \tag{4.23}$$

and

$$\gamma_i = \sum_{k=1}^{4} \sum_{j=1}^{n} a_{ji}^{(k)} c_j$$

Let

$$d_i = f_i'(0), \qquad i = 1, 2, 3, \ldots, n, \quad \text{and}$$

$$D = \operatorname{diag}(d_1, d_2, d_3, \ldots, d_n) \tag{4.24}$$

It can be established that A-protection for (4.22) is equivalent to the condition

$$\rho(DM) > 1 \tag{4.25}$$

where $\tilde{M} = \sum_{k=1}^{4} M^{(k)}$. Notice that $\tilde{M}$ is an $n \times n$ matrix unlike (4.22), which is $4n \times 4n$. The significance and interpretation of the pattern (4.22) will be pursued elsewhere.

The natural extension of (4.22) involving 2^r clusters leads to a backward migration matrix of the form

$$M = \sum_{\boldsymbol{\epsilon}} M^{(\boldsymbol{\epsilon})} \otimes P^{\boldsymbol{\epsilon}} \tag{4.26}$$

where the sum is extended over the 2^r, r-tuples $\boldsymbol{\epsilon} = (\epsilon_1, \epsilon_2, \ldots, \epsilon_r)$, $\epsilon_i = +1$ or 0. Here $P^{(\boldsymbol{\epsilon})} = J^{\epsilon_1} \otimes J^{\epsilon_2} \otimes \cdots \otimes J^{\epsilon_r}$ ($\otimes$ indicates Kronecker product) and

$$J = \left\| \begin{matrix} 0 & 0 & \ldots & 0 & 1 \\ 0 & 0 & \ldots & 1 & 0 \\ \vdots & & & & \vdots \\ 1 & 0 & \ldots & 0 & 0 \end{matrix} \right\|$$

is an $n \times n$ matrix having unity running down the reverse diagonal and zero elements elsewhere. Of course $J^0 = I$, $M^{(\boldsymbol{\epsilon})} = \| m_{ij}^{(\boldsymbol{\epsilon})} \|_{i,j=1}^{n}$. It is instructive to illustrate (4.26) where $r = 2$. Then we have four $\boldsymbol{\epsilon}$ choices, (0,0), (0,1), (1,0), (1,1), and the $P^{(\boldsymbol{\epsilon})}$ alternatives are

$$P^{(0,0)} = I = \left\| \begin{matrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \end{matrix} \right\| \qquad P^{(1,0)} = \left\| \begin{matrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \end{matrix} \right\|$$

$$P^{(0,1)} = \left\| \begin{matrix} 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \end{matrix} \right\| \qquad P^{(1,1)} = \left\| \begin{matrix} 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 0 \\ 0 & 1 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{matrix} \right\|$$

For the product form (4.26) we have explicitly

$$M^{(1,0)} \otimes P^{(1,0)} = \left\| \begin{matrix} 0 & 0 & M^{(1,0)} & 0 \\ 0 & 0 & 0 & M^{(1,0)} \\ M^{(1,0)} & 0 & 0 & 0 \\ 0 & M^{(1,0)} & 0 & 0 \end{matrix} \right\|$$

The representation (4.26) then reduces to that of (4.22) implementing the obvious specialization.

Returning to the general case, we stipulate that the selection functions only vary among the demes of a cluster, not between clusters. Accordingly, the local selection functions within a cluster are given by $\{f_1(x), f_2(x), \ldots, f_n(x)\}$ and set $d_i = f_i'(0)$, $D = \operatorname{diag}(d_1, d_2, \ldots, d_n)$. *Extending (4.25) we find that A-protection occurs in the model of (4.26) if and only if*

$$\rho\Big(D \sum_{\epsilon} M^{(\epsilon)}\Big) > 1$$

which involves the spectral radius of a matrix of order n, reduced from that of order $n \cdot 2^r$.

XIII. Circulant Block Migration Structures

Let $M_1, M_2, \ldots, M_p$ be p n-deme migration matrices and let γ_i be nonnegative scalars satisfying $\sum_{i=1}^{p} \gamma_i = 1$. Consider the block circulant $pn \times pn$ matrix

$$\tilde{M} = \left\| \begin{matrix} \gamma_1 M_1 & \gamma_p M_p & \cdots & \gamma_2 M_2 \\ \gamma_2 M_2 & \gamma_1 M_1 & \cdots & \gamma_3 M_3 \\ \vdots & & & \\ \gamma_p M_p & \gamma_{p-1} M_{p-1} & \cdots & \gamma_1 M_1 \end{matrix} \right\| \tag{4.27}$$

This is a multideme structure that superimposes a simple circulant isolation-by-distance migration matrix (2.19) on a cluster pattern (e.g., some seaweeds drift with currents carrying along some arthropod populations). It is possible to reduce the calculation of the eigenvalues and eigenvectors of M of order np to p matrices each of order n. Sufficient conditions for the existence of a protected polymorphism (or more specifically, A-protection) in this model are set forth in Appendix D.

XIV. A Deme Cluster Seed Load Process

Consider the basic migration matrix to be that of (2.23)—directional flow with a distinguished deme. Recall (Section 2) that this migration matrix can be interpreted, for example, as a model of seed load involving say, at most p periods of dormancy. It is often relevant to expand each deme into a cluster of demes, the clustering perhaps reflecting other characteristics of the plant populations. The associated backward migration matrix then takes the form

$$\tilde{M} = \left\| \begin{matrix} A_1 & A_2 & A_3 & \cdots & A_{p-1} & A_p \\ B_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & B_2 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & & \vdots \\ 0 & 0 & 0 & \cdots & B_{p-1} & 0 \end{matrix} \right\| \tag{4.28}$$

where the matrices A_k and B_k, $k = 1, 2, \ldots, p$, are of size $n \times n$. Pertaining to (4.28) we envision n colonies of plants admitting seed dispersal between and within colonies coupled to a possible latent period of inactivity. The distributed seeds tend to germinate within p generations of dormancy. A number of conditions on behalf of a protected polymorphism for the block migration pattern of (4.28) are set forth in Section 13. We also deal with the more general block migration matrix

$$\tilde{M} = \left\| \begin{matrix} R_1 & A_2 & A_3 & \cdots & A_{p-1} & A_p \\ B_1 & R_2 & 0 & & 0 & 0 \\ 0 & B_2 & R_3 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & & & \vdots \\ 0 & 0 & 0 & \cdots & B_{p-1} & R_p \end{matrix} \right\| \tag{4.29}$$

where the R_k matrices superimpose a type of frictional force that maintains a seed constitution in its same state.

5. THE INFLUENCE OF LEVELS AND FORMS OF MIGRATION ON THE EXISTENCE OF A PROTECTED POLYMORPHISM

This section is concerned with which migration patterns provide protection for a given selection regime rather than which selection regimes provide protection for a given migration pattern. More specifically, we compare the relative innate tendencies for protection of various migration patterns independent of the selection regime.

It is useful to classify migration matrices though four qualitative criteria in order to assess their effects on protection. We designate these *very small migration, small to moderate mobility rates, moderate to uniform mixing rates,* and *strongly oscillating migration patterns.* A precise mathematical formulation follows the biological description of these concepts.

i. Very small migration entails almost isolated demes. It is the circumstance under which speciation is generally assumed to occur. It would be engendered by a physical environment such as impassable water separating islands or inhospitable mountains separating certain insect populations in canyons. Ethological factors could also be responsible for very small migration, if, for example, some primates seldom leave the troop they are born into. Reduced fertility resulting from interpopulational crosses may entail very small gene flow even if mating is random between the populations.

ii. Small to moderate mobility rates might be considered the most natural migration patterns in many biological contexts. Most isolation-by-distance migration structures including the classical stepping-stone migration model fall into this category.

iii. Moderate to uniform mixing migration rates are essentially what is represented by Levene migration patterns. The migration process leaves the demes indistinguishable until selection has taken its toll. Some classes of organisms that possibly fit this life-style include the polychaetes (marine worms), which are principally sessile but in mating engage in swarming maneuvers and then mostly settle back to available habitats.

iv. Strongly oscillating migration patterns are present when the demes in the habitats are altered drastically by migration, i.e., the genetic compositions of demes in a habitat in succeeding generations are only weakly correlated. An extreme case (mathematically, not biologically) is temporal variation whereby a given habitat inherits en masse the deme that was subjected to a different habitat the previous generation.

A mathematical formulation of these concepts follows.

i. A backward migration matrix M corresponds to "very small" gene flow per generation if M differs very slightly from the identity matrix I. Specifically, migration flow is very small if results for no migration hold valid in accordance with the theory of small parameters (Karlin and McGregor, 1972*b*).

ii. There are two mathematical descriptions that well capture the notion of "small to moderate" flow patterns. (a) The first proposes that the backward migration matrix M be symmetrizable to a positive semidefinite matrix. A migration matrix M is symmetrizable to a positive definite matrix if M admits the representation

$$M = E_1 K E_2 \tag{5.1}$$

where E_1 and E_2 are positive diagonal matrices and K is positive definite. This condition is fulfilled, in particular, for the variable-homing-rate models of Section 2, part III, and the stepping-stone migration model of Section 2, part IV, provided the exchange rates among contiguous demes are not excessive. A positive definite migration matrix can be viewed as a moderate extension of the identity matrix and concomitantly entails small to moderate gene flow. (b) A second mathematical representation of low to moderate gene flow is a totally positive matrix of order 2 (TP_2) (see Appendix B). The class of totally positive matrices has wide scope and is usually not symmetrizable. TP_2 matrices strongly resemble isolation-by-distance migration forms possibly very appropriate for population distributions along a transect or a suitable one-dimensional terrain. A TP_2 matrix enjoys the property that for each i the probability density in j given by $\{m_{ij}\}_{j=1}^{N}$ has a unimodal shape. The TP_2 matrices inherit many properties similar to positive definite matrices. The descriptions (a) and (b) coincide for 2×2 migration matrices.

iii. In quantitative terms, an approximately uniform flow pattern is mostly reflected by migration matrices M entailing all but one of its eigenvalues close to zero. A matrix M of rank one conforms to this description as exemplified by the Levene population subdivision model being a rank-one matrix. Matrices close to rank-one (or low-rank) matrices characterize generalized "uniform" flow patterns.

iv. A mathematical description of this class consists of specifying a lack of the properties specified in (i), (ii), and (iii). The prototype case is migration reflecting temporal selection variation.

The classifications above are too diverse to allow a ranking of them with respect to protection. However, very low migration provides the greatest opportunity for maintenance of a polymorphism. Several partial orderings of matrices entail a loss of protection as one passes from class (i) through class (ii) to class (iii). Highly oscillatory gene flow exemplified in class (iv) encompasses both high and low opportunities for protection.

Within the framework of the foregoing qualitative classifications of migration patterns, we pass to partial orderings of individual matrices which may reflect on the likelihood of protection. The first two orderings appear in Karlin (1976), and we present here proofs and further amplifications that these orderings are consistent with extent of protection. Subsequent orderings reflect natural notions for which the necessary constraints for protection have not been completely elucidated.

A. The first notion for comparing migration flow states that M_3 is *more mixing* than M_1 and M_2, in symbols

$$M_3 > M_1, \qquad M_3 > M_2 \tag{5.2}$$

if $M_3 = M_1 M_2$, M_1 and M_2 commute, and M_i ($i = 1, 2, 3$) are each *symmetrizable to a positive definite matrix*. Thus, this partial ordering applies only to matrices in qualitative class (ii).

The motivation behind this ordering is that multiple migrations should induce more mixing. The commutativity requirement makes the definition symmetric. The constraint to positive definite matrices precludes choices like

$$M_1 = M_2 = \begin{Vmatrix} 0 & 1 \\ 1 & 0 \end{Vmatrix}, \qquad M_3 = M_1 M_2 = \begin{Vmatrix} 1 & 0 \\ 0 & 1 \end{Vmatrix}$$

for which it is manifestly unnatural to think of $M_3 = I$ as more mixing than M_1 and M_2.

We now state the theorem that we formally prove in Appendix E.

THEOREM 5.1. *For the soft selection model* [see Section 1, part (iii)], *if* $M_3 > M_1$ *as defined above in (5.2), then*

$$\rho(M_3 D) < \rho(M_1 D) \tag{5.3}$$

where D *is a positive diagonal matrix.*

Thus, where the multideme population determined by the migration–selection parameter set $\{M_1, D\}$ *entails A-protection, then with the migration pattern* M_3 [*which is less mixing than* M_1 *in the sense of (5.2)*] *and the same selection structure of* D, *protection of the A-allele is, a fortiori, assured.*

In particular, if M possesses the representation (5.1), then for each integer k we have (M^k is the kth power of M under matrix multiplication)

$$\rho(M^{k+1} D) \le \rho(M^k D) \tag{5.4}$$

It is important to underscore the fact that the relation (5.3) is not universally correct with respect to any two *comparable migration patterns*. In fact, consider a system of two subpopulations having equal deme sizes with homogeneous migration matrix

$$M = \begin{Vmatrix} 1-\gamma & \gamma \\ \gamma & 1-\gamma \end{Vmatrix}$$

It is elementary to check that M_{γ_1} is more mixing than M_{γ_2} in the sense of definition (5.2) if and only if $\gamma_1 > \gamma_2$. However, for any $D = \mathrm{diag}(\mathrm{d}_1, \mathrm{d}_2)$, $\rho(M_\gamma D)$ decreases to a minimum attained when $\gamma = \frac{1}{2}$ and subsequently increases. Of course, each M_γ for $\gamma > \frac{1}{2}$ is *not* symmetrizable to a positive definite matrix.

B. *Rates of homing*. The following second criterion for comparison of two migration patterns seems natural.

Let $M^{(1)} = \| m_{ij}^{(1)} \|$ *and* $M^{(2)} = \| m_{ij}^{(2)} \|$ *be two (backward) migration matrices. If for each* i

$$m_{ij}^{(2)} \ge m_{ij}^{(1)} \qquad \text{for all } i \ne j \tag{5.5}$$

then it is suggestive to say that $M^{(2)}$ *is more mixing than* $M^{(1)}$. *We write the relation of (5.5) compactly as*

$$M_2 \gg M_1 \tag{5.6}$$

The relation (5.5) tells us that after migration the number of inhabitants in deme $\mathcal{P}_i$ originating from any deme other than $\mathcal{P}_i$ is larger for the migration matrix $M^{(2)}$ than for $M^{(1)}$ and this property holds for all i.

A set of matrices comparable in the sense of (5.5) incorporates the one-parameter family

$$M^{(\alpha)} = (1 - \alpha)I + \alpha M \qquad (M \text{ is a fixed stochastic matrix}) \tag{5.7}$$

[The Deakin migration pattern (2.2) is a special example of (5.7) with $M = \| e_i c_j \|$, $e_i \equiv 1$.] We can interpret $1 - \alpha$ as the innate propensity of an organism to actively home, independent of selection and deme sizes. A proportion α of the population follows the migration pattern M. When $\alpha = 0$ all demes are strictly isolated, and when $\alpha = 1$ the migration behavior of the total population per generation is summarized by M.

It is trivial to check that $M^{(\alpha_1)}$ is more mixing [in the sense of definition (5.5)] than $M^{(\alpha_2)}$ if and only if $\alpha_1 > \alpha_2$.

Allowing for dispersal rates to vary with the deme origin we obtain an n-parameter family of matrices (defining $\delta_{ii} = 1$, $\delta_{ij} = 0$ for $i \ne j$).

$$m_{ij}^{(\boldsymbol{\alpha})} = (1 - \alpha_i)\delta_{ij} + \alpha_i m_{ij}, \qquad i, j = 1, \ldots, N \tag{5.8}$$

$$[M = \| m_{ij} \|, \qquad \boldsymbol{\alpha} = (\alpha_1, \ldots, \alpha_N)]$$

Obviously, the matrix $M^{(\boldsymbol{\alpha})}$ suggests more mobility than $M^{(\boldsymbol{\beta})}$ constructed with dispersal parameter sets $\boldsymbol{\alpha} = (\alpha_1, \alpha_2, \ldots, \alpha_N)$ and $\boldsymbol{\beta} = (\beta_1, \beta_2, \ldots, \beta_N)$, respectively, if $\alpha_i \ge \beta_i$ for every i.

To what extent does "more mixing" in the sense of (5.6) increase or decrease the opportunities of a protected polymorphism? Comparison of the migration structure $M^{(\boldsymbol{\alpha})}$ and $M^{(\boldsymbol{\beta})}$ with n parameters is formidable and does not point to a consistent relationship. In fact, decreasing only the first component α_1 *need not* enhance or curtail the occurrence of a protected polymorphism.

For the case of a uniform homing rate [the model of (5.7)], we find, independent of the selection gradient, that the likelihood in favor of a protected polymorphism becomes stronger as the degree of mobility diminishes (α decreases).

The following general result is correct.

THEOREM 5.2. *We focus on the soft selection model with the one-parameter family of migration matrices of (5.7). Let D be a diagonal matrix with positive terms on the diagonal induced by the spatial array of AA-selection parameters* [see after (1.12)]. *Then*

$$\rho(M^{(\alpha)}D) = \rho(\alpha) \tag{5.9}$$

is a decreasing function of α.

A formal proof is given in Appendix E.

This monotonicity in (5.9) does not always apply in the hard selection model. It is correct for the homogeneous Deakin migration matrix (2.2).

It follows that if a protected polymorphism exists for a level of homing $1 - \alpha_0$, and migration structure $M^{(\alpha)}$ as in (5.7), then a protected polymorphism is assured for any increased level of homing.

The general intuitive notion that with $M_2 \gg M_1$, then polymorphism under M_1 entails polymorphism under M_2 is false. Indeed, the choice

$$M_2 = \begin{Vmatrix} .5 & .5 \\ .5 & .5 \end{Vmatrix}, \qquad M_1 = \begin{Vmatrix} .5 & .5 \\ 0 & 1 \end{Vmatrix}, \qquad D = \begin{Vmatrix} 2 & 0 \\ 0 & 1 \end{Vmatrix}$$

provides $\rho(M_2D) > \rho(M_1D)$ counter to the intuitive notion.

C. *Indices of migration mixing*. Another approach in assessing migration strength is by means of various sets of indices. The following are of biological interest bearing intuitive merit and/or are tied to procedures in statistical discriminant analysis.

The stationary population deme frequency vector $\boldsymbol{\xi} = (\xi_1, \xi_2, \ldots, \xi_N)$ of the migration matrix M [$\boldsymbol{\xi}M = \boldsymbol{\xi}$, $(\boldsymbol{\xi}, \mathbf{e}) = 1$] describes the long-term population distribution that would be established if only the migration process and no selection differentials operate over many generations. Thereby in a preliminary manner we can summarize the effects of M by its invariant frequency vector $\boldsymbol{\xi}$. Associated with $\boldsymbol{\xi}$ there exist a hierarchy of measures of dispersion: for example, its entropy ($-\sum_{i=1}^{N} \xi_i \log \xi_i$), the coefficient of variation ($C_{\boldsymbol{\xi}} = \sum k\xi_k/[\sum k^2\xi_k - (\sum k\xi_k)^2]^{1/2}$), the midrange of $\boldsymbol{\xi}$, percentile statistics, etc.

In terms of these indices we may propose that $M^{(1)}$ is *weakly* more mixing than $M^{(2)}$ if one or several of the index values for $\boldsymbol{\xi}^{(1)}$ exceed those of $\boldsymbol{\xi}^{(2)}$. One justification for this method of comparisons derives from the

conditions (1.18) and (1.19b) that involve M only through $\boldsymbol{\xi}$. With $\boldsymbol{\xi}^{(1)}$ and $\boldsymbol{\xi}^{(2)}$ it is possible to offer comparisons without further restricting the class of fitness regimes.

D. Under stochastic ordering comparisons where the population range conforms to an intrinsic arrangement of demes (as when correlated with geographical or ecological parameters or other hierarchical determinations), the migration matrix M can reflect isolation-by-distance properties. A useful assumption in these circumstances has M a totally positive matrix. In this context it is appropriate to employ the notions of stochastic orderings of distributions in comparing migration structures.

E. *Migration comparisons relative to a selection regime*. Because protection depends on the selection regime as well as on the migration pattern, it is natural to consider when a migration pattern is more mixing with respect to a selection regime.

In this vein, we say that $M^{(1)}$ is more mixing than $M^{(2)}$ with respect to a class $\mathfrak{D} = \{D\}$ of fitness arrays if

$$\rho(M^{(1)}D) \geq \rho(M^{(2)}D) \qquad \text{for all } D \in \mathfrak{D}$$

or a weaker notion proposes for the comparison

$$\prod_{i=1}^{N} d_i^{\xi_i^{(1)}} \geq \prod_{i=1}^{N} d_i^{\xi_i^{(2)}} \qquad \text{for } D \in \mathfrak{D}$$

or

$$\sum_{i=1}^{N} d_i\xi_i^{(1)} \geq \sum_{i=1}^{N} d_i\xi_i^{(2)}$$

We symbolize either ordering by $\boldsymbol{\xi}^{(1)} > \boldsymbol{\xi}^{(2)}$ ($\mathfrak{D}$). Thus, if $\mathfrak{D}$ consists of all monotone decreasing $\mathbf{d}$, then an elementary analysis proves that $\boldsymbol{\xi}^{(1)} > \boldsymbol{\xi}^{(2)}$ if and only if $\sum_{i=1}^{k} (\xi_i^{(1)} - \xi_i^{(2)}) \geq 0$, $k = 1, 2, \ldots, N$. When $\mathfrak{D}$ consists of all fitness vectors that describe convex sequences, then $\boldsymbol{\xi}^{(1)} > \boldsymbol{\xi}^{(2)}$ if and only if $\sum_{i=1}^{N} i\xi_i^{(1)} = \sum_{i=1}^{N} i\xi_i^{(2)}$ and $\sum_{k=1}^{l} [\sum_{i=1}^{k} (\xi_i^{(1)} - \xi_i^{(2)})] \geq 0$ for all $k, l = 1, \ldots, N$.

6. THE INFLUENCE OF MORE OR LESS HETEROGENEOUS ENVIRONMENTS ON THE EXISTENCE OF A PROTECTED POLYMORPHISM

There are many qualitative and heuristic discussions on the relations between environmental heterogeneity and the occurrence of polymorphisms, e.g., Hanson (1966), Dobzhansky (1967), Powell (1971), Goodhart (1963).

There is a tendency to measure diversity (or heterogeneity) of an environment by a single index. Common choices include the variance of selection values (or of an associated ecological parameter), the cumulative deviations of selection values (absolute or relative), the interquartile range of selection values, the information index (entropy) for a selection gradient, and other indices correlated with those above. A real-valued index for measuring heterogeneity compels essentially a single scaling over all environments. An environment is intrinsically complex and its diversity probably cannot be summarized in a single value. It should also be evident that not all environments are comparable with each other. We now discuss several concepts for ascertaining when an environment $\mathscr{E}$ is regarded "more heterogeneous" than a second environment $\mathscr{E}'$.

Consider an environmental selection regime $\mathscr{E}$ characterized by the local selection functions $\{f_1(x), f_2(x), \ldots, f_N(x)\}$ with f_i for definiteness of the form (1.2) associated with the viability parameters

$$\begin{array}{cccc} AA & Aa & aa & \\ v_i & 1 & w_i & i = 1, 2, \ldots, N \end{array}$$

In this model the environment is determined by the array of selection parameters

$$\mathbf{v} = (v_1, v_2, \ldots, v_N) \quad \text{and} \quad \mathbf{w} = (w_1, w_2, \ldots, w_N) \tag{6.1}$$

We say that the selection regime $\{\mathbf{v}, \mathbf{w}\}$ *is more heterogeneous than the selection regime induced by the parameters*

$$\mathbf{v}' = (v_1', v_2', \ldots, v_N') \quad \textit{and} \quad \mathbf{w}' = (w_1', w_2', \ldots, w_N') \tag{6.2}$$

if $\mathbf{v}'$ *is "an average" of* $\mathbf{v}$ *and* $\mathbf{w}'$ *is "an average" of* $\mathbf{w}$.

We now make precise the first proposal of "averaging" applied to vectors. A matrix $A = \| a_{ij} \|$ is said to be *doubly stochastic* if

$$a_{ij} \geq 0, \qquad \sum_{j=1}^{N} a_{ij} = \sum_{i=1}^{N} a_{ij} = 1, \qquad i, j = 1, 2, \ldots, N \tag{6.3}$$

(all the row and column sums are 1).

The collection of all doubly stochastic matrices is denoted by $\mathscr{A}$. *Now we stipulate* $\mathbf{v}'$ *is an average of* $\mathbf{v}$ *provided there exists a matrix A in* $\mathscr{A}$

such that

$$\mathbf{v}' = A\mathbf{v}, \textit{ that is, } v_i' = \sum_{j=1}^{N} a_{ij} v_j, \qquad i = 1, 2, \ldots, N \tag{6.4}$$

The foregoing averaging preserves the aggregate selection effects, namely,

$$\sum_{i=1}^{N} v_i' = \sum_{i=1}^{N} v_i = v \tag{6.5}$$

Moreover, the relationship (6.4) tends to reduce the variation of the v_i values. For example, the variance of the $\mathbf{v}'$ vector is diminished: $\sum_{i=1}^{N} (v_i')^2 \leq \sum_{i=1}^{N} (v_i)^2$ and more generally for any convex function φ, $\sum_{i=1}^{N} \varphi(v_i') \leq \sum_{i=1}^{N} \varphi(v_i)$.

The specific averaging matrix having $a_{ij} = 1/N$ for all i, j converts $\mathbf{v}$ into the constant (homogeneous) environmental selection pattern with $v_i' = v/N$, $i = 1, 2, \ldots, n$.

We now state the first formal definition.

Definition 6.1. *The environmental selection gradient* $\{\mathbf{v}', \mathbf{w}'\} = \mathscr{E}'$ *is more homogeneous than the environmental selection gradient* $\{\mathbf{v}, \mathbf{w}\} = \mathscr{E}$ (in the first stochastic ordering sense) *if* $\mathbf{v}'$ *is an average of* $\mathbf{v}$ *and* $\mathbf{w}'$ *is an average of* $\mathbf{w}$ *in the sense of (6.4).*

Formally, the averaging relationship is equivalent to the existence of A and B in $\mathscr{A}$ (not necessarily the same), such that

$$\mathbf{v}' = A\mathbf{v} \quad \text{and} \quad \mathbf{w}' = B\mathbf{w} \tag{6.6}$$

In particular, for a prescribed aggregate level of selection coefficients $v = \sum v_i$ and $w = \sum w_i$ relative to the AA and aa genotypes, respectively, the constant selection gradient with the constant selection coefficients

$$v_i' = \frac{v}{N} \quad \text{and} \quad w_i' = \frac{w}{N}, \qquad i = 1, 2, \ldots, N$$

is *more homogeneous* than any other environmental gradient with a selection array having the same cumulative selection effects v and w.

The following question is natural. How does increased heterogeneity of the environmental selection gradient correlate with the realization of protection for alleles A and a and the maintenance of polymorphism?

Definition 6.1 provides the simplest framework for dealing with this problem. The averaging concept is appealing but is unnatural for reasons explained below. It is not correct that the existence of a protected polymorphism is more likely in a more heterogeneous environment (taken in the sense of Definition 6.1). The weakness is that Definition 6.1 refers only to selection gradients and does not take account of the nature and interactions of selection with gene flow.

We now extend the method of comparing selection gradients in a manner that meshes better with the underlying migration structure. Let M be a fixed backward migration matrix having principal left and right eigenvectors $\boldsymbol{\xi}$ and $\mathbf{e}$, respectively, for the eigenvalue 1, that is,

$$\boldsymbol{\xi} M = \boldsymbol{\xi}, \qquad M\mathbf{e} = \mathbf{e} = (1, 1, \ldots, 1), \qquad \boldsymbol{\xi} = (\xi_1, \xi_2, \ldots, \xi_N) \tag{6.7}$$

and $\boldsymbol{\xi}$ normalized to satisfy $\sum_{i=1}^{N} \xi_i = 1$.

Let $\mathscr{A}(\boldsymbol{\xi}, \mathbf{e})$ *consist of the collection of all nonnegative matrices A satisfying (6.7).* $\mathscr{A}(\boldsymbol{\xi}, \mathbf{e})$ *constitutes a convex closed set of matrices including M.*

The rank-one matrix $J = \| e_i \xi_j \|$, $e_i \equiv 1$, is also a member of $\mathscr{A}(\boldsymbol{\xi}, \mathbf{e})$. When $\boldsymbol{\xi} = \mathbf{e}$, plainly $\mathscr{A}(\mathbf{e}, \mathbf{e})$ coincides with the collection of all doubly stochastic matrices $\mathscr{A}$ described previously.

Definition 6.2. *Consider two arrays of selection coefficients* $\mathbf{v} = (v_1, v_2, \ldots, v_N)$ *and* $\mathbf{v}' = (v_1', v_2', \ldots, v_N')$ *reflecting two different environmental selection gradients* $\mathscr{E}$ *and* $\mathscr{E}'$, *respectively.* (To ease the exposition we have focused on comparing sets of *AA*-genotype selection parameters. The extensions to selection arrays involving other genotypes or general selection functions are straightforward.) *We say that* $\mathscr{E}'$ *is less heterogeneous than* $\mathscr{E}$ *with respect to the migration structure M if the relation*

$$\mathbf{v}' = A\mathbf{v} \text{ holds for some } A \in \mathscr{A}(\boldsymbol{\xi}, \mathbf{e}) \tag{6.8}$$

The least heterogeneous environment in the hierarchy implicit to the above definition is the constant vector $\bar{\mathbf{v}} = (\bar{v}_1, \bar{v}_2, \ldots, \bar{v}_N)$ with $\bar{v}_i = \sum_{i=1}^{N} v_i \xi_i = v_{\boldsymbol{\xi}}$ for all i.

For $\mathbf{v}'$ determined as in (6.8) the analog of (6.5) is

$$\sum_{i=1}^{N} v_i' \xi_i = \sum_{i=1}^{N} v_i \xi_i \tag{6.9a}$$

It also follows that $\sum_{i=1}^{N} \xi_i (v_i' - v_{\boldsymbol{\xi}})^2 \le \sum_{i=1}^{N} \xi_i (v_i - v_{\boldsymbol{\xi}})^2$ and generally for any convex function φ,

$$\sum_{i=1}^{N} \xi_i \varphi(v_i') \le \sum_{i=1}^{N} \xi_i \varphi(v_i) \tag{6.9b}$$

showing that the environmental selection variance (*weighting subpopulation i* by the factor ξ_i) is smaller for environment $\mathscr{E}'$ than for environment $\mathscr{E}$.

The following general result holds in many circumstances.

Principle 6.1. *Let M be a backward migration matrix. Let* $\mathscr{E}$ *and* $\mathscr{E}'$ *be two environmental selection gradients such that* $\mathscr{E}'$ *is less heterogeneous than* $\mathscr{E}$ *with respect to the migration structure M in the sense of Definition 6.2. Symbolically, we write* $\mathscr{E}' < \mathscr{E}$. *Define D′ to be the diagonal selection matrix associated with the fitness values of* $\mathscr{E}'$, *that is,* $D' = \operatorname{diag}(d_1', d_2', \ldots, d_N')$ *where* $d_i' = 1/v_i'$ *and the diagonal matrix D is determined analogously from the selection coefficients* $\{v_1, v_2, \ldots, v_N\}$. *Then*

$$\rho(MD) \ge \rho(MD') \tag{6.10}$$

Accordingly, protection of the A-allele is more likely in the more heterogeneous environment $\mathscr{E}$ *over that of* $\mathscr{E}'$.

For the extreme case $\mathbf{v}' = (v_{\boldsymbol{\xi}}, v_{\boldsymbol{\xi}}, \ldots, v_{\boldsymbol{\xi}})$, $v_{\boldsymbol{\xi}} = \sum_{i=1}^{N} v_i \xi_i$, *then* $\mathscr{E}' < \mathscr{E} = \{v_1, v_2, \ldots, v_N\}$ *and indeed (6.10) holds by virtue of the inequality* $\rho(MD) \ge \sum_{i=1}^{N} v_i \xi_i$ *provided M is of the form (5.1)* [compare also to (1.19)].

Comparison of the models of hard and soft selection with reference to the existence of a protected polymorphism reduces to an important case of Principle 6.1. It can be proved in many cases that *the environment of soft selection* $\mathscr{E}^{(S)}$ *is more heterogeneous than the environment of hard selection* $\mathscr{E}^{(H)}$ *in the sense of Definition 6.2.* (Karlin and Campbell, 1981).

We would expect from Principle 6.1 that the phenomenon of a protected polymorphism is more facile under soft selection than under hard selection. Where local fitnesses also influence the migration flow, the resulting environmental structure amalgamates to a more homogeneous population behavior entailing increased possibilities for total fixation.

The validity of Principle 6.1 is established in a number of examples including the stepping-stone migration pattern for a monotone cline model, and in the Deakin migration form and other cases (see Section 7). This fact for the Deakin case was uncovered first by Christiansen (1975).

Principle 6.1 is not correct in complete generality without imposing some restrictions on the migration structure.

It is also relevant to introduce the mechanism of *nonlinear averaging environments*. Thus, in place of straight linear average as in (6.8), namely,

$$v_i' = \sum_{j=1}^{N} a_{ij} v_j, \qquad w_i' = \sum_{j=1}^{N} b_{ij} w_j \qquad \text{where } A, B \in \mathscr{A}(\xi, \mathbf{e}) \tag{6.11}$$

we also consider via parameters α and β the nonlinear set of averages

$$v_i'(\alpha) = \left(\sum_{j=1}^{N} a_{ij} [v_j]^{\alpha} \right)^{1/\alpha} \quad \text{and} \quad w_i'(\beta) = \left(\sum_{j=1}^{N} b_{ij} [w_j]^{\beta} \right)^{1/\beta} \tag{6.12}$$

The case $\alpha = \beta = 1$ recovers (6.11). The case $\alpha = 0$ (i.e., the well-defined limit $\alpha \to 0$) produces the generalized geometric mean average

$$v_i'(0) = \prod_{j=1}^{N} v_j^{a_{ij}} \tag{6.13}$$

The quantities (6.12) are monotonic functions in α and β approaching $\max_i v_i$ as $\alpha \to \infty$ and $\min_i v_i$ as $\alpha \to -\infty$.

For protection (say A-protection) to exist it is sufficient that [see (1.12)] $\rho(MD^{(v)}) > 1$ where $D^{(v)}$ is the diagonal matrix $D^{(v)} = \operatorname{diag}(d_1^{(v)}, d_2^{(v)}, \ldots, d_N^{(v)})$ with $d_i^{(v)} = 1/v_i$. $D^{(v)}$ is the relevant diagonal fitness matrix for A-protection.

Consider a collection of selection environments $\mathscr{E}^{(k)}$ with corresponding diagonal fitness arrays

$$\mathbf{d}^{(k)} = (d_1^{(k)}, d_2^{(k)}, \ldots, d_N^{(k)}), \qquad k = 1, 2, \ldots, r \tag{6.14}$$

Associated with the collection (6.14) we can construct a hierarchy of "more homogeneous" selection environments by appropriate scalings and averages relative to $\{\mathscr{E}^{(k)}\}$. In particular, a *generalized geometric mean environment* of $\{\mathscr{E}^{(k)}\}$ is delimited by the fitness array

$$\mathbf{d}^{(g)} = (d_1^{(g)}, d_2^{(g)}, \ldots, d_N^{(g)}) \tag{6.15}$$

involving the component fitness values

$$d_i^{(g)} = \prod_{k=1}^{N} (d_i^{(k)})^{\eta_k}, \qquad i = 1, 2, \ldots, N \tag{6.16}$$

where $\eta_k > 0$ are suitable weights, $\sum_{k=1}^{r} \eta_k = 1$. The important special case $\eta_k = 1/r$, $k = 1, 2, \ldots, r$, produces

$$d_i^{(g)} = \left(\prod_{k=1}^{r} d_i^{(k)} \right)^{1/r} \tag{6.17}$$

as the classical "geometric mean" selection environment based on $\{\mathbf{d}^{(k)}\}$.

Another "more homogeneous" selection regime involves the fitness values (referred to henceforth as the harmonic mean selection environment $\mathscr{E}^*$)

$$d_i^{(h)} = \left[\sum_{k=1}^{r} \eta_k (d_i^{(k)})^{-1} \right]^{-1}, \qquad i = 1, 2, \ldots, N \tag{6.18}$$

Intuitively, there is a general contention that increased homogeneity in the spatial selection regime diminishes the occurrence of polymorphism. The next theorem establishes that the "more homogeneous" *geometric mean environment* (6.16) independent of the migration structure engenders less polymorphic realizations as compared with the individual selection regimes $\mathscr{E}^{(k)}$, $k = 1, 2, \ldots, r$. More precisely, we have

THEOREM 6.1. *Suppose non-A-protection occurs for each selection regime* $\mathscr{E}^{(k)}$ *such that*

$$\rho(MD^{(k)}) \le 1 \qquad \textit{for all } k = 1, 2, \ldots, r \tag{6.19}$$

Then

$$\rho(MD^{(g)}) \le 1 \tag{6.20}$$

and unless all $D^{(k)}$ *coincide, strict inequality holds in (6.20).*

It is useful to state the conclusion of Theorem 6.1 in contrapositive form. Accordingly, if the geometric average environment assures protection, $\rho(MD^{(g)}) > 1$, then necessarily $\rho(MD^{(k)}) > 1$ for at least one $\mathscr{E}^{(k)}$, that is, A-protection prevails in at least one of the component environments.

PROOF. The result of (6.20) emanates on the basis of the strict log convexity property of the function $\rho(MD)$ with respect to the matrix variable D to the effect that

$$\rho(MD^{(g)}) \le \prod_{k=1}^{r} [\rho(MD^{(k)})]^{\eta_k} \tag{6.21}$$

The previous theorem does not extend to other average environments in general, and in particular we present an example below [(6.22)] that demonstrates that it is not valid for harmonic mean environments. This counterexample is dependent on high migration flow. The following result applies under more restrictive migration levels.

THEOREM 6.2. *Let* **M** *be symmetrizable to a positive definite matrix* [see (5.1)] *and consider the environments of (6.14). We set* $\rho(MD^{(k)}) = \rho_k$, $k = 1, 2, \ldots, r$. *Then for the generalized arithmetic average selection regime*

$$\bar{d}_i = \sum_{k=1}^{r} \eta_k d_i^{(k)}, \qquad i = 1, 2, \ldots, N \quad (\eta_k > 0, \quad \textstyle\sum \eta_k = 1)$$

we have

$$\rho(M\bar{D}) \le \sum_{k=1}^{r} \eta_k \rho_k = \rho \tag{6.22}$$

In particular, $\rho(MD^{(k)}) \le 1$ *for all k implies* $\rho(M\bar{D}) \le 1$.

It is possible to construct two-deme population models where

$$\rho(MD) > \rho(MD^{(k)}), \qquad k = 1, 2, \ldots, r$$

(opposite to the implications of Theorem 6.2) holds for a harmonic mean environment

$$D^{(*)} = \operatorname{diag}\left(\frac{1}{A(1/\mathbf{d})}\right)$$

with

$$M = \begin{pmatrix} 1-m & m \\ m & 1-m \end{pmatrix}, \qquad m > \frac{1}{2},$$
$$A = \begin{pmatrix} 1-\alpha & \alpha \\ \alpha & 1-\alpha \end{pmatrix}, \qquad D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix} \tag{6.23}$$

(Karlin and Campbell, 1981).

7. CONDITIONS FOR A PROTECTED POLYMORPHISM AND ALLELE PROTECTION FOR SEVERAL BASIC MIGRATION MODELS

We present in this section the conditions for protection for several of the basic migration models of Section 2. Whenever tractable we will ascertain explicitly the spectral radius $\rho(MD)$ [M is the backward migration matrix, D the matrix of relevant selection parameters; cf. (1.12)]. Where the calculation of $\rho(MD)$ is prohibitive, we will rely on the bounds established in (1.18) and (1.19).

Generalized Deakin Migration Patterns

On the basis of the developments of Appendix C, we can determine the exact conditions assuring A-protection for the forward migration matrix of (2.4) involving a variable set of homing parameters. To this end, let $D = \operatorname{diag}(d_1, d_2, \ldots, d_N)$ be the diagonal matrix expressing the reciprocal of the differential viability values relevant for protection of allele A [see before equation (1.13)].

For the model of (2.4) and (2.5) the A-allele is protected if at least one of the following two relations hold. Either

$$\left(\frac{1-\alpha_i}{\gamma_i}\right) d_i \ge 1 \qquad \textit{for some } i \tag{7.1}$$

or $(1 - \alpha_i)d_i < \gamma_i$ *holds for all i and the inequality*

$$\sum_{i=1}^{N} \frac{\alpha_i c_i d_i}{[\gamma_i - (1-\alpha_i)d_i]} > 1 \textit{ holds} \tag{7.2}$$

On the other hand, if both inequalities (7.1) and (7.2) are reversed, then the fixation state **0** *(fixation of allele a) is locally stable and the A-allele will go extinct when initially rare.*

For the extended model of (2.11), A-protection is in force if and only if the following conditions hold: either

$$\kappa_i = \frac{(1-\alpha_i)c_i d_i}{\gamma_i} \ge 1 \qquad \textit{for some } i \tag{7.3}$$

or where $\kappa_i < 1$ *for all* i, *the relation*

$$\sum_{i=1}^{N} \frac{\delta_i \alpha_i c_i d_i}{\gamma_i - (1 - \alpha_i) c_i d_i} > 1 \text{ holds} \tag{7.4}$$

For the specialization to a uniform homing rate, i.e., with $\alpha_1 = \alpha_2 = \ldots = \alpha_N (= \alpha)$, then γ_i are equal respectively to c_i and the conditions for protection of the A-allele as displayed in (7.1)–(7.2) agree with the findings of Christiansen (1974), namely, A-protection occurs if

$$(1 - \alpha) \geq w_i \text{ for some } i$$

or (7.5)

$$\alpha \sum_{i=1}^{N} \frac{c_i}{w_i + \alpha - 1} > 1 \qquad \text{where we have written } w_i \text{ for } \frac{1}{d_i}$$

Christiansen (1974) observed for the standard Deakin migration form, corresponding to (2.2), that with protection of the A-allele at an outbreeding level α_0, then protection of that allele is guaranteed for any reduced outbreeding rate $\alpha \leq \alpha_0$. Thus, an increase of relative isolation while precluding absolute isolation more expeditiously promotes variable selection influences engendered by the separate demes leading to more polymorphism.

The foregoing fact is subsumed as a special case of a very general result (Theorem 5.2). For any migration matrix M and diagonal D,

$$\rho([(1 - \alpha)I + \alpha M]D) \text{ strictly decreases in } \alpha \tag{7.6}$$

Actually, in the Deakin model the quantity of (7.6) decreases convexly as α increases. The fact of (7.6) further entails that the *strength of A-protection, as measured by the relevant spectral radius, increases with decreasing outbreeding* (increasing homing) *rates*.

The conclusion of (7.6) also prevails for the corresponding migration–selection model in the formulation of hard selection.

Examination of (7.2) reveals that it is possible to increase a single homing rate and reduce or even abrogate the event of A-protection. This stands in contrast with the result for a constant homing rate (uniform across the population range) where an increased homing propensity enhances the strength of A-protection.

We examine the influence of selection heterogeneity for the constant-homing-rate Deakin migration matrix (Section 2, part II). Let $\mathbf{w} = (w_1, w_2, \ldots, w_N)$ be the underlying viability values of the *aa* genotype. Consider the stochastic matrix (2.2) with a normalized left eigenvector given by the vector of premigration adult deme sizes composing the components of $\mathbf{c}$.

Consider a stochastic matrix A, i.e., A nonnegative, which satisfies $A\mathbf{e} = \mathbf{e}$, $\mathbf{e} = (1, 1, \ldots, 1)$, and $\mathbf{c}A = \mathbf{c}$. We construct the new selection parameters

$$\mathbf{w}' = A\mathbf{w}, \qquad \mathbf{w}' = (w'_1, w'_2, \ldots, w'_N)$$

so that the components of $\mathbf{w}'$ represent viability values of a selection array "less heterogeneous" relative to the Deakin migration matrix (in the sense of Definition 6.2) over the selection environment corresponding to $\mathbf{w}$.

We prove on the basis of the precise conditions (7.5) that protection for $\mathbf{w}$ implies protection for $\mathbf{w}'$. In fact, it is elementary to discern that the relation $1 - \alpha \geq w'_i$ for some i entails $1 - \alpha \geq w_i$ for some i. Indeed, suppose to the contrary that $(1 - \alpha)\mathbf{e} < \mathbf{w}$. Applying A to both sides we obtain $(1 - \alpha)\mathbf{e} = (1 - \alpha)A\mathbf{e} < A\mathbf{w} = \mathbf{w}'$ and the stipulation $1 - \alpha \geq w'_i$ for some i is violated. Suppose next that

$$(1 - \alpha)\mathbf{e} < \mathbf{w}' \quad \text{and} \quad \alpha \sum_{i=1}^{N} \frac{c_i}{w'_i + \alpha - 1} > 1$$

The function $\phi(x) = 1/(x + \alpha - 1)$ is convex for $x > 1 - \alpha$ and the fact of (6.9b) applies (as $\mathbf{c}A = \mathbf{c}$) to yield the inequality

$$\alpha \sum_{i=1}^{N} \frac{c_i}{w_i + \alpha - 1} \geq \alpha \sum_{i=1}^{N} \frac{c_i}{(A\mathbf{w})_i + \alpha - 1}$$

It follows that for the *homogeneous* (uniform homing) *Deakin migration structure the opportunity of a protected polymorphism is enhanced under a more heterogeneous selection environment in the sense of Principle 6.1. In particular, protection in the hard selection Deakin model entails protection in the corresponding soft selection model.*

We hasten to point out that with the model (2.5) involving variable homing rates over the separate niches, Principle 6.1 is not universally valid; indeed, by appropriate choice of the homing rates, protection for the hard selection environment can occur while protection in the soft selection model is lacking.

Protection for the Model of Directional Migration Pattern with a Distinguished Major Deme Dispersing or Receiving Migrants to "Subordinate" Demes

Consider a backward migration matrix of the form

$$M = \begin{Vmatrix} r_1 & p_1 & 0 & 0 & \cdots & 0 \\ q_2 & r_2 & p_2 & 0 & \cdots & 0 \\ q_3 & 0 & r_3 & p_3 & \cdots & 0 \\ \cdot & & \cdot & \cdot & \cdot & \cdot \\ \cdot & & & \cdot & \cdot & \cdot \\ \cdot & & & & \cdot & \cdot \\ q_{N-1} & 0 & 0 & \cdot & r_{N-1} & p_{N-1} \\ q_N & 0 & 0 & \cdot & \cdot & \cdot\, r_N \end{Vmatrix}, \quad \begin{aligned} &r_i + q_i + p_i = 1, \\ &q_i > 0,\ p_i > 0,\ r_i \geq 0, \\ &i = 1, \ldots, N-1 \end{aligned} \qquad (7.7)$$

Interpretations and relevance of this migration pattern are discussed in Section 2, part VI.

Where the migration propensity is in the other direction away from the distinguished deme, (7.7) is replaced by

$$M = \begin{Vmatrix} a_1 & a_2 & a_3 & & a_N \\ b_2 & c_2 & 0 & & 0 \\ 0 & b_3 & c_3 & & 0 \\ & \cdot & \cdot & & \cdot \\ & & \cdot & \cdot & \cdot \\ & & & \cdot & \cdot \\ & & & b_N & c_N \end{Vmatrix}, \quad \begin{aligned} &a_i > 0,\ \sum_{i=1}^{N} a_i = 1, \\ &b_i + c_i = 1, \text{ and} \\ &b_i > 0,\ i = 2, 3, \ldots, N \end{aligned} \qquad (7.8)$$

With respect to the migration structures (7.7) and (7.8), the formal calculations of the spectral radius $\rho(MD)$ are accessible. To this end, choose an irreducible nonnegative matrix (not necessarily stochastic, i.e., the row sums need not all add up to unity) of the form

$$G = \begin{Vmatrix} r_1 & b_1 & 0 & 0 & \cdots & 0 \\ a_2 & r_2 & b_2 & 0 & \cdots & 0 \\ a_3 & 0 & r_3 & b_3 & \cdots & 0 \\ & & \cdot & \cdot & & \cdot \\ & & & \cdot & \cdot & \cdot \\ & & & & \cdot & \cdot \\ a_{N-1} & 0 & \cdots & & r_{N-1} & b_{N-1} \\ a_N & 0 & \cdots & & 0 & r_N \end{Vmatrix} \qquad (7.9)$$

with $a_i \geq 0$, $r_i \geq 0$, $b_i > 0$, $i = 1, 2, \ldots, N$.

The following result is pertinent in assessing protection in the case of the migration structure of (7.7).

Let G be an irreducible nonnegative matrix of the form (7.9). Then $\rho(G) > 1$ *if and only if either*

$$r_i \geq 1 \qquad \textit{for some } i \qquad (7.10\text{a})$$

or

$$r_i < 1 \qquad \textit{for all } i \quad \textit{and} \quad r_1 + \sum_{k=2}^{N} a_k \frac{\prod_{i=1}^{k-1} b_i}{\prod_{i=2}^{k} (1 - r_i)} > 1 \ \textit{holds} \qquad (7.10\text{b})$$

EXAMPLE. If $r_i \equiv 1 - \alpha$, $p_i = \alpha$, $q_i = 0$, $2 \leq i \leq N - 1$, $q_N = \alpha$ in (7.7) and $D = \operatorname{diag}(d_1, d_2, \ldots, d_N)$, then $\rho(MD) > 1$ if and only if either

$$(1 - \alpha) d_i \geq 1 \qquad \text{for some } i \qquad (7.11\text{a})$$

or the unique solution λ_0 of

$$\prod_{i=1}^{N} [\lambda - (1 - \alpha) d_i] = \alpha^N \prod_{i=1}^{N} d_i \qquad (7.11\text{b})$$

that is larger than $\max_{1 \leq i \leq N}[(1 - \alpha) d_i]$, exceeds 1.

For this example, Principle 6.1 prevails. That is, a "more homogeneous" selection environment with respect to M diminishes the chance of a protected polymorphism. The corresponding result with general parameters in (7.7) is not always valid; a counterexample appears in Karlin and Campbell (1981).

Consider the special case of (7.7) with $r_i \equiv 0$ (as in the model for seed load germination). Let $P_i = \prod_{k=1}^{i} p_k$, $i \geq 1$, $P_0 = 1$, and $D_i = \prod_{k=1}^{i} d_k$; then A-protection, that is, $\rho(MD) > 1$, occurs if and only if $\sum_{i=2}^{N} a_i > 1$ where $a_i = q_i P_{i-1} D_i$ [cf. (7.10)].

The calculation of the spectral radius of (7.8) paraphrases the analysis corresponding to (7.7). For

$$H = \begin{Vmatrix} \alpha_1 & \alpha_2 & \alpha_3 & \cdots & \alpha_N \\ \beta_2 & \gamma_2 & 0 & \cdots & 0 \\ 0 & \beta_3 & \gamma_3 & \cdots & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & & \cdot & \cdot \\ \cdot & \cdot & & & \cdot\,\cdot \\ 0 & 0 & 0 & \cdots & \beta_N \gamma_N \end{Vmatrix}$$

we establish that $\rho(H) > 1$ *if and only if either* $\gamma_i \ge 1$ *for some* $i \ge 2$ *or that all* $\gamma_i < 1$, *and then*

$$\alpha_1 + \sum_{k=2}^{N} \alpha_k \frac{B_k}{R_k} > 1 \textit{ holds} \tag{7.12}$$

where

$$B_k = \prod_{i=2}^{k} \beta_i, \qquad R_k = \prod_{i=2}^{k} (1 - \gamma_i)$$

Nonhomogeneous Linear Stepping-Stone Migration

The demes are located in an ordered fashion as described in Section 2, part IV. In each generation, immigration occurs to neighboring demes. Due to differences in deme sizes and local endemic rates of migration, the backward migration matrix takes the form

$$M = \left\| \begin{matrix} r_1 & p_1 & 0 & & \cdots & 0 \\ q_2 & r_2 & p_2 & & \cdots & 0 \\ 0 & q_3 & r_3 & & \cdots & 0 \\ & & \ddots & \ddots & \ddots & \\ & & & q_{N-1} & r_{N-1} & p_{N-1} \\ 0 & \cdots & & & q_N & r_N \end{matrix} \right\| \tag{7.13}$$

where $r_i \ge 0$, $q_i > 0$, $p_i > 0$, $r_i + q_i + p_i = 1$. [See (2.15) for a specific determination of the migration parameters p_i, q_i, r_i expressed in terms of the relative deme sizes and an innate exchange rate between contiguous demes.] We impose, henceforth, the mild requirement that all principal minors of (7.13) are nonnegative. For the homogeneous stepping-stone migration mode with exchange rate m, the foregoing assumption is satisfied provided $m \le \frac{1}{4}$, i.e., that at most 50% of the population in any deme per generation moves. Define $\pi_j = p_{j-1}p_{j-2}\cdots p_1/q_jq_{j-1}\cdots q_2, j \ge 2$, $\pi_1 = 1$. An application of (1.19) affirms that

$$\rho(MD) > 1 \tag{7.14}$$

holds if

$$\sum_{i=1}^{N} d_i\pi_i \Big/ \sum_{i=1}^{N} \pi_i \tag{7.15}$$

(See Appendix D.)

For the special homogeneous stepping-stone migration form with equal deme sizes

$$M = \left\| \begin{matrix} 1-m & m & 0 & & & 0 \\ m & 1-2m & m & & & \vdots \\ & \ddots & \ddots & \ddots & & \vdots \\ & & & m & 1-2m & m \\ 0 & 0 & 0 & \cdots & m & 1-m \end{matrix} \right\| \tag{7.16}$$

and in this case protection of the A-allele is assured if

$$\frac{1}{N} \sum_{i=1}^{N} d_i \ge 1 \tag{7.17}$$

8. PROTECTION IN A MULTICLUSTER MIGRATION STRUCTURE*

In order to ascertain explicitly the spectral radius $\rho(M\tilde{D})$ with M the hybrid generalized multicluster migration structure of the form (3.7) and (3.18), it is natural to stipulate that the selection parameters summarized in $\tilde{D}$ of order $N \times N$ admit the representation $\tilde{D} = D \otimes I$ where $D = \operatorname{diag}(d_1, d_2, \ldots, d_m)$ is interpreted as in (3.3). Consider M of the form (3.18a). To evaluate $\rho(M\tilde{D})$, it suffices to exhibit a positive eigenvector $\mathbf{z} \gg 0$ satisfying

$$M\tilde{D}\mathbf{z} = \lambda_0\mathbf{z} \tag{8.1}$$

and then by appeal to the Frobenius theory of positive matrices we deduce that $\lambda_0 = \rho(M\tilde{D})$ (see Appendix B). We try a Kronecker product form $\mathbf{z} = \mathbf{y} \otimes \mathbf{e}$ with $\mathbf{y} = (y_1, y_2, \ldots, y_m)$ to be determined and $\mathbf{e}$ a vector

---

* Multiuniform migration as in Section 3, part VII.

of only unit components. Recall that $M\bar{D} = (1/r)\sum_{i=1}^{r} L_iD \otimes F_i$ and as $F_i\mathbf{e} = \mathbf{e}$ for all i it is clear that by specifying $\mathbf{y}$ as the eigenvector corresponding to the spectral radius of $\hat{L} = [(1/r)\sum_{i=1}^{r} L_i]D$ we deduce

$$\rho(M\bar{D}) = \rho(\hat{L}) \tag{8.2}$$

It is of independent interest and instructive to discuss first the homogeneous case (3.9). The spectral radius of $\rho(M\bar{D})$ reduces to $\rho(K)$ with

$$\begin{aligned} K &= (a - \beta_1)\bar{C}CD + n(\beta_1 - \beta_2)\bar{C}CD + n\beta_2\bar{C}U_mCD \\ &= \Delta + n\beta_2 \left\| \frac{1}{\gamma_i} c_jd_j \right\|_{i,j=1}^{m} \end{aligned} \tag{8.3}$$

where $\Delta = \operatorname{diag}(\delta_1, \delta_2, \ldots, \delta_m)$, $\gamma_i = ac_i + \beta_1(n-1)c_i + n\beta_2(1 - c_i)$, $i = 1, 2, \ldots, m$, and

$$\delta_i = (a - \beta_1)\frac{c_id_i}{\gamma_i} + n(\beta_1 - \beta_2)\frac{c_id_i}{\gamma_i}, \qquad i = 1, 2, \ldots, m \tag{8.4}$$

The result of Appendix C, subsection I, establishes

$$\rho(M\bar{D}) = \rho(K) > 1 \text{ if and only if} \tag{8.5}$$

$$\delta_i \geq 1 \text{ for some } i \tag{8.6}$$

or

$$\delta_i < 1 \text{ for all } i = 1, 2, \ldots, m$$

and

$$n\beta_2 \sum_{i=1}^{m} \frac{c_id_i}{\gamma_i(1 - \delta_i)} > 1 \tag{8.7}$$

The conditions (8.7) displayed in terms of the parameters a, β_1, β_2, m, n read as

$$\frac{[(a - \beta_1) + n(\beta_1 - \beta_2)]c_id_i}{ac_i + \beta_1(n-1)c_i + n\beta_2(1 - c_i)} \geq 1 \text{ for some } i \tag{8.7a}$$

or the inequalities (8.7a) are reversed for all i and

$$n\beta_2 \sum_{i=1}^{m} \times \frac{c_id_i}{[ac_i + \beta_1(n-1)c_i + n\beta_2(1 - c_i)] - (a - \beta_1)c_id_i - n(\beta_1 - \beta_2)c_id_i} > 1 \tag{8.7b}$$

Recall that a, β_1, and β_2 are nonnegative and are constrained such that

$$a + (n-1)\beta_1 + (m-1)n\beta_2 = 1 \tag{8.7c}$$

When $n \uparrow \infty$, increase in the number of demes per cluster, such that the populations are locally replicated retaining the corresponding selection regime, the possibilities for a protected polymorphism are varied. For example, for a deme cluster of size c_i satisfying $c_im > 1$ and $d_i > (mc_i - 1)/mc_i$, A-protection is assured when $n \uparrow \infty$. However, if d_i is small (close to zero) and also $c_im > 1$ holds, while $d_i \approx 1$ when $c_im < 1$, then A-protection is impossible with n large.

On the other hand, as the number of clusters m is increased and allele A is favored in some cluster ($d_i > 1$ for some i), then the contingencies for A-protection are facilitated.

We consider next the more elaborate deme cluster model of (3.18). Again, we observe that the corresponding $\bar{L}$ of (3.18a) has the form

$$\bar{L} = \bar{\Delta} + \bar{R} \tag{8.8}$$

where

$$\bar{\Delta} = \operatorname{diag}(\bar{\delta}_1, \bar{\delta}_2, \ldots, \bar{\delta}_m), \qquad \bar{\delta}_i = \frac{1}{\hat{\gamma}_i}[(a_i - b_i)c_id_i + n(b_i - u_iv_i)c_id_i]$$

and $\bar{R}$ is the rank-one matrix $\bar{R} = n\,\|(v_iu_j/\hat{\gamma}_i)\,d_j\|$ and $\hat{\gamma}_i$ are defined in (3.18c). We can apply the procedure of Appendix C to obtain the result $\rho(\bar{L}) > 1$ if and only if either

$$\bar{\delta}_i \geq 1 \text{ for some } i \tag{8.9}$$

or

$$\bar{\delta}_i < 1 \text{ for all } i \text{ and } n\sum_{i=1}^{m} \frac{v_iu_id_i}{\hat{\gamma}_i(1 - \bar{\delta}_i)} > 1 \tag{8.10}$$

In Section 1 we underscored [see (1.18)–(1.19)] the sufficient conditions for protection in terms of the principal left eigenvector of the backward migration matrix. Consider the backward migration matrix of (3.9), namely,

$$M = (a - \beta_1)\bar{C}C \otimes I_n + (\beta_1 - \beta_2)\bar{C}C \otimes U_n + \beta_2\bar{C}U_mC \otimes U_n \quad (8.11)$$

If we denote by $\boldsymbol{\xi}$ the principal left eigenvector for the matrix $n([(a - \beta_1)/n]\bar{C}C + (\beta_1 - \beta_2)\bar{C}C + \beta_2\bar{C}U_mC)$, then $\boldsymbol{\xi} \otimes \mathbf{e}_n$, where $\mathbf{e}_n$ is the n-dimensional vector of ones, is the left eigenvector of M.

More generally, we may put superscripts on a and β_1 and consider a backward migration matrix of the form $\hat{M} = \bar{C}[\mathrm{diag}(a^i - \beta_1^i)]C \otimes I_n + \bar{C}[\mathrm{diag}(\beta_1^i - \beta_2)]C \otimes U_n + \beta_2\bar{C}U_mC \otimes U_n$. Where $\boldsymbol{\xi}$ is the left eigenvector for $\bar{C}[(1/n)\,\mathrm{diag}(a^i - \beta_1^i) + \mathrm{diag}(\beta_1^i - \beta_2) + \beta_2U_m]C$, $\boldsymbol{\xi} \otimes \mathbf{e}_n$ is the left eigenvector of $\hat{M}$. Properly normalized we need to work with $(1/n)\boldsymbol{\xi} \otimes \mathbf{e}$.

In conformance with (1.18), a sufficient condition for protection has

$$\left(\prod_{i=1}^{m} d_i^{\xi_i}\right) > 1$$

The dependence on the number m of clusters and the nature of the migration exchange among clusters mainly enter via the coordinates of $\boldsymbol{\xi}$. The spectral radius bounds

$$\rho(M\bar{D}) \geq \left(\prod_{i=1}^{m} d_i^{\xi_i}\right)$$

suggest that the degree of clustering will not qualitatively affect the opportunities for polymorphism although it will tend to attenuate the strength of the polymorphism (the local rate of attraction is reduced).

9. CONDITIONS FOR PROTECTION IN THE STAR MIGRATION STRUCTURE

We adhere to the notations of (3.20)–(3.28). It would be helpful for the reader to review the discussion as set forth there. Let M be the migration matrix displayed in (3.25). We also stipulate that the local selection regimes depend on the distance to the central deme obeying the relations (3.28).

In establishing conditions for A-protection, we need to determine $\rho(M\hat{D}) = \rho(\hat{D}M)$ with $d_i = f_i'(0)$ and $\hat{D}$ is the diagonal matrix

$$\hat{D} = \left\|\begin{array}{c|c} d_0 & 0\ldots0 \\ \hline 0 & D \otimes I_n \\ \vdots & \\ 0 & \end{array}\right\| \quad (9.1)$$

where $D = \mathrm{diag}(d_1, d_2, \ldots, d_m)$. The matrix $M\hat{D}$ has the form

$$M\hat{D} = \left\|\begin{array}{c|c} \dfrac{a_0c_0}{\gamma_0}d_0, & \dfrac{b_{10}c_1}{\gamma_0}d_1, \ldots, \dfrac{b_{10}c_1}{\gamma_0}d_1, \dfrac{b_{20}c_2}{\gamma_0}d_2, \ldots, \dfrac{b_{20}c_2}{\gamma_0}d_2, \ldots \\ \hline \dfrac{a_1c_0}{\gamma_1}d_0 & \\ \vdots & \hat{L}D \otimes I_n \\ \dfrac{a_1c_0}{\gamma_1}d_0 & \\ \dfrac{a_2c_0}{\gamma_2}d_0 & \\ \vdots & \end{array}\right\| \quad (9.2)$$

with $\hat{L} = \|\hat{l}_{ij}\|_1^m$ and $\hat{l}_{ij} = c_jb_{ji}/\gamma_i$

Cognizance of the character of $M\hat{D}$ suggests that we seek a positive eigenvector

$$M\hat{D}\mathbf{x} = \lambda\mathbf{x} \qquad [\text{with } \lambda = \rho(M\hat{D})] \quad (9.3)$$

of the form

$$\begin{aligned} \mathbf{x} &= (x_0, \underbrace{x_1, \ldots, x_1}_{n}, \underbrace{x_2, \ldots, x_2}_{n}, \ldots, \underbrace{x_m, \ldots, x_m}_{n}) \quad (9.4) \\ &= (x_0, \bar{\mathbf{x}} \otimes \mathbf{e}) \end{aligned}$$

where $\bar{\mathbf{x}} = (x_1, x_2, \ldots, x_m)$ and $\mathbf{e} = (1, 1, \ldots, 1)$, the latter involving

n components. The conditions of (9.3) reduce to the $m + 1$ equations

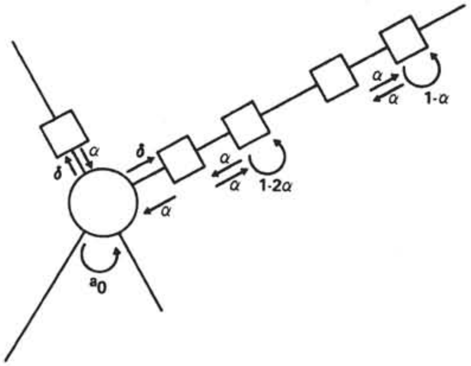
$$\begin{aligned} \frac{a_0 c_0 d_0}{\gamma_0} x_0 + \frac{n}{\gamma_0} \sum_{j=1}^{m} d_j c_j b_{j0} x_j &= \lambda x_0 \\ \frac{a_i c_0 d_0}{\gamma_i} x_0 + \sum_{j=1}^{m} d_j \hat{l}_{ij} x_j &= \lambda x_i, \qquad i = 1, 2, \ldots, m \end{aligned} \tag{9.5}$$

or equivalently the spectral radius of $M\hat{D}$ coincides with that of the $(m + 1) \times (m + 1)$ matrix

$$\bar{L}\bar{D} = \left\| \begin{matrix} \dfrac{a_0 c_0 d_0}{\gamma_0} & \dfrac{n b_{10} c_1 d_1}{\gamma_0} & \dfrac{n b_{20} c_2 d_2}{\gamma_0} & \cdots & \dfrac{n b_{m0} c_m d_m}{\gamma_0} \\ \dfrac{a_1 c_0 d_0}{\gamma_1} & \hat{l}_{11} d_1 & \hat{l}_{12} d_2 & \cdots & \hat{l}_{1m} d_m \\ \vdots & \vdots & \vdots & & \vdots \\ \dfrac{a_m c_0 d_0}{\gamma_m} & \hat{l}_{m1} d_1 & \hat{l}_{m2} d_2 & \cdots & \hat{l}_{mm} d_m \end{matrix} \right\| \tag{9.6}$$

where $\bar{L}$ and $\bar{D}$ are of order $m + 1$ and $\bar{D} = \operatorname{diag}(d_0, d_1, \ldots, d_m)$.

Some examples are worth recording. Assume a homogeneous stepping-stone pattern along each ray and equal relative deme sizes



Of course δ (= a_1 in the previous notation) and a_0 are restricted by the

normalization $n\delta + a_0 = 1$. Then M reduces to

$$M = \left\| \begin{array}{ll} \dfrac{a_0}{\gamma_0}, \overbrace{\dfrac{\alpha}{\gamma_0}, \ldots, \dfrac{\alpha}{\gamma_0}}^{n}, 0, \ldots, 0, \ldots, 0 & \\ n\left\{ \begin{matrix} \dfrac{\delta}{\gamma_1} \\ \dfrac{\delta}{\gamma_1} \\ \vdots \\ \dfrac{\delta}{\gamma_1} \end{matrix} \right. & \qquad B \otimes I_n \\ \begin{matrix} 0 \\ \vdots \\ 0 \end{matrix} & \end{array} \right\| \tag{9.7}$$

with

$$B = \left\| \begin{matrix} \dfrac{1 - 2\alpha}{\gamma_1} & \dfrac{\alpha}{\gamma_1} & 0 & \cdots & 0 & 0 \\ \alpha & 1 - 2\alpha & \alpha & \cdots & 0 & 0 \\ \vdots & & & & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 1 - 2\alpha & \alpha \\ 0 & 0 & 0 & \cdots & \alpha & 1 - \alpha \end{matrix} \right\| \tag{9.8}$$

$\gamma_0 = a_0 + n\alpha$, $\gamma_1 = \delta + 1 - \alpha$.

The matrix $\bar{L}$ for this example becomes

$$\bar{L} = \left\| \begin{matrix} \dfrac{a_0}{a_0 + n\alpha} & \dfrac{n\alpha}{a_0 + n\alpha} & 0 & 0 \cdots & 0 \\ \dfrac{\delta}{\delta + 1 - \alpha} & \dfrac{1 - 2\alpha}{\delta + 1 - \alpha} & \dfrac{\alpha}{\delta + 1 - \alpha} & 0 \cdots & 0 \\ 0 & \alpha & 1 - 2\alpha & \alpha \cdots & 0 \\ \vdots & & & \ddots & \\ \vdots & & & & 1 - \alpha \end{matrix} \right\|$$

The version of $\tilde{L}$ with relative deme sizes $\{c_0, c_1, \ldots, c_m\}$ depending on the distance from the center superimposed on a homogeneous stepping-stone migration model is

$$\tilde{L} = \left\| \begin{matrix} \frac{a_0 c_0}{\gamma_0} & \frac{n\alpha c_1}{\gamma_0} & 0 & 0 & \cdots \\ \frac{\delta c_0}{\tilde{\gamma}_1} & \frac{(1-2\alpha)c_1}{\tilde{\gamma}_1} & \frac{\alpha c_2}{\tilde{\gamma}_1} & 0 & \\ 0 & \frac{\alpha c_1}{\tilde{\gamma}_2} & \frac{(1-2\alpha)c_2}{\tilde{\gamma}_2} & \frac{\alpha c_3}{\tilde{\gamma}_2} & \\ & & \ddots & \ddots & \ddots \\ & & & \frac{\alpha c_{m-1}}{\tilde{\gamma}_m} & \frac{(1-\alpha)c_m}{\tilde{\gamma}_m} \end{matrix} \right\| \tag{9.10}$$

The $\tilde{\gamma}_i$ are normalizing constants guaranteeing that the row sums for $\tilde{L}$ add to unity.

A sufficient condition for protection with the above tridiagonal matrix [cf. (7.15)] for $\alpha < \frac{1}{2}$ is

$$\sum_{i=0}^{m} d_i \pi_i > 1 \tag{9.11}$$

where

$$\pi_k = \frac{1}{K} \frac{n\alpha}{\delta} \frac{c_k \gamma_k}{c_0 \gamma_0}, \qquad k = 1, 2, \ldots, m,$$

$$\pi_0 = 1, \qquad K = 1 + \frac{n\alpha}{\delta c_0 \gamma_0} \sum_{k=1}^{m} c_k \gamma_k$$

10. PROTECTION IN A MULTIDEME POPULATION SUBJECT TO SEASONAL VARIATIONS IN SELECTION INTENSITIES*

The associated backward migration matrix $\tilde{M}$ is given in (4.4) and the local selection functions follow the format of (4.2). The selection coefficients relevant to appraising the maintenance of A-protection are summarized by the $Np \times Np$ diagonal matrix

$$\tilde{D} = \operatorname{diag}(D^{(1)}, D^{(2)}, \ldots, D^{(p)}) \tag{10.1}$$

where $D^{(k)} = \operatorname{diag}(d_1^{(k)}, d_2^{(k)}, \ldots, d_N^{(k)})$, $k = 1, 2, \ldots, p$, and $d_i^{(k)} = f'_{k,i}(0)$. The condition for A-protection is, of course,

$$\rho(\tilde{M}\tilde{D}) > 1 \tag{10.2}$$

It is easy to establish the evaluation

$$\rho(\tilde{M}\tilde{D}) = [\rho(MD^{(p)} \cdots MD^{(2)}MD^{(1)})]^{1/p} \tag{10.3}$$

and, of course, the matrix $\prod_{k=1}^{p} MD^{(k)} = MD^{(p)} \cdots MD^{(2)}MD^{(1)}$ is reduced to size $N \times N$.

When $M = \| e_i c_j \|_1^N$ is a Levene migration matrix, then

$$\rho(\tilde{M}\tilde{D}) = \left(\prod_{k=1}^{p} \sum_{j=1}^{N} c_j d_j^{(k)} \right)^{1/p} \tag{10.3a}$$

Where M is positive definite (or symmetrizable to a positive definite matrix, e.g., Deakin-type migration), we can achieve the upper bound

$$\rho(\tilde{M}\tilde{D}) \leq \left(\prod_{k=1}^{p} \rho(MD^{(k)}) \right)^{1/p} \tag{10.4}$$

This inequality shows that when $\prod_{k=1}^{p} \rho(MD^{(k)}) < 1$, the A allele is unprotected. In particular, if A-allele fixation is a stable state for every season, then allele A monomorphism is stable for the complete temporal cycle. On the other hand, if A-allele fixation is stable in a geometric mean sense, then it is stable for the p-season model.

In terms of the model (4.5), where the migration rates also vary seasonally, the condition for A-protection extending (10.2) and (10.3) becomes

$$\rho(M^{(p)}D^{(p)} \cdots M^{(2)}D^{(2)}M^{(1)}D^{(1)}) > 1 \tag{10.5}$$

With two seasons the ascertainment of A-protection requires that $\rho(M^{(2)}D^{(2)}M^{(1)}D^{(1)})$ exceed 1.

It is useful to record the sufficient conditions for (10.2) and (10.5) based on (1.18). We consider first the case of $M^{(1)} = M^{(2)} = \cdots = M^{(p)}$

---

* Model IX, Section 4.

(migration does not change seasonally), while the selection forces vary. Let $\boldsymbol{\xi}$ be the normalized left eigenvector of eigenvalue 1, that is, $\boldsymbol{\xi}$ satisfies for M, $\boldsymbol{\xi} M = \boldsymbol{\xi}$, $\langle \boldsymbol{\xi}, \mathbf{e} \rangle = \sum_{i=1}^{N} \xi_i = 1$. Then $\mathbf{z} = (\boldsymbol{\xi}/p, \boldsymbol{\xi}/p, \ldots, \boldsymbol{\xi}/p)$ is a corresponding left eigenvector for the extended migration matrix $\tilde{M}$. Appealing to (1.18) produces the estimate

$$\rho(\tilde{M}\tilde{D}) \geq \left(\prod_{k=1}^{p} \prod_{i=1}^{N} (d_i^{(k)})^{\xi_i/p} \right) = \prod_{i=1}^{N} \left(\left(\prod_{k=1}^{p} d_i^{(k)} \right)^{\xi_i} \right)^{1/p} \tag{10.6}$$

The quantity

$$d_i^* = \left(\prod_{k=1}^{p} d_i^{(k)} \right)^{1/p}$$

is exactly the temporal geometric mean of the selection values. The stationary distribution in deme $\mathcal{P}_i$ due to population structure and migration pattern has components $\{\xi_1, \xi_2, \ldots, \xi_N\}$. The inequality

$$\rho(\tilde{M}\tilde{D}) \geq \prod_{i=1}^{N} (d_i^*)^{\xi_i} \tag{10.7}$$

summarizes (10.6) where the right side resembles the formula (1.18). It should be emphasized that the right side of (10.6) is a weighted geometric mean with weights that depend on the migration structure. It is virtually folklore and ofttimes a declared tenet (e.g., Felsenstein, 1976; Hedrick *et al.*, 1976) that the selection expression of temporal variation operates through a geometric mean of the separate seasonal effects. The relation (10.6) can be interpreted as only partly consistent with this tenet subject to the caveat that its validity is only an approximation as a lower bound to the relevant spectral radius.

It is useful to extend (10.6) encompassing the situation where the migration rates could differ between seasons. In this circumstance

$$\tilde{M} = \left\| \begin{array}{cccccc} 0 & 0 & 0 & \ldots & 0 & M^{(p)} \\ M^{(1)} & 0 & 0 & \ldots & 0 & 0 \\ 0 & M^{(2)} & 0 & \ldots & 0 & 0 \\ \vdots & & & & & \vdots \\ 0 & 0 & 0 & \ldots & M^{(p-1)} & 0 \end{array} \right\| \tag{10.8}$$

where $M^{(k)}$ is the backward migration matrix in passing from the kth to the $(k+1)$th season. A left eigenvector for $\tilde{M}$ [of (10.8)] has components

$$\mathbf{z} = \left(\frac{\boldsymbol{\xi}^{(1)}}{p}, \frac{\boldsymbol{\xi}^{(2)}}{p}, \ldots, \frac{\boldsymbol{\xi}^{(p)}}{p} \right) \tag{10.9}$$

where $\boldsymbol{\xi}^{(k)}$ is the stationary frequency distribution for the matrix $M^{(k)}$.

Then the version of (10.6) in the variable (seasonal) migration context becomes

$$\rho(\tilde{M}\tilde{D}) \geq \prod_{i=1}^{N} \left(\prod_{k=1}^{p} (d_i^{(k)})^{\xi_i^{(k)}} \right)^{1/p} \tag{10.10}$$

11. COMPARISONS FOR PROTECTION WITH MIGRATION ONCE EACH CYCLE VERSUS ONCE EACH GENERATION

In the case where selection parameters are varying over time, it would be useful if we could identify a set of selection parameters (some sort of average) that would serve as a sufficient statistic in determining protection. We consider here the Levene backward migration matrix

$$M = \left\| \begin{array}{cccc} c_1 & c_2 & \ldots & c_N \\ c_1 & c_2 & \ldots & c_N \\ \vdots & \vdots & & \vdots \\ c_1 & c_2 & \ldots & c_N \end{array} \right\|, \qquad \sum_{i=1}^{N} c_i = 1$$

When there are p seasons with associated selection vectors $\mathbf{d}^{(k)}$, $k = 1, 2, \ldots, p$, the criterion for protection for this model is

$$\left(\prod_{k=1}^{p} \langle \mathbf{c}, \mathbf{d}^{(k)} \rangle \right)^{1/p} > 1 \tag{11.1}$$

where $\langle \mathbf{c}, \mathbf{d}^{(k)} \rangle = \sum_{i=1}^{N} c_i d_i^{(k)}$ is the inner product.

As we are multiplying spectral radii, a natural candidate for an average is $(\prod_{j=1}^{p} \circ\, \mathbf{d}^{(j)})^{1/p}$ whose entries are the pth roots of the p-fold Schur product. (The Schur product of two vectors is the vector with components equal to the product of the corresponding components.) We are therefore interested in the statistic

$$\sum_{i=1}^{N} c_i \left(\prod_{k=1}^{p} d_i^{(k)} \right)^{1/p} \tag{11.2}$$

Application of a form of the generalized arithmetic-geometric mean inequality to (11.2) gives

$$\left(\prod_{k=1}^{p} \sum_{i=1}^{N} c_i d_i^{(k)} \right)^{1/p} \geq \sum_{i=1}^{N} c_i \left(\prod_{k=1}^{p} d_i^{(k)} \right)^{1/p} \tag{11.3}$$

Hence, a sufficient condition for protection, but not a sufficient statistic for deciding A-protection, is that the right side of (11.3) exceeds 1.

Another comparison pertains to taking the product rather than geometric mean of the $\mathbf{d}^{(k)}$, which may be relevant when considering multivoltine species. If only one season is suitable for migration, and matings occur within demes for the other generations, the question can be asked what the effect on protection would be if migration were not restricted to once a cycle (year). The answer is not as apparent as the previous case.

For fixed Levene migration matrix C and varying fitness vectors $\mathbf{d}^{(i)}$ (we write $D^{(i)}$ for the diagonal matrix with vector $\mathbf{d}^{(i)}$ on the diagonal), the criterion for protection becomes that the spectral radius $\rho(\prod_{k=1}^{p} CD^{(k)}) > 1$ or explicitly $\prod_{k=1}^{p} (\sum_{j=1}^{N} d_j^{(k)} c_j) > 1$.

If no migration occurs until the close of the seasonal cycle, the criterion for protection is $\rho(C \prod_{k=1}^{p} D^{(k)}) > 1$ or $\sum_{j=1}^{N} c_j (\prod_{k=1}^{p} d_j^{(k)})^{1/p} > 1$.

In the case where the $\mathbf{d}^{(\nu)}$ are similarly ordered, i.e.,

$$(d_j^{(k)} - d_j^{(l)})(d_i^{(k)} - d_i^{(l)}) > 0 \text{ for all } i, j, k, l \tag{11.4}$$

(e.g., $d_i^{(k)}$ is increasing in k for each i), a standard rearrangement inequality states $\prod_k \sum_j c_j d_j^{(k)} \leq \sum_j c_j (\prod_k d_j^{(k)})$ or protection with migration every generation entails protection with a single migration per cycle.

Biologically, constraint (11.4) tacitly implies that the niches can be ordered by the relative magnitudes of their fitness parameters independent of the generation in the cycle (e.g., dry areas are most hard hit by a drought).

In the case of just two generations per cycle (e.g., winter/summer), it is possible that the condition $(d_j^{(k)} - d_j^{(l)})(d_i^{(k)} - d_i^{(l)}) < 0$ for all i, j, k, l is satisfied (dissimilar arrangements). Then the inequality is reversed

to $\prod_i \sum_j c_j d_j^{(i)} \geq \sum_j c_j \prod_i d_j^{(i)}$, signifying that protection is enhanced if migration is changed from once a cycle to once a generation.

12. PROTECTION IN A CLUSTER HOMING AND MAINLY DIRECTIONAL MIGRATION PATTERN

The population structure for this model is described in Section 4, part X, involving the backward migration matrix (4.7). Let the A-allele fitness coefficients for the multideme model of (4.7) be

$$d_i^{(k)}, \qquad i = 1, 2, \ldots, n_k, \qquad \text{applying in deme } \mathcal{P}_i^{(k)} \tag{12.1}$$

and form the extended diagonal matrix

$$\bar{D} = \operatorname{diag}(D^{(1)}, D^{(2)}, \ldots, D^{(p)}),$$
$$D^{(k)} = \operatorname{diag}(d_1^{(k)}, d_2^{(k)}, \ldots, d_{n_k}^{(k)}) \tag{12.2}$$

The criterion for A-protection, $\rho(\tilde{M}\bar{D}) > 1$, in the case at hand is equivalent to the conditions (Appendix C, Result C.3)

(i) $e_i^{(k)} d_i^{(k)} \geq 1$ *for some* i *and* k, *or* (12.3a)

(ii) $e_i^{(k)} d_i^{(k)} < 1$ *for all* i *and* k, *and*

$$\sum_{i=1}^{n_k} \frac{a_i^{(k)} b_i^{(k)} d_i^{(k)}}{1 - e_i^{(k)} d_i^{(k)}} > 1 \textit{ for some } k, \qquad 1 \leq k \leq p \tag{12.3b}$$

or

(iii) $e_i^{(k)} d_i^{(k)} < 1$ *for all* i *and* k *and all the inequalities of (12.3b) are reversed and*

$$(-1)^p \prod_{k=1}^{p} \langle \mathbf{v}^{(k)} \circ \mathbf{d}^{(k)}, (A_k - I)^{-1} \mathbf{u}^{(k)} \rangle > 1 \tag{12.4}$$

holds. (The notation $\mathbf{z} \circ \mathbf{w}$ denotes the Schur product vector whose components are the products of the corresponding components of $\mathbf{z}$ and $\mathbf{w}$).

Where $a_i^{(k)} = b_i^{(k)} = 0$, only the conditions of (i) and (iii) are relevant and (12.4) takes the explicit form

$$(-1)^p \prod_{k=1}^{p} \sum_{i=1}^{n_k} \frac{v_i^{(k)} d_i^{(k)} u_i^{(k)}}{e_i^{(k)} d_i^{(k)} - 1} > 1 \tag{12.5}$$

The expression (12.4) can be expanded explicitly to

$$(-1)^p \prod_{k=1}^{p} \sum_{i=1}^{n_k} \frac{v_i^{(k)} d_i^{(k)} u_i^{(k)}}{(e_i^{(k)} d_i^{(k)} - 1)} - \frac{1}{1 + \sum_{i=1}^{n_k} \frac{b_i^{(k)} d_i^{(k)} a_i^{(k)}}{e_i^{(k)} d_i^{(k)} - 1}} \sum_{i=1}^{n_k} v_i^{(k)} d_i^{(k)} u_i^{(k)} r_i^{(k)} s_i^{(k)} \tag{12.6}$$

where

$$r_i^{(k)} = \frac{a_i^{(k)}}{e_i^{(k)} d_i^{(k)} - 1} \quad \text{and} \quad s_i^{(k)} = \frac{d_i^{(k)} b_i^{(k)}}{e_i^{(k)} d_i^{(k)} - 1} \tag{12.7}$$

The above conditions (12.4)–(12.7) indicate a hybrid elaborate geometric-arithmetic averaging of the parameters. The migration scheme itself is a mixed directional–seasonal flow pattern with variable cluster homing tendencies.

13. PROTECTION IN A MULTIDEME SEED LOAD PROCESS*

The model of seed dormancy or facultative germination allowing at most p periods of dormancy is described in Section 2 within the framework of a migration pattern having a distinguished deme (see part VI, Section 2). Thus, a seed can exist in one of p environments where being in environment deme $\mathcal{P}_1$ will mean actual germination while being in deme positions 2 to $(p - 1)$ correspond to length of dormancy. We now superimpose a block of demes on each of the previous states inducing the backward migration matrix

---

* See Section 4, part XIII.

$$M = \begin{Vmatrix} A_1 & A_2 & A_3 & \ldots & A_p \\ B_1 & 0 & 0 & \ldots & 0 \\ 0 & B_2 & 0 & \ldots & 0 \\ \vdots & & & & \vdots \\ 0 & \ldots & & B_{p-1} & 0 \end{Vmatrix} \tag{13.1}$$

where all the component matrices A_i and B_j are of order $n \times n$. Let each term of $(D^{(1)}, D^{(2)}, \ldots, D^{(p)})$ be a diagonal positive matrix reflecting the selection coefficients relevant to A-protection across the various demes in the various states.

The relevant matrix for discerning A-protection becomes

$$MD = \begin{Vmatrix} \bar{A}_1 & \bar{A}_2 & \bar{A}_3 & \ldots & \bar{A}_p \\ \bar{B}_1 & 0 & 0 & \ldots & 0 \\ 0 & \bar{B}_2 & 0 & \ldots & 0 \\ \vdots & & & & \\ 0 & 0 & 0 & \bar{B}_{p-1} & 0 \end{Vmatrix} \tag{13.2}$$

where $\bar{A}_k = A_k D_k$ and $\bar{B}_k = B_k D_k$, $k = 1, 2, \ldots$.

It can be proved that A-protection occurs if and only if the *spectral radius* of the matrix T defined in (13.3) exceeds 1,

$$\rho(T) = \rho(\bar{A}_1 + \bar{A}_2 \bar{B}_1 + \bar{A}_3 \bar{B}_2 \bar{B}_1 + \cdots + \bar{A}_p \bar{B}_{p-1} \bar{B}_{p-2} \cdots \bar{B}_1) > 1 \tag{13.3}$$

The matrix T is $n \times n$ compared to (13.2), which is $np \times np$. Thus, for $n = 2$, T is a 2×2 matrix and $\rho(T)$ is explicitly calculable. Moreover, when the $n \times n$ matrices A_k and B_k are of the form

$$A_k = \Delta_k + R_k, \qquad B_k = E_k + S_k, \qquad k = 1, 2, \ldots \tag{13.4}$$

with Δ_k, E_k diagonal positive and R_k, S_k of rank one, the evaluation attendant to (13.3) can be explicitly done following the form of Result C.2 in Appendix C.

14. DEME SIZE DISTRIBUTIONS AND ALLELE PROTECTION

We now examine the effect of the arrangement of deme sizes on the strength of A-protection. The problem can be more precisely formulated as follows. What is the arrangement of deme sizes $(c_1, c_2, \ldots, c_N)$ in relation to the fitness array $\{d_1, d_2, \ldots, d_N\}$ that maximizes $\rho(MD)$ and, therefore, increases the likelihood of A-protection? Equivalently, how could a prescribed set of selection effects be distributed coupled to the migration structure to ensure greater opportunities for protection of the A allele? We consider this problem in this section for a number of specific migration patterns.

Let M be of rank-one migration form (Levene structure):

$$M = \| e_i c_j \|_1^N, \qquad e_i \equiv 1 \tag{14.1}$$

Then

$$\rho(MD) = \sum_{i=1}^{N} c_i d_i$$

It is standard to show $\sum_{i=1}^{N} c_i d_i$ is maximized, assuming without loss of generality c_i is monotone increasing when d_i is arranged increasing and is minimized for the arrangement d_i decreasing.

For the Deakin model,

$$M = (1 - \alpha)I + \alpha C \tag{14.2}$$

(entailing a uniform homing propensity superimposed on the Levene structure) the criterion for protection requires [see (7.5)] that either

(i) $(1 - \alpha)d_i > 1$ holds for some i,

or

(ii)

$(1 - \alpha)d_i \le 1$ for all i, for the inequality $\alpha \sum_{i=1}^{N} \dfrac{c_i d_i}{1 + (\alpha - 1)d_i} > 1$ to hold

The first condition (i) is independent of the ordering of $\{c_j\}$ so we may assume without loss of generality that it is not met, and concentrate on maximizing the sum in (ii) with respect to all orderings of $\{d_i\}$. The expression of condition (ii) may be exhibited more suggestively in the form

$$\alpha \sum_{i=1}^{N} c_i \left(\frac{1}{1/d_i + (\alpha - 1)} \right) \tag{14.3}$$

We note, subject to the constraint $(1 - \alpha)d_i < 1$ [imposed in (ii)], that the function $1/[1/d_i + (\alpha - 1)]$ is monotone increasing in the variables d_i. Thus, the stipulation c_i increasing in concordance with d_i increasing tends to maximize $\rho(MD)$, while the arrangement d_i decreasing coupled to c_i increasing minimizes the spectral radius.

For the model involving differential habitat homing rates $\{\alpha_i\}_1^N$, it is *not* correct that the "optimal maximizing $\rho(MD)$" distribution of $\{\alpha_i\}$ is concordant with the ordering of $\{c_i\}$.

We can also deal with the complementary question: What order of premigration deme sizes $\{c_i\}$ maximizes the likelihood of protection for prescribed $\{d_i\}$ in the context of the above two models? The foregoing argument shows that $\{c_i\}$ should be similarly ordered with $\{d_i\}$ for the Levene migration pattern. An identical result is obtained in the presence of a uniform homing factor.

We can analyze this problem for the case of variable homing behavior if one assumes that $\{\alpha_i\}$ and $\{d_i\}$ are fixed. We may assume, without loss of generality, that $(1 - \alpha_i)d_i$ are less than one for all i. In order to increase the likelihood of protection we seek the arrangement of $\{c_i\}$ maximizing

$$\sum_{i=1}^{N} c_i \frac{\alpha_i}{1/d_i + (\alpha_i - 1)} \tag{14.4}$$

If the quantity (14.4) exceeds 1 for some ordering of $\{c_i\}$, then the same inequality persists where $\{c_i\}$ are ordered concordant with the sequence $\{\alpha_i/[d_i^{-1} + (\alpha_i - 1)]\}$.

We proved (Karlin, 1977*b*) that a dominant allele is protected if and only if

$$\sum_{i=1}^{N} \xi_i w_i > 1 \tag{14.5}$$

where w_i is the fitness of the recessive genotype (fitness values w_i, 1, 1 for genotypes *aa*, *Aa*, *AA*, respectively) in deme $\mathcal{P}_i$ for a general migration matrix with left principal eigenvector $\boldsymbol{\xi} = (\xi_1, \xi_2, \ldots, \xi_N)$. It follows that the optimal ordering of deme sizes for A-protection has $\{\xi_i\}$ similarly ordered to the fitness values $\{w_i\}$.

Consider the stepping-stone migration model having backward migration matrix (2.14) with $m \le \frac{1}{4}$ signifying an a priori migration propensity per individual of less than 0.50. Where the deme sizes increase, $c_1 \le c_2 \le \cdots \le c_N$, (or decrease) over the population range, $\{c_i \gamma_i\}$ also increase (decrease), [γ_i are defined in (2.16)], and then

$$\sum_{i=1}^{N} \xi_i w_i = \frac{\sum_{i=1}^{N} c_i\gamma_i w_i}{\sum_{i=1}^{N} c_i\gamma_i} \tag{14.6}$$

is largest (smallest) if the fitness values ($w_1, w_2, \ldots, w_N$) also occur in increasing order, i.e., $w_1 \le w_2 \le \cdots \le w_N$.

When c_i are not monotone, then $\{c_i\gamma_i\}$ and $\{c_i\}$ are not necessarily similarly ordered. The optimal arrangement of w_i maximizing A-protection corresponds to the ordering of $\{c_i\gamma_i\}$.

The values $\{\gamma_i\}$ can be interpreted as the relative sizes of the demes after migration, while $\{c_i\}$ is the array of deme sizes prior to migration. The magnitudes of the products, $\{c_i\gamma_i\}$ [or equivalently the geometric means, $(c_i\gamma_i)^{1/2}$, of the sizes before and after migration], meshed concordantly with the magnitudes of the array of aa-genotype fitness values, $\{w_i\}$ appear to be essential in the comparison. Thus, the optimal arrangement of the fitnesses, $\{w_i\}$, to ensure A-protection or, equivalently, the maximum of (14.6) is achieved when $\{w_i\}_1^N$ and $\{c_i\gamma_i\}_1^N$ exhibit the same arrangements in their relative magnitudes. In particular, if $c_{i_1}\gamma_{i_1} \le c_{i_2}\gamma_{i_2} \le \cdots \le c_{i_N}\gamma_{i_N}$, then the ordering of $\{w_i\}$ among demes $\{\mathcal{P}_i\}_1^N$, according to $w_{i_1} \le w_{i_2} \le \cdots \le w_{i_N}$, yields the maximum in (14.6) relative to all permutations of the values of $\{w_i\}_1^N$ among the demes.

In the nonhomogeneous homing model (2.11), the arrangement of the magnitudes of $\{w_i\}$ concordant with $\{c_i\gamma_i\delta_i\}$ maximizes the likelihood of A-protection. The quantities $\{c_i\alpha_i\delta_i\}$ do not lend themselves to easy interpretation except in the uniform homing case, $\alpha_1 = \alpha_2 = \ldots = \alpha_N = \alpha$, where ξ_i reduces to c_i, $i = 1, 2, \ldots, N$. The factor $c_i\delta_i$ can be construed as the relative population size after migration, while the multiplier α_i measures the extent of outcrossing from deme $\mathcal{P}_i$. The magnitudes of $\{\alpha_i c_i\gamma_i\}$ coupled with fitness values $\{w_i\}$ determine the strength of A-protection relative to all prescriptions of the given $\{w_i\}$ among the demes. The extent to which these sequences are concordant in their arrangement of effects confers increased likelihood in maintaining a-protection.

Observe that

$$\prod_{i=1}^{N} (w_i)^{\xi_i} = \exp\left[\sum_{i=1}^{N} \xi_i \log w_i\right]$$

is also maximal where the sequences $\{\xi_i\}$ and $\{w_i\}$ are concordant in relative sizes. Using this fact and inspection of the possible inequality

$$\prod_{i=1}^{N} w_i^{\xi_i} < 1 < \sum_{i=1}^{N} \xi_i w_i$$

suggests that increasing the chances of A-protection ipso facto decreases the likelihood of a-protection. Accordingly, the existence of a protected polymorphism that maintains both A and a alleles requires a compromise in the assignment of fitness values $\{w_i\}$ among the demes relative to the migration factors $\{\xi_i\}_1^N$.

15. TWO DEAKIN MIGRATIONS PER GENERATION

When considering a population of organisms that mate in certain areas ($\mathcal{M}_j$) but undergo viability selection in separate habitats ($\mathcal{P}_i$), one possible schematization of the life cycle is as follows:

$$\begin{array}{l}\text{Diploid juveniles before selection} \xrightarrow{\text{selection}} \text{Diploid adults after selection} \xrightarrow{\text{migration}} \text{Shed gametes} \rightarrow \\ \rightarrow \text{Gametes unite (mating)} \rightarrow \text{Zygotes} \xrightarrow{\text{migration}} \text{Diploid juveniles before selection} \rightarrow\end{array}$$

where selection occurs in $\mathcal{P}_i$ and gametes are shed and unite to form zygotes in $\mathcal{M}_j$. Consider a series of mating areas $\{\mathcal{M}_j\}$ and a series of maturing habitats $\{\mathcal{P}_i\}$ with general migration forms between them. Viability selection will not necessarily act on a subpopulation with Hardy–Weinberg proportions, thus necessitating carrying two sets of frequencies through all calculations. However, as the problem of protection essentially concerns only haploids, one set of frequency values suffices. It is the ascertainment of protection that we are concerned with here.

We shall assume heterozygotes all have fitness 1 and the fitness of the common homozygote is designated by σ_i. We further assume that there are the same number of mating ($\mathcal{M}$) and maturing ($\mathcal{P}$) areas that either are coincident or are associated in some natural manner such that the forward migration matrices $\mathcal{P} \rightarrow \mathcal{M}$ and $\mathcal{M} \rightarrow \mathcal{P}$ have the form $(1 - \alpha)I + \alpha G$ and $(1 - \beta)I + \beta H$, respectively, where I is the identity and G and H are rank-one stochastic matrices. Composition gives the forward migration matrix $\mathcal{P} \rightarrow \mathcal{P}$ as

$$[(1 - \alpha)I + \alpha G][(1 - \beta)I + \beta H] \tag{15.1}$$

which is appropriate as we are only concerned with the disposition of the rare alleles, mostly found in heterozygous individuals.

The calculation of the forward migration matrix over the whole cycle obtained by composition of the two component forward migration matrices is strongly dependent on the assumption of no selection between the migrations. We stress that the relative deme sizes are not normalized after the first migration, but are consistent with the premigration deme sizes and the migration pattern (M). Following the standard recipe, the backward migration matrix is given by

$$M = \Gamma^{-1}F'C \tag{15.2}$$

where C is the diagonal matrix of the relative sizes of $\{\mathcal{M}_i\}$ before migration, the prime designates transpose, and Γ^{-1} normalizes M producing a row stochastic matrix.

In the usual manner we shall designate by D the diagonal matrix with entries $1/\sigma_i$ representing the marginal viabilities of the heterozygotes. Protection then occurs if $\rho(MD) > 1$.

We note that

$$\begin{aligned} F &= [(1-\alpha)I + \alpha G][(1-\beta)I + \beta H] \\ &= (1-\alpha)(1-\beta)I + \beta H + \alpha(1-\beta)G \end{aligned} \tag{15.3}$$

is the sum of a diagonal and two rank-one matrices. However, the particular nature of G and H (both share their principal eigenvector) reduces F to the sum of a diagonal and one rank-one matrix. This is most easily seen by writing

$$g_{ij} = g_j, \qquad h_{ij} = h_j \tag{15.4}$$

Hence,

$$\beta H + \alpha(1-\beta)G = R \text{ such that } r_{ij} = \beta h_j + \alpha(1-\beta)g_j \tag{15.5}$$

The backward migration matrix, in accordance with the standard recipe, is given by

$$M = \Gamma^{-1}F'C = \Gamma^{-1}[(1-\alpha)(1-\beta)I + R]'C \tag{15.6}$$

where C is diagonal and gives the relative premigration deme sizes and

Γ is diagonal with

$$\gamma_i = (1-\alpha)(1-\beta)c_i + \beta h_i + \alpha(1-\beta)g_i$$

We now display explicitly the criterion for protection $\rho(MD) > 1$, as derived in Appendix C.

For the foregoing model, protection occurs if either

(i) $$\frac{(1-\alpha)(1-\beta)c_i d_i}{(1-\alpha)(1-\beta)c_i + \beta h_i + \alpha(1-\beta)g_i} > 1 \text{ for some } i$$

or (i) does not hold and

(ii) $$\sum_{i=1}^{N} \frac{[\beta h_i + \alpha(1-\beta)g_i]c_i d_i}{(1-\alpha)(1-\beta)c_i(1-d_i) + \beta h_i + \alpha(1-\beta)g_i} > 1$$

is in force.

16. MAINTENANCE OF PROTECTION WITH CHANGES IN POPULATION SUBDIVISION

The following questions are of interest. (a) Does protection of allele A persist in the two separate parts of a previously single population having allele A protected? (b) Is protection of allele A maintained for a combined population composed from two isolated populations after removal of the migration barrier where allele A was protected in each of the two source populations? (c) It is of interest to ascertain the similarities and contrasts in the equilibrium gene frequency patterns that accrue from an enlarged neutral zone where in other respects the environmental selection–migration structure is unchanged.

Let $\bar{M} = \| \bar{m}_{ij} \|_{i,j=1}^{r}$ be the backward migration matrix for the population consisting of demes $\bar{\mathcal{P}} = \{\bar{\mathcal{P}}_1, \bar{\mathcal{P}}_2, \ldots, \bar{\mathcal{P}}_r\}$ carrying associated A-allele fitness values $\{\bar{d}_1, \bar{d}_2, \ldots, \bar{d}_r\}$. Furthermore, let $\hat{M} = \| \hat{m}_{ij} \|_1^s$ be the backward migration matrix for the population range comprised of the demes $\hat{\mathcal{P}} = \{\hat{\mathcal{P}}_1, \hat{\mathcal{P}}_2, \ldots, \hat{\mathcal{P}}_s\}$ and corresponding fitness values $\{\hat{d}_1, \hat{d}_2, \ldots, \hat{d}_s\}$. Consider now the coupled multideme complex entailing some migration flow between the extreme demes $\bar{\mathcal{P}}_r$ and $\hat{\mathcal{P}}_1$. The enlarged backward migration matrix (involving now $r + s$ demes) takes the form

$$M = \begin{array}{cc||cccccccc||}
 & & \multicolumn{4}{c}{\overbrace{\hphantom{\bar m_{11}\cdots\bar m_{r,r}-\lambda}}^{r}} & \multicolumn{4}{c}{\overbrace{\hphantom{\hat m_{11}-\mu\ \hat m_{12}\cdots\hat m_{1s}}}^{s}} \\
\bar{\mathcal{P}} & 1 & \bar m_{11} & \cdots & & \bar m_{1r} & 0 & 0 & \cdots & 0 \\
 & 2 & \bar m_{21} & \cdots & & \bar m_{2r} & 0 & 0 & \cdots & 0 \\
 & \vdots & \vdots & & & \vdots & & & & \\
 & r-1 & \bar m_{r-1,1} & \cdots & & \bar m_{r-1,r} & 0 & 0 & \cdots & 0 \\
 & r & \bar m_{r,1} & \cdots & & \bar m_{r,r} - \lambda & \lambda & 0 & \cdots & 0 \\
\hat{\mathcal{P}} & 1 & 0 & \cdots & 0 & \mu & \hat m_{11} - \mu & \hat m_{12} & \cdots & \hat m_{1s} \\
 & 2 & 0 & \cdots & 0 & 0 & \hat m_{21} & \hat m_{22} & \cdots & \hat m_{2s} \\
 & \vdots & \vdots & & & & & & & \\
 & s & 0 & & 0 & 0 & \hat m_{s1} & \hat m_{s2} & \cdots & \hat m_{ss}
\end{array} \tag{16.1}$$

The migration rates $\lambda > 0$ and $\mu > 0$ are, of course, constrained such that $\bar m_{rr} - \lambda > 0$ and $\hat m_{11} - \mu > 0$.

The following result bears on questions (a) and (b).

THEOREM 16.1. (i) *The removal of a migration barrier between $\bar{\mathcal{P}}$ and $\hat{\mathcal{P}}$ producing the backward migration matrix (16.1) where in each separate range (i.e., for $\bar{\mathcal{P}}$ and for $\hat{\mathcal{P}}$) allele A is protected, the combined population $\mathcal{P} = \{\bar{\mathcal{P}}, \hat{\mathcal{P}}\} = \{\bar{\mathcal{P}}_1, \ldots, \bar{\mathcal{P}}_r, \hat{\mathcal{P}}_1, \ldots, \hat{\mathcal{P}}_s\}$ has allele A again protected.*

(ii) *Division of $\mathcal{P}$ having allele A protected into two contiguous parts preserves A-protection in at least one of its parts.*

The following example suggests that Theorem 16.1 [part (ii)] is not necessarily intuitive. Consider a three-range selection gradient (in a clinal situation)

$$\underbrace{\overset{P_1}{\square}\cdots\overset{P_{l_1}}{\square}}_{-}\quad\underbrace{\overset{P_{l_1+1}}{\square}\cdots\overset{P_{l_2}}{\square}}_{+}\quad\underbrace{\overset{P_{l_2+1}}{\square}\cdots\overset{P_n}{\square}}_{-} \tag{16.2}$$

where allele A is advantageous in the intermediate zone but disadvantageous in the outer parts. Suppose the selection migration structure has allele A protected in the whole population. Interposing a barrier in the + zone divides the population into two sectors

$$\underbrace{\overset{P_1}{\square}\cdots\overset{P_{l_1}}{\square}}_{-}\ \underbrace{\overset{P_{l_1+1}}{\square}\cdots\overset{P_{l_1+k}}{\square}}_{+}\quad\Big|\quad\underbrace{\overset{P_{l_1+k+1}}{\square}\cdots\overset{P_{l_2}}{\square}}_{+}\ \underbrace{\overset{P_{l_2+1}}{\square}\cdots\overset{P_n}{\square}}_{-} \tag{16.3}$$

where in the separate parts the number of demes favorable to allele A may conceivably be too small to compel A-protection. Theorem 16.1 [part (ii)] asserts that at least one of the population sectors maintains A-protection.

The converse is not generally correct. No encompassing conclusions apply for a population composed from two parts where in one part allele A is protected, while in the other part extinction of allele A is possible.

The Influence of Neutral Demes

It is of interest to investigate in the equilibrium gene frequency patterns that occur with the enlargement, contractions, or other modifications of the neutral zone where in other respects the selection regime and migration pattern remain unaltered. Our first statement on this topic is as follows.

PROPOSITION 16.1. *The existence of a protected polymorphism is unaffected by the addition of neutral demes at the boundary of the population range.*

Moreover, the resulting equilibrium frequency arrays and their stability characteristics in the enlarged system (i.e., the original population augmented with the new neutral boundary demes) *coincide with the equilibrium frequency configurations at the common demes.*

The foregoing result is perhaps intuitive. However, the effects accruing from adding new neutral demes into the midst of the population range are a more recondite matter as we now elaborate. In order that the formulation be well defined, we envision an original population composed of two groups of demes $\mathcal{A} = (\mathcal{A}_1, \ldots, \mathcal{A}_k)$ and $\mathcal{B} = (\mathcal{B}_1, \ldots, \mathcal{B}_l)$ subject to the backward migration matrix

$$M = \begin{array}{c||ccccccc||}
k & a_{11} & \ddots & a_{1k} & 0 & 0 & & 0 \\
 & \vdots & & \vdots & \vdots & \vdots & & \vdots \\
 & a_{k-1,1} & \cdots & a_{k-1,k} & 0 & 0 & & 0 \\
 & a_{k1} & \cdots & a_{kk} & a & 0 & & 0 \\
l & 0 & & b & b_{11} & b_{12} & \cdots & b_{1l} \\
 & & & & b_{21} & b_{22} & & \\
 & \vdots & & \vdots & \vdots & & & \vdots \\
 & 0 & & 0 & b_{l1} & \cdots & & b_{ll}
\end{array} \tag{16.4}$$

where $\mathcal{A}$ and $\mathcal{B}$ communicate only by gene flow between the specific demes $\mathcal{A}_k$ and $\mathcal{B}_1$ with corresponding rates $\mathcal{A}_k \xleftarrow{a} \mathcal{B}_1$ and $\mathcal{A}_k \xrightarrow{b} \mathcal{B}_1$, $a > 0$, $b > 0$. The total population obviously involves $k + l$ demes.

The associated fitness values in the ordering of (16.4) are given by

$$(d_1, d_2, \ldots, d_k, d_1', d_2', \ldots, d_l') \tag{16.5}$$

We examine the new situation created by interposing between demes $\mathcal{A}_k$ and $\mathcal{B}_1$ a new *neutral* deme (labeled $\mathcal{P}_0$) producing thereby the population arrangement

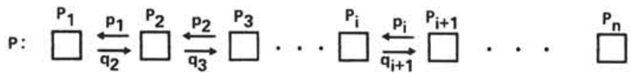
$$\{\mathcal{A}_1, \mathcal{A}_2, \ldots, \mathcal{A}_k, \mathcal{P}_0, \mathcal{B}_1, \ldots, \mathcal{B}_l\} \tag{16.6}$$

In retaining the migration structure of (16.4), we stipulate the backward migration matrix for (16.6) as

$$\tilde{M} = \begin{array}{c|cccccccc|} & d_1 & \ldots & d_k & d_0 = 1 & d_1' & d_2' & \ldots & d_l' \\ \mathcal{A}_1 & a_{11} & & a_{1k} & 0 & 0 & 0 & & 0 \\ \vdots & \vdots & & \vdots & \vdots & \vdots & \vdots & & \vdots \\ \mathcal{A}_2 & a_{k1} & & a_{kk} & a & 0 & 0 & \ldots & 0 \\ \mathcal{P}_0 & 0 & \ldots & m & 1-2m & m & 0 & \ldots & 0 \\ \mathcal{B}_1 & 0 & \ldots & 0 & b & b_{11} & b_{12} & \ldots & b_{1l} \\ & 0 & \ldots & 0 & 0 & b_{21} & b_{22} & \ldots & b_{2l} \\ \vdots & \vdots & & \vdots & \vdots & \vdots & \vdots & & \vdots \\ \mathcal{B}_l & 0 & \ldots & 0 & 0 & b_{l1} & b_{l2} & & b_{ll} \end{array} \tag{16.7}$$

signifying that the proportion of migrants per generation entering the neutral deme from the population range $\mathcal{A}$, i.e., through $\mathcal{A}_k$, and the rate of gene flow into $\mathcal{P}_0$ arising from the demes of $\mathcal{B}$ (via $\mathcal{B}_1$) are *the same* ($= m$; $0 < m < 1/2$). *This requirement is essential* for the validity of Theorem 16.2 (below) as attested to by Example 16.1 below.

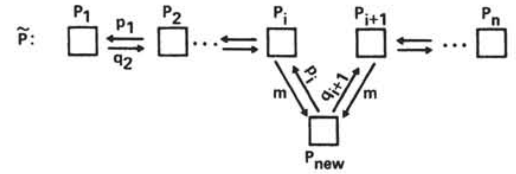
It may clarify the formulation by presenting a pictoral representation for a generalized stepping-stone migration model. Accordingly, consider the original multideme clinal population $\mathcal{P}$ in the linear arrangement



(16.8a)

where p_i and q_i indicate the obvious backward migration rates.

The augmented population $\mathcal{P}$ is taken coincidént with $\mathcal{P}$ apart from the introduction of a new neutral deme between demes $\mathcal{P}_i$ and $\mathcal{P}_{i+1}$ following the schematization



(16.8b)

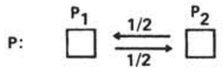
THEOREM 16.2. *Consider a population system* $\mathcal{P} = \{\mathcal{A}_1, \ldots, \mathcal{A}_k, \mathcal{B}_1, \ldots, \mathcal{B}_l\}$ *composed of two parts. Assume the migration mixing for* $\mathcal{P}$ *is described by the matrix M of (16.4) which is assumed symmetrizable to a symmetric (not necessarily positive definite) matrix* [cf. (5.1)]. *Interposing a new neutral deme between* $\mathcal{A}_k$ *and* $\mathcal{B}_1$ *subject to the migration forces expressed by the backward migration matrix* $\tilde{M}$ *of (16.7)* (where the flow into the new neutral deme from both parts is the same, while in all other respects the population structure is unchanged) *does not diminish the extent of protection. Formally,*

$$\rho(MD) > 1 \textit{ implies } \rho(\tilde{M}\tilde{D}) > 1 \tag{16.9}$$

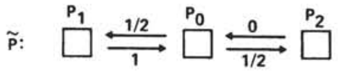
The conditions for $\mathcal{P}$ are satisfied for a clinal geographical arrangement of demes governed by a stepping-stone migration mode even allowing for variable local exchange rates. In this case, the neutral deme can be introduced at any position along the cline [see (16.8b)].

In particular, Theorem 16.2 declares that when allele A is protected in $\mathcal{P}$ of (16.8a), then allele A remains protected in $\tilde{\mathcal{P}}$ of (16.8b).

EXAMPLE 16.1. The requirement of equal migration flow in both directions into the new neutral demes is essential for the validity of Theorem 16.2. In fact, the two-deme model with homogeneous migration exchange as depicted



having fitness parameters obeying $0 < d_1 < 1 < d_2 < 2$, $d_1 + d_2 > 2$, and $d > [d_1(2 - d_2)/4] + d_1 + d_2$ has $\rho(MD) = [(d_1 + d_2)/2] > 1$, but the augmented system



interposing a neutral deme in the center, but with unequal migration input into $\mathcal{P}_0$ from the demes $\mathcal{P}_1$ and $\mathcal{P}_2$, has $\rho(\tilde{M}\tilde{D}) < 1$, i.e., allele A is unprotected.

The same situation prevails for the modified example with migration rates from the left and right into the neutral deme of magnitudes $1 - \epsilon$ and ϵ, respectively (with ϵ positive and small).

The result of Theorem 16.2 in conjunction with the foregoing example establishes that although a neutral deme confers no selective advantage to either allele, yet unless this locality is influenced to the same extent by the population sectors on its right and left the persistence of a protected polymorphism can be attenuated and even eliminated. It is striking that Theorem 16.2 applies to any clinal population structure provided only that the migration flow into the neutral deme is the same from the right and left portions of the population range independent of local deme sizes, unequal local migration rates among demes, or differences in reciprocal directions.

The Influence of the Multiplicity of Neutral Demes and the Existence of a Protected Polymorphism

We have seen that the addition of neutral demes with equal flow into them from the neighboring demes preserves the phenomenon of a protected polymorphism. Our next result asserts that in natural circumstances a sufficient accretion of neutral demes can ensure protection of an allele where ab initio no protection existed. The precise statement is as follows.

THEOREM 16.3. *Consider a multideme population $\mathcal{P} = \{\mathcal{P}_1, \mathcal{P}_2, \ldots, \mathcal{P}_n\}$ with the property that deme $\mathcal{P}_{i_0}$ connects in $\mathcal{P}$ only via demes $\mathcal{P}_{i_0-1}$ and $\mathcal{P}_{i_0+1}$ or equivalently the i_0th row of the backward migration matrix exhibits only three consecutive nonzero elements:*

$$M = \left\| \begin{matrix} & & \cdot & & \\ & & \cdot & & \\ 0 \ldots 0 & q_{i_0} & \ddots r_{i_0} & p_{i_0} & 0 \ldots 0 \\ & & \cdot & & \\ & & \cdot & & \end{matrix} \right\| \text{ row } i_0\text{th}$$

where $q_{i_0}p_{i_0} > 0$, $q_{i_0} + r_{i_0} + p_{i_0} = 1$. Suppose deme $\mathcal{P}_{i_0}$ is A-advantageous connoting $d_{i_0} > 1$. Then by addition of enough neutral demes on both sides of $\mathcal{P}_{i_0}$, protection of allele A can be guaranteed for $\mathcal{P}$.

(Actually, an upper estimate of the number of neutral demes needed to ensure A-protection is

$$k \geq \frac{1 - r_{i_0}d_{i_0}}{d_{i_0} - 1} \tag{16.10}$$

The condition $r_{i_0}d_{i_0} \geq 1$ means that there is already protection of allele A independent of the nature of selection in the other demes. More generally, for a migration matrix M and fitness values summarized in D, then

$$m_{i_0,i_0}d_{i_0} \geq 1 \text{ for some } i_0, \qquad 1 \leq i_0 \leq n \tag{16.11}$$

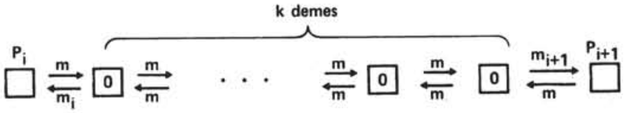
entails $\rho(MD) > 1$. Actually, the condition (16.11) assures that allele A increases in the subpopulation $\mathcal{P}_{i_0}$ when rare even if all demes lack allele A.

Another sufficient condition extending (16.11) noted by Christiansen (1974) follows. Let $(MD)_{(k)}$ represent the contraction of the matrix MD to a prescribed subset of the same k rows and columns, $k < n$. Then

$$\det[I_k - (MD)_k] \leq 0 \text{ implies } \rho(MD) > 1 \tag{16.12}$$

In words, the above condition assures protection for allele A even if there are only k populations containing the allele at the initial generation.

For the general clinal migration structure it is established in Karlin and Richter-Dyn (1976) that by an addition of k neutral demes between demes $\mathcal{P}_i$ and $\mathcal{P}_{i+1}$ with homogeneous migration mode as depicted



the corresponding equilibrium states are identical to those arising with a reduction of the migration rate between demes $\mathcal{P}_i$ and $\mathcal{P}_{i+1}$ by a factor of $1/(k+1)$. Interpretation of Theorem 16.3 coupled to this remark reveals that the addition of neutral demes effectively operates to diminish gene flow among the demes. We pointed out in Section 6 (see also Karlin and

McGregor, 1972*b*) that significantly reduced migration rates enhance the prospects of polymorphisms.

17. DISCUSSION AND SUMMARY

Spatial and temporal variation in environment are thought to be important factors in the maintenance of genetic variation in populations. Classical examples of populations that have been partitioned into subpopulations with intrinsic selection effects include industrial melanism in moths (Cain and Sheppard, 1952; Ford, 1975), shell color and banding pattern in snails (Ford, 1975; Jones *et al.*, 1977), adaptive responses to heavy-metal tolerance in plants (Jain and Bradshaw, 1966), growth modifications of some sea cliff plant populations (Aston and Bradshaw, 1966), diallozyme representations on alcohol tolerance in *Drosophila melanogaster* (Clarke, 1979), some enzyme adjustments of fish populations to conditions of salinity and temperature [e.g., *Fundulus heteroclitus* (Mitton and Koehn, 1975)], and maintenance of area effects (Goodhart, 1963). For other examples, see Dobzhansky (1956, 1967), Wright (1969), Koehn (1969), Antonovics (1971), Bradshaw (1971), Bryant (1974), McDonald and Ayala (1974), Powell (1975), Soule (1976).

It is also widely recognized that migration may play an important, even dominant role in producing clines and polymorphisms in that important sources of variability in natural populations can be genes and gene complexes transferred from other populations. In all cases the maintenance of a polymorphism is probably due to a complex interaction of environmental heterogeneity and genetic factors, the relative importance of which varies over the population range.

Delineation of how genetic variability should be related to physical or biotic environmental heterogeneity is difficult. Measures of environmental heterogeneity are usually set forth in dichotomous terms, e.g., fine versus coarse, variable versus constant, unstable versus stable, central versus marginal. These characterizations are ambiguous and in all respects open to subjective interpretations.

A general hypothesis proposes that organisms living in "stable environments" should be genetically depauperate. The case of deep-sea organisms is cited as representative of a stable environment. Presumably, subterranean terrestrial situations also present constant environmental conditions. It is argued that deep-sea populations are highly specialized (Grassle, 1972) and, therefore, there is much species diversity but little genetic variability within these species populations. This conclusion is contested on the basis of other studies (e.g., Ayala *et al.*, 1975).

It is suggested that in "constant environments" organisms become narrowly niched, specialized, and genetically homogeneous. Concomitantly, there may be high species diversity if predation and related ecological disturbances are not present (Clarke, 1979). Some data on genetic variability among subterranean mammals conform to this hypothesis (Nevo, 1978).

A heuristic argument for more individual gene homozygosity in "variable environments" proceeds as follows. Individuals able to cope with a wide variety of environmental conditions are more fit because they can utilize and exploit many food resources, etc. Therefore, some generalized chromosomal composition would be selected for that increases the overall fitness but simultaneously reduces the genetic variability by selecting against alleles that lower the overall fitness. Then the population would contain few alleles at an average locus.

It has also been suggested by Bretsky and Lorenz (1969) and Bretsky (1970) that extinction patterns in the fossil record could be explained on the basis of a positive correlation between genetic variability and environmental stability. That is, organisms in stable (coarse-grain) environments are expected to have less variable gene pools owing to specialized adaptation and as a consequence they are less able to adapt to major environmental changes and concomitantly experience higher rates of extinction.

Intimately related to the above theme is the controversy of the extent of genetic variability in marginal populations as compared to central ones (Carson, 1958; Dobzhansky, 1967; see the discussion and review of Lewontin, 1974, pp. 148–151). It is often suggested that peripheral (marginal) populations of a species tend to be less polymorphic than central populations, but the data on this proposition are ambiguous. Chromosomal inversion polymorphisms in certain *Drosophila* collections (mainly on chromosome III) appear to be more frequent in central populations and there is some controversy as to the cause. In these cases distinctions are made between chromosomal versus genic polymorphism.

A number of verbal dictums abound in the evolutionary literature concerning the relationships inherent to selection–migration environmental parameters, population structure, and patterns of gene frequency variation. We paraphrase some of these: (i) Polymorphism will be more likely to occur in temporally more variable environments while unlikely to exist in constant environments. (ii) Greater heterogeneity in spatial selection gradients enhances polymorphism. (iii) Decreased migration flow in a population entails more cases of polymorphism. (iv) More population division facilitates the establishment of polymorphism. These statements include undefined and vague concepts. What is meant by one migration pattern involving relatively less migration flow than a second migration pattern? Is there a consistent scale (or a vector of indices) by which to assess rate of mobility, or degrees of isolation? By what criteria is a prescribed selection gradient judged more heterogeneous (or more stable) than another selection structure? Undoubtedly, not all environmental grains are comparable. What are meaningful sets of measures of heterogeneity in both ecological and genetic (fitness) terms? A common measure used involves the variance taken over time and space of some environmental variable. This is obviously too restrictive.

There are marked differences in the way selection, migration, and population structure influence the occurrence and nature of a protected polymorphism. With this in mind, we have suggested natural classes of migration forms that reflect environmental profiles, systematic and fluctuating selection effects, behavioral and physiological attributes, and population structure parameters. It is of value to highlight a number of concepts and factors of the interactive influences operating on migration–selection dynamics.

(a) The notion of population subdivision that involves separate habitat sites can often be characterized by a myriad of social, behavioral, geographical, ecological, historical, and other criteria. (b) Multiple stages of migration per generation. Multiple mating areas and consequences of migration of juveniles versus adults and zygotes versus gametes. (c) Local (usually variable) rates of homing and related measures of isolation. (d) The distributional characteristics of the migration process. (e) The influence of variable deme sizes and their arrangement over the population range. (f) Geographical and hierarchical characteristics implicit and explicit to population structure.

Our results are of three kinds. We set forth some general principles that are valid for all migration forms independent of the selection regimes. We also provide results and properties that depend on the level and/or form of the migration–selection interaction. Third, we determine explicit conditions for the existence of a protected polymorphism over a spectrum of models. These results are interpreted and contrasted for specific classes of migration forms that are of interest in some natural situations for purposes of better understanding the interrelationships of the factors under (a)–(f) in elucidating forms and levels of polymorphism.

We have dealt with several canonical classes of migration patterns: e.g., the possibility of variable homing rates with respect to deme sites, island structures, isolation-by-distance structures, periodic patterns, migration flow entailing a major and a subordinate deme, and hybrid compositions of these that are particularly amenable to analysis and reasonably biologically motivated. These supplement the classic Wright island model (1943), the stepping-stone migration form (Malécot, 1959), the Levene population subdivision model (Levene, 1953; Prout, 1968), and (constant homing) migration patterns (Deakin, 1966). Our analysis is especially revealing for the hybrid migration structures described in Tables III and IV (Section 1). We emphasize the generalized multiuniform migration form (part VII, Section 3), which depicts subpopulation clusters where each cluster consists of an array of demes not unlike "societies" within "nations." The generalized star migration form (part VIII, Section 3) can be considered as being composed of a string of colonies, primarily communicating through a central population. The attendant analysis may be used to describe situations of population expansion out of a central locality or of centripetal migration. The formulations of parts IX and X (Section 4) allow treatment of seasonal variation in selection intensity in a multideme context. The Kronecker product model (XI) involves demes classified by a sequence of independent criteria.

We now summarize a number of the main findings and interpretations of the results.

1. Previous attempts to summarize sufficient conditions for allele protection in a subdivided population emphasize either a simple geometric or an arithmetic average of fitness values over the population range. I previously observed (Karlin, 1976) that it is unnatural in proposing a meaningful sufficient "average" statistic that does not weight the effects of variation in demes sizes, differences in local migration rates, the existence of multistage migration tendencies, range variance, and other attributes of the migration distributions in its calculation. Only in the simplest constructions (the Levene population subdivision model or on a single population subject to cyclic temporal selection) do the simple average of selection values have meaning.

The conditions for protection involve *compositions of properly "weighted" geometric and arithmetic means*. The hybridization is well exemplified in models VII–XIII (see Sections 3 and 4 and 8–12), reflecting a hierarchical pattern of spatial clustering, homing tendencies, and temporal variation.

2. Whereas under uniform (independent of habitat site) homing tendencies, allelic protection is enhanced with increased homing, this conclusion is not generally applicable in the presence of nonhomogeneous homing rates. The homing tendency in the latter case acts as an interdemic selection factor interacting with local selection.

3. With a hierarchical population structure as reflected by a Kro-

necker product of migration matrices (model XI), i.e., where the population deme classifications are based on independent criteria, the condition for protection reduces precisely to the geometric mean of the protection endowment contributed from each tier. In contrast, if the deme definitions depend on correlated characteristics, the balances implying protection are more recondite and do not factor. Each case can be worked out explicitly. The special nature of the migration structure has to be accounted for under these conditions.

4. The conditions for protection for many of the examples reflect a hierarchical structure [e.g., see (9.11) and (10.10) and also (12.3a) and (12.3b)]. Thus, the first condition of (12.3a) is fulfilled if protection of the A-allele is overwhelming in at least one of the demes. When this is not the case, then protection can still be achieved by virtue of its "aggregate" selection advantage conveyed by a cluster of demes. A further basis for protection may arise from interactions over several deme clusters. This is essentially the significance of the inequality (12.3b). The potential for A-protection induced by a subgroup of clusters is embodied in the inequality of (12.4).

5. The analyses of the multicluster migration patterns (models VII–XIV) establish that increased clustering generally enhances the opportunities for a protected polymorphism. This concept requires cautious interpretation as clustering can abrogate heterogeneity effects when nonuniformly applied.

6. We considered the question of comparing the chance of protection for a multideme population under a cyclically (seasonally) varying selection regime where migration occurs once each season as against migration occurring once each generation encompassing a full round of seasons. The results and discussion in Section 11 with proper standardizations suggest that migration every season is advantageous in maintaining polymorphism if each migration phase does not entail excessive redistribution of the population. Technically, this requires the migration matrix be equivalent to a positive definite matrix as is the case with the Deakin form (model II), but not necessarily for the distinguished deme migration pattern (model VI).

7. We posed in Section 14 the problem of determining the "optimal" arrangement of deme sizes $\{c_i\}$ relative to a prescribed distribution of the spatial fitness values, homing rates, and other migration parameters, that would maximize the opportunities to obtain a protected allele. For simple Levene population subdivision we found that the deme sizes and relevant selection values should be *similarly ordered.* The relationship is more subtle for other migration patterns (see Section 14 for other results and further discussion).

8. To what extent is the degree and extent of protection maintained with changes in population subdivision? More specifically, in Section 16 we ask: (a) Does protection of an allele persist in the two separate parts of a previously single population having allele A protected? Is protection of allele A maintained for a combined population composed from two isolated populations where the allele in question was previously protected in each of the two source populations? (b) It is of interest to ascertain the similarities and contrasts in the equilibrium gene frequency patterns that accrue from an enlarged neutral zone where in other respects the selection–migration structure is unchanged.

We highlight the statement of Theorem 16.2, which establishes that the existence of a protected polymorphism is maintained with the introduction of a new neutral deme into the population range receiving the same amount of migration contributions from the subpopulations on its right and left. Moreover, we found that a sufficient accretion of neutral demes can ensure protection of an allele where previously no protection existed. Effectively, addition of neutral demes to the population range operates to diminish gene flow among the demes and thereby (in line with Theorem 5.2) enhances the opportunities for protection.

9. There is a tendency to assess environmental heterogeneity by a single index. Common proposals include the variance and/or range of selection values (or of an associated ecological parameter), or some cumulative deviation measure of (absolute or relative) selection values, information (entropy) content for a selection gradient, or other indices usually correlated with those above. A real-valued index for measuring heterogeneity compels essentially a single scaling over all environments. Intrinsically, an environment is complex and cannot be summarized in a single value. Surely it is evident that not all environments are comparable.

A number of approaches are set forth that partially order the degree and nature of heterogeneity with respect to two multideme selection structures for a given migration pattern (Section 6). In this perspective, the following general principle has broad validity.

PRINCIPLE 6.1. *Let M be a backward migration matrix. Let $\mathscr{E}$ and $\mathscr{E}'$ be two environmental selection gradients such that $\mathscr{E}'$ is less heterogeneous than $\mathscr{E}$ with respect to the migration structure M in the sense of Definition 6.2. Then the existence of a protected polymorphism is more likely in the more heterogeneous environment $\mathscr{E}$ over that of $\mathscr{E}'$.*

Comparison of the models of hard and soft selection in terms of the existence of a protected polymorphism reduces to an important case of

Principle 6.1. More explicitly, *the environment of soft selection* $\mathscr{E}^{(\mathrm{S})}$ *is more heterogeneous than the environment of hard selection* $\mathscr{E}^{(\mathrm{H})}$ *in the sense of Definition 6.2* (see Section 6 and also Karlin and Campbell, 1981).

The validity of Principle 6.1 is established in a number of examples including the stepping-stone migration pattern for a monotone selection gradient, the Deakin migration form with a general selection pattern, the major and subordinate deme migration model, and other cases. However, Principle 6.1 is not correct in complete generality, but its validity appears to have wide scope.

In line with Principle 6.1, Theorem 6.1 asserts that the "more homogeneous" *geometric mean environment,* independent of the migration structure, engenders less polymorphic realizations as compared with its component selection regimes. This theorem does not, in general, extend to other averaged environments [example (6.23)].

10. Various ways of distinguishing "more" from "less" migration for a multideme population are introduced in Section 5. We established in this section quite generally that less (but nonzero) migration increases the chance of a protected polymorphism.

In the case of *very small migration flow* the degree of environmental heterogeneity coupled to the initial frequency state plays a decisive role in the evolutionary development of the population. With selection forces favoring different genotypes in different demes, one or another of the alleles predominate in each deme. The average level of heterozygosity is low but the level of polymorphism is large. The emerging gene frequency arrays are considerably heterogeneous. The exclusive contingency of avoiding polymorphism for any sets of initial conditions is that a single allele has selective advantage throughout the population range (cf. Karlin and McGregor, 1972*a,b*).

With a homogeneous selection gradient involving local heterozygote advantage, a relatively homogeneous polymorphic frequency state is achieved expressing a high average heterozygosity.

A mixture of underdominance, directional and overdominant spatially varying selection expression can produce a wide variety of stable polymorphic and/or fixation states and the actual equilibrium established depends sensitively on the initial frequency conditions.

For *small to moderate mobility rates,* result (5.2) tells us that the strength of a protected polymorphism increases with the extent of isolation of demes. It is important to caution that this result applies in general form only if the outward dispersal rate is diminished uniformly independent of the deme sites. A diminished migration rate at a particular deme while the other migration rates remain constant can engender the opposite effect, making fixation more likely.

Increasing strength of protection means that the fixation states are more repellant and that each allelic frequency is represented at a substantial frequency in at least one deme. There appears to be no relationship between the strength of a protected polymorphism and the form of the polymorphic equilibrium. We expect considerable heterogeneity in gene frequency with low migration rates. For moderate migration, more monomorphic outcomes are realized unless substantial heterozygote advantage is operating in each deme.

Under *moderate to uniform mixing migration rates,* the selection effect contribution of the demes substantially blend. The outcomes now depend in a complex manner on all parameters of the model, producing both fixation and polymorphic possibilities with fixation occurrences usually more frequent unless other forces are involved.

For *strongly oscillating migration patterns,* protection is again more likely than with uniform mixing. There appears to be a threshold level of medium migration flow such that the maintenance of a stable polymorphism is minimal at that rate of migration.

11. With population subdivision and moderate migration flow, a sufficient condition for the existence of, say, protection of the *A*-allele is

$$\sum_{i=1}^{N} \xi_i d_i \geq 1 \tag{17.1}$$

where $\{d_i\}_{i=1}^{N}$ related to the spatial array of selection values and the components of $(\xi_1, \xi_2, \ldots, \xi_N)$ reflect the influence of migration and varying deme sizes [see (1.18) and (1.19)]. We have ascertained in Appendix D the $\boldsymbol{\xi}$ vector for all the migration schemes of Sections 2–4.

For a cyclically (seasonally) varying set of selection effects $\{d_i\}_1^N$ of period length N, a sufficient condition for protection is

$$\prod_{i=1}^{N} (d_i)^{\xi_i} > 1 \tag{17.2}$$

The generalized arithmetic-geometric mean inequality $\sum_{i=1}^{N} \xi_i d_i > \prod_{i=1}^{N} d_i^{\xi_i}$ shows that protection of the *A*-allele is more easily maintained with spatial as compared to temporal variation in selection coefficients. This suggests that spatial rather than temporal heterogeneity of the environments is a more powerful force for producing and maintaining polymorphism. For temporal heterogeneity the determining factor is a generalized geometric mean of fitness values, while in spatial heterogeneity a generalized arithmetic mean of fitness values is critical. It should be emphasized that we are comparing the same average levels of selection in the two cases.

The contrast is more manifest with small cumulative selection effects ($\sum_{i=1}^{N} | d_i - 1 |$ small). Then (17.1) is essentially equivalent to

$$\sigma^2 > \bar{d} \text{ with } \sigma^2 = \sum_{i=1}^{N} \xi_i(d_i - \bar{d})^2 \quad \text{and} \quad \bar{d} = \sum_{i=1}^{N} d_i\xi_i$$

while (17.2) reduces to $\sigma^2/2 > \bar{d}$. Thus, with temporally fluctuating selection intensities the above inequality (by a factor $\frac{1}{2}$) brings less likelihood of protection.

12. Various authors have emphasized that "average heterozygosity seems to increase with increasing environmental variability." Most *averages* are usually computed by weighting population parameters equally over space and/or time. We have determined that it is unnatural when constructing the average to improperly scale the effects of deme sizes, differences in local migration rates, and the spectrum of selection influences.

The relative deme sizes are often used to define the global heterozygosity index $\sum_{i=1}^{N} c_i x_i(1 - x_i)$ where $\{c_i\}$ specify the relative deme size and x_i is the equilibrium frequency of the A allele in the ith deme. The left eigenvector of the Deakin backward migration matrix is $\mathbf{c}$, i.e., $\mathbf{c}M = \mathbf{c}$. Hence, employing the left eigenvector of the backward migration matrix to weight the local heterozygosity may provide a more natural way to extend the global heterozygosity index. The left eigenvector occurs intrinsically in the analysis of multideme population genetic models, and can be interpreted as the arrangement of local deme sizes under the influence of a continuing process of migration with due account of population structures. In the stepping-stone model the relevant left eigenvector displays components related to the geometrical mean of the local population sizes before and after migration. In the case of dominant alleles, the principal left eigenvector rather than the local deme sizes is the weighting that extends results for the Deakin migration structure (where the two coincide) to more general migration patterns (Karlin, 1977*b*).

13. The analysis we have presented should be extended to encompass more alleles, more loci, more habitats, more general migration patterns, and more general selection schemes. It is essential to attempt a more complete classification of the formal structures while seeking to elucidate functional relations between parameter specifications of the pertinent biological, environmental factors and the realized allele frequency patterns.

APPENDIX A. KRONECKER PRODUCTS OF MATRICES

We record for ready reference several facts concerning Kronecker products of matrices. A detailed development of this topic can be found in many linear algebra texts.

Definition A.1. (Kronecker product of matrices). Let A be an $m \times n$ real matrix and B of order $l \times k$. The Kronecker product of A and B, written $A \otimes B$, is constructed explicitly as the partitioned matrix of size $ml \times nk$ of the form

$$A \otimes B = \begin{Vmatrix} a_{11}B & a_{12}B & \cdots & a_{1n}B \\ a_{21}B & a_{22}B & \cdots & a_{2n}B \\ \vdots & \vdots & & \vdots \\ a_{m1}B & a_{m2}B & \cdots & a_{mn}B \end{Vmatrix} \qquad (A.1)$$

The operation $A \otimes B$ obeys the distributive and associative laws and commutes with scalar multiplication. More specifically, we have

$$(A + B) \otimes C = A \otimes C + B \otimes C, \qquad A \otimes (B + C) = A \otimes B + A \otimes C,$$
$$(A \otimes B) \otimes C = A \otimes (B \otimes C), \qquad (\gamma A) \otimes B = A \otimes (\gamma B) = \gamma(A \otimes B)$$

for any real γ.

The next concept is a specialization of Definition A.1.

Definition A.2. (The Kronecker product of two vectors $\mathbf{a}$ and $\mathbf{b}$). Let $\mathbf{a} = (a_1, a_2, \ldots, a_m)$ and $\mathbf{b} = (b_1, b_2, \ldots, b_n)$ be real vectors of m and n components, respectively. The Kronecker product of $\mathbf{a}$ and $\mathbf{b}$ (written $a \otimes b$) is the Kronecker product of the $1 \times n$ and $1 \times m$ matrices induced by the vectors $\mathbf{a}$ and $\mathbf{b}$, respectively. In component form, we have

$$a \otimes b = (a_1b_1, a_1b_2, \ldots, a_1b_n, a_2b_1, \ldots, a_2b_n, \ldots, a_mb_1, a_mb_2, \ldots, a_mb_n) \qquad (A.2)$$

Let ϕ be a polynomial in two variables ξ and η with real coefficients

$$\phi(\xi, \eta) = \sum_{i,j=0}^{p} c_{ij}\xi^i\eta^j$$

The following theorem details the relationship between the eigenvalues of A, B, and

$$\phi(A, B) = \sum_{i,j=0}^{p} c_{ij} A^i \otimes B^j \tag{A.3}$$

THEOREM A.1. *If* $\lambda_1, \lambda_2, \ldots, \lambda_m$ *are the eigenvalues of the* $m \times m$ *matrix* A *and* $\mu_1, \mu_2, \ldots, \mu_n$ *the eigenvalues of the* $n \times n$ *matrix* B*, then the eigenvalues of the matrix* $\phi(A, B)$ *defined in (A.3) consist of the mn numbers* $\phi(\lambda_r, \mu_s)$, $r = 1, 2, \ldots, m$; $s = 1, 2, \ldots, n$.

COROLLARY A.1.

(i) *The eigenvalues of* $A \otimes B$ *are the mn numbers* $\lambda_r\mu_s$, $r = 1, 2, \ldots, m$; $s = 1, 2, \ldots, n$.

(ii) *Moreover, if* $A\mathbf{a} = \lambda\mathbf{a}$ *and* $B\mathbf{b} = \mu\mathbf{b}$*, then the relation*

$$A \otimes B(\mathbf{a} \otimes \mathbf{b}) = \lambda\mu(\mathbf{a} \otimes \mathbf{b}) \text{ holds} \tag{A.4}$$

The fact highlighted next serves decisively for a variety of applications.

Let A and C be $m \times m$ real matrices, B and D each of size $n \times n$. The identity

$$(A \otimes B)(C \otimes D) = AC \otimes BD \tag{A.5}$$

is valid.

In particular, let A be an $m \times m$ matrix, B an $n \times n$ matrix, $\mathbf{a}$ and $\mathbf{a}'$ m-vectors, $\mathbf{b}$ and $\mathbf{b}'$ n-vectors. Then

$$(A \otimes B) \cdot (\mathbf{a} \otimes \mathbf{b}) = A\mathbf{a} \otimes B\mathbf{b}$$

$$(\mathbf{a} \otimes \mathbf{b}, \mathbf{a}' \otimes \mathbf{b}') = (\mathbf{a}, \mathbf{a}')\,(\mathbf{b}, \mathbf{b}')$$

where $(\mathbf{x}, \mathbf{y})$ denotes the scalar product of the two vectors $\mathbf{x}$ and $\mathbf{y}$.

APPENDIX B. SOME BACKGROUND INFORMATION ON NONNEGATIVE MATRICES*

Let C be an $n \times n$ nonnegative matrix (i.e., all elements are nonnegative). C is said to be irreducible if some power C^k exhibits only positive entries. Henceforth, unless stated otherwise, we assume that C is *nonnegative and irreducible*.

a. The spectral radius $\rho(C)$ is a positive simple eigenvalue of C. There exist unique (up to a scalar multiple) right and left corresponding positive eigenvectors

$$\mathbf{u} = (u_1, u_2, \ldots, u_n) \quad \text{and} \quad \mathbf{v} = (v_1, v_2, \ldots, v_n), \qquad u_i > 0,$$
$$v_i > 0 \text{ for all } i \tag{B.1}$$

satisfying

$$C\mathbf{u} = \rho(C)\mathbf{u}, \qquad \mathbf{v}C = \rho(C)\mathbf{v} \tag{B.2}$$

Where $C = M$ is a migration matrix, then of course $\rho(M) = 1$ and $\mathbf{u} = (1, 1, \ldots, 1)$. If $C = \| c_{ij} \|$ is a doubly stochastic matrix, i.e., $c_{ij} \geq 0$, $\sum_{j=1}^{n} c_{ij} = \sum_{i=1}^{n} c_{ij} = 1$, $i, j = 1, \ldots, n$, then $\mathbf{v} = \mathbf{u} = (1, 1, \ldots, 1)$.

b. The following characterizations of the spectral radius for nonnegative matrices will serve in a multitude of ways.

Let C be a nonnegative matrix. Then

$$\rho(C) = \sup_{\mu \in \Delta} \mu$$

$$\text{where } \Delta = \{\mu \mid \mu \text{ real and } A\mathbf{x} \geq \mu\mathbf{x} \text{ for some } \mathbf{x} \geq 0,\ \mathbf{x} \neq 0\} \tag{B.3}$$

(The notation $\mathbf{z} \geq \mathbf{w}$ signifies that $\mathbf{z} - \mathbf{w}$ is a nonnegative vector.)

$$\text{If there exists } \mathbf{y} \gg 0 \text{ (strictly positive) satisfying } C\mathbf{y} \leq \gamma\mathbf{y}, \quad \gamma > 0, \text{ then } \rho(C) \leq \gamma \tag{B.4}$$

An elementary deduction from (B.3) establishes that for two nonnegative matrices, B dominating componentwise A,

$$A \leq B \tag{B.5a}$$

then

$$\rho(A) \leq \rho(B) \tag{B.5b}$$

Another useful consequence of the characterization (B.3) is the fact

$$\rho(C) > \rho(C_{(k)}) \tag{B.6}$$

---

* For details see Chapter 17 of Gantmacher (1959).

where C is irreducible nonnegative and $C_{(k)}$ is the contraction of the matrix C to a kth-order principal submatrix.

Another useful criterion ensuring $\rho(C) \geq 1$ is the inequality

$$\det[I_k - C_{(k)}] \leq 0 \tag{B.7}$$

Indeed, the characteristic polynomial $I(\lambda) = \det[\lambda I_k - C_{(k)}]$ is plainly positive for $\lambda \to \infty$ and the hypothesis (B.7) implies that $I(\lambda)$ vanishes for some $\lambda \geq 1$. By the Frobenius theorem, $\rho(C_{(k)})$ is the largest positive root of $I(\lambda)$ and therefore $\rho(C) > \rho(C_{(k)}) \geq 1$.

c. A matrix C is called (strictly) totally positive if every minor of C is (positive) nonnegative. The matrix C is said to be oscillatory totally positive if A is totally positive and some power A^k is strictly totally positive. A matrix C is said to be (strictly) totally positive of order r (abbreviated TP_r) if every minor of order $\leq r$ is (positive) nonnegative.

d. A real matrix C is called positive definite if C is symmetric and

$$(C\mathbf{z}, \mathbf{z}) = \sum_{i,j=1}^{n} c_{ij} z_i z_j > 0$$

with equality only if $\mathbf{z} = \mathbf{0}$.

e. A symmetric (positive definite) matrix admits only real (positive) eigenvalues. The sets of eigenvalues of two successive principal submatrices *interlace*.

APPENDIX C. SOME COMPARISONS OF PRINCIPAL EIGENVALUES FOR VARIOUS CLASSES OF MATRICES

The main task of this and the following appendices is to elaborate the mathematical apparatus needed to validate most of the results reported in Sections 5–16. It will ease the exposition to divide the analysis into four subsections.

I. We concentrate on a nonnegative irreducible matrix of the form

$$\| p_{ij} \|_{i,j=1}^{n} = P = E + R \qquad \text{with } E = \operatorname{diag}(e_1, \ldots, e_n), \quad e_i > 0 \tag{C.1}$$

(it suffices to have $e_i + r_{ii} > 0$), and

$$R = \| u_i v_j \|_{i,j=1}^{n}, \qquad u_i v_j \geq 0 \text{ for all } i \text{ and } j$$

The above class of matrices underlie the homing migration patterns of Section 2, part III, and the multicluster models of Section 3, part VII.

It is convenient to introduce the compact notation $\mathbf{u} = (u_1, u_2, \ldots, u_n)$ and $\mathbf{v} = (v_1, v_2, \ldots, v_n)$. The symbol $\langle \mathbf{z}, \mathbf{w} \rangle = \sum_{i=1}^{n} z_i w_i$ stands for the inner product of the indicated vectors.

Our analysis seeks to ascertain exact conditions assuring $\rho(P) > 1$ (that is, that the spectral radius of P exceeds 1). To this end, a formula for C^{-1} where

$$C = K + R \qquad \text{(provided } K^{-1} \text{ exists) and } R \text{ is of rank 1} \tag{C.2a}$$

is needed and familiar. In fact, C^{-1} exists if and only if

$$\gamma = 1 + \langle \mathbf{v} K^{-1}, \mathbf{u} \rangle \neq 0 \tag{C.2b}$$

and then

$$C^{-1} = K^{-1} - \frac{1}{\gamma} S, \qquad \text{where } S \text{ is of rank 1 of the form } \| s_i r_j \|_1^n \tag{C.2c}$$

having $\mathbf{r} = \mathbf{v} K^{-1}$ and $\mathbf{s} = K^{-1}\mathbf{u}$.

With the information (C.2) at hand, it is suggestive to write $P - \lambda I = (E - \lambda I) + R = K(\lambda) + R$.

We examine two cases: We assume to ease the argument that $u_i v_j > 0$ and avoid technical details of no real import.

Case (i). Suppose $e_{i_0} \geq 1$ (or suppose $e_{i_0} + u_{i_0} v_{i_0} > 1$) for some i_0. Let $\mathbf{z}^{(i_0)} = (0, \ldots, 0, 1, 0, \ldots, 0)$ where the 1 appears only at the i_0th component. Because P is a nonnegative irreducible matrix, the condition $e_{i_0} \geq 1$ manifestly entails $P\mathbf{z}^{(i_0)} \geq \mathbf{z}^{(i_0)}$ precluding equality. An account of this inequality and a classical characterization of the spectral radius for nonnegative matrices ensure $\rho(P) > 1$ (Appendix B, point b).

Case (ii). Suppose $e_i < 1$ for all i. In order to determine $\rho(P)$ we consider $P{-}\lambda I$. In this circumstance with each $\lambda \geq 1$ manifestly $(E - \lambda I)^{-1}$ exists. By the prescription of (C.2), $(P - \lambda I)^{-1}$ exists if

$$\gamma(\lambda) = 1 + \langle \mathbf{v}, (E - \lambda I)^{-1} \mathbf{u} \rangle \neq 0 \tag{C.3a}$$

That is, provided

$$\gamma(\lambda) = 1 + \sum_{i=1}^{n} \frac{v_i u_i}{e_i - \lambda} \neq 0 \tag{C.3b}$$

Obviously $\gamma(\infty) = 1$ and as $e_i < 1 \le \lambda$ for all i we find that $\gamma(\lambda)$ is monotone increasing and vanishes somewhere on the range $1 < \lambda < \infty$ if and only if $\gamma(1) < 0$ and then $\rho(P) > 1$ as the spectral radius is the largest positive eigenvalue of P (Appendix B). To sum up, if $e_i < 1$ for all i, then $\rho(P) > 1$ if and only if

$$\sum_{i=1}^{n} \frac{v_i u_i}{1 - e_i} > 1 \tag{C.4}$$

II. We extend the above analysis to the estimation of $\rho(P)$ where P now has the form

$$P = E + A + R$$

where

$$E = \operatorname{diag}(e_1, \ldots, e_n), \qquad e_i + a_i b_i > 0$$
$$A = \| a_i b_j \|_1^n, \qquad R = \| u_i v_j \|_1^n \tag{C.5}$$

and satisfying

$$a_i b_j \ge 0 \quad \text{and} \quad u_i v_j \ge 0 \text{ for all } i \text{ and } j \tag{C.6}$$

We distinguish two cases:

If $e_i \ge 1$ for some i or $e_i < 1$ for all i and $\sum_{i=1}^{n} [a_i b_i/(1 - e_i)] > 1$, then

$$\rho(P) \ge \rho(E + A) > 1 \tag{C.7}$$

the first inequality due to the ordering $P \ge E + A$ and the last inequality ensues from the result of subsection I.

Case (iii). $e_i < 1$ for all i and $\sum_{i=1}^{n} [a_i b_i/(1 - e_i)] < 1$. The latter condition assures that $C(\lambda) = E + A - \lambda I$ is invertible for all $\lambda > 1$. To check whether $P(\lambda) = P - \lambda I$ is nonsingular, we apply the criterion of (C.2). As the spectral radius of the positive matrix $E + A$ is at most 1, it follows for $\lambda > 1$ that $[\lambda I - (E + A)]^{-1}$ is also a positive matrix, that is, $-C(\lambda)^{-1}$ is a positive matrix. Actually,

$$C(\lambda)^{-1} = \operatorname{diag}\left[\frac{1}{e_1 - \lambda}, \ldots, \frac{1}{e_n - \lambda}\right] - \frac{1}{\gamma}\left\| \left(\frac{a_i}{e_i - \lambda}\right)\left(\frac{b_j}{e_j - \lambda}\right) \right\| \text{ where } \gamma = 1 + \sum_{i=1}^{n} \frac{a_i b_i}{e_i - \lambda}$$

by (C.2). From the analysis of (C.2) we find, when $\lambda > 1$, that

$$P(\lambda) \text{ is invertible if and only if } \delta(\lambda) = 1 + \langle \mathbf{v}, C(\lambda)^{-1}\mathbf{u} \rangle \ne 0 \tag{C.8}$$

Observe that $[-C(\lambda)^{-1}]$ is strictly decreasing (i.e., componentwise) as λ traverses 1 to ∞. Therefore $\delta(\lambda)$ vanishes for some λ on the range $1 < \lambda < \infty$ if and only if $\langle \mathbf{v}, (I - E - A)^{-1}\mathbf{u} \rangle > 1$.

To sum up: let P have the form (C.5) subject to (C.6). *Then* $\rho(P) > 1$ *if and only if either* (i) $e_i \ge 1$ *for some i; or* (ii) $e_i < 1$ *for all i and* $\sum_{i=1}^{n} [a_i b_i/(1 - e_i)] > 1$; *or* (iii) $e_i < 1$ *for all i*, $\sum_{i=1}^{n} [a_i b_i/(1 - e_i)] \le 1$; *and*

$$\langle \mathbf{v}, (I - E - A)^{-1}\mathbf{u} \rangle > 1 \tag{C.9}$$

In line with (C.2) we have $(I - E - A)^{-1} = (I - E)^{-1} - \gamma^{-1}\tilde{A}$ where $\tilde{A} = \| \tilde{a}_i \tilde{b}_j \|$ having $\tilde{\mathbf{a}} = (\tilde{a}_1, \ldots, \tilde{a}_n)$, $\tilde{\mathbf{b}} = (\tilde{b}_1, \ldots, \tilde{b}_n)$, $\tilde{a}_i = (1 - e_i)^{-1}a_i$, $\tilde{b}_i = (1 - e_i)^{-1}b_i$, $\gamma = 1 + \sum_{i=1}^{n} (1 - e_i)^{-1}a_i b_i$.

In terms of the components, the condition (C.9) can be expressed explicitly as

$$\sum_{i=1}^{n} \frac{u_i v_i}{1 - e_i} - \frac{1}{\gamma}\left(\sum_{i=1}^{n} \frac{u_i a_i}{1 - e_i}\right)\left(\sum_{j=1}^{n} \frac{b_j v_j}{1 - e_j}\right) > 1$$

III. The result of subsection II can be generalized to the following general setup. Let

$$P = E + C^{(1)} + C^{(2)} + \cdots + C^{(r)} \tag{C.10}$$

where $E = \operatorname{diag}(e_1, e_2, \ldots, e_n)$, $e_i > 0$, and

$$C^{(k)} = \| a_i^{(k)} b_j^{(k)} \|_{i,j=1}^n, \qquad a_i^{(k)} b_j^{(k)} \ge 0 \text{ for all } i, j, k \tag{C.11}$$

Adapting straightforwardly the analysis of subsection II we find:

RESULT C.1. *Let P have the form (C.10) satisfying (C.11). Then* $\rho(P) > 1$ *if and only if one of the following conditions hold:*

(i) *either* $e_i \ge 1$ *for some i*

or

(ii) $e_i < 1$ *for all i, and for some l*, $1 \le l \le r - 1$,

$$\langle \mathbf{a}^{(k)}, (I - E - C^{(1)} - \cdots - C^{(k-1)})^{-1}\mathbf{b}^{(k)} \rangle \le 1, \; k = 1, \ldots, l$$

while

$$\langle \mathbf{a}^{(l+1)}, (I - E - C^{(1)} - \cdots - C^{(l)})^{-1}\mathbf{b}^{(l+1)}\rangle > 1 \qquad \text{(C.12)}$$

IV. We next extend the methods of subsections I–III to handle matrices that consist of blocks on the diagonal each of the structure (C.10) and involving off the diagonal general rank-one matrices. To this end, consider a matrix composed of p^2 blocks

$$X = \left\| \begin{matrix} A_1 & 0 & \cdots & 0 \\ 0 & A_2 & & 0 \\ & & \ddots & \\ 0 & 0 & \cdots & A_p \end{matrix} \right\| + \left\| \begin{matrix} 0 & 0 & \cdots & 0 & R_{1p} \\ R_{21} & 0 & & 0 & 0 \\ 0 & R_{32} & & & \\ \vdots & & \ddots & \vdots & \vdots \\ 0 & 0 & & R_{p,p-1} & 0 \end{matrix} \right\| \qquad \text{(C.13)}$$

where all the R's are rank-one matrices, viz.,

$$R_{k+1,k} = \| u_i^{(k+1)} v_j^{(k)} \|_{i=1,j=1}^{n_{k+1},n_k}, \qquad k = 1, 2, \ldots, p \text{ (interpret } p + 1 = 1)$$

and where each A_k is a nonsingular matrix of order n_k. We presently ascertain exact conditions assuring that X be invertible.

A little manipulation and ingenuity suggests to try an inverse for X of the form

$$Y = \left\| \begin{matrix} A^{-1} & 0 & \cdots & 0 \\ 0 & A_2^{-1} & \cdots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \cdots & A_p^{-1} \end{matrix} \right\| + \left\| \begin{matrix} a_{11}S_{11} & a_{12}S_{12} & \cdots & a_{1p}S_{1p} \\ a_{21}S_{21} & & & \\ \vdots & & & \vdots \\ a_{p1}S_{p1} & & \cdots & a_{pp}S_{pp} \end{matrix} \right\| \qquad \text{(C.14)}$$

where each $S_{\lambda,\mu}$ is an appropriate rank-one matrix and a_{ij} are constants to be determined. We display

$$S_{\lambda,\mu} = \| w_i^{(\lambda)} z_j^{(\mu)} \|_{i=1,j=1}^{n_\lambda,n_\mu}, \qquad \lambda, \mu = 1, \ldots, p \qquad \text{(C.15)}$$

Performing the multiplication XY and equating the outcome to the identity

matrix leads to the equations

$$\begin{gathered} 0 = \mathrm{a}_{k+1,l} \| (\mathrm{A}_{k+1}\mathbf{w}^{(k+1)})_i \mathrm{z}_j^{(l)} \| + \mathrm{a}_{kl} \| \mathrm{u}_i^{(k+1)} \mathrm{z}_j^{(l)} \| \langle \mathbf{v}^{(k)}, \mathbf{w}^{(k)} \rangle, \\ l = 1, 2, \ldots, k-1, k+1, \ldots, p, \qquad k = 1, \ldots, p \end{gathered} \qquad \text{(C.16)}$$

$$\begin{aligned} 0 = {} & \| u_i^{(k+1)} (\mathbf{v}^{(k)} A_k^{-1})_j \| + a_{k+1,k} \| (A_{k+1}\mathbf{w}^{(k+1)})_i z_j^{(k)} \| \\ & + a_{k,k} \langle \mathbf{v}^{(k)}, \mathbf{w}^{(k)} \rangle \| u_i^{(k+1)} z_j^{(k)} \|, \qquad k = 1, 2, \ldots, p \end{aligned} \qquad \text{(C.17)}$$

In order to be able to combine the matrices of each equation, we prescribe the vectors $\mathbf{w}^{(k)}$ and $\mathbf{z}^{(l)}$ by the formulas

$$\mathbf{w}^{(k)} = A_k^{-1}\mathbf{u}^{(k)}, \qquad k = 1, 2, \ldots, p \qquad \text{(C.18)}$$

and

$$\mathbf{z}^{(l)} = \mathbf{v}^{(l)} A_l^{-1} \qquad l = 1, 2, \ldots, p \qquad \text{(C.19)}$$

With the determinations of (C.18) and (C.19), the equations of (C.16) and (C.17) will hold provided the constants $a_{\lambda\mu}$ obey the relations

$$\begin{gathered} a_{k+1,l} = -a_{k,l} \langle \mathbf{v}^{(k)}, A_k^{-1}\mathbf{u}^{(k)} \rangle, \\ l = 1, 2, \ldots, k-1, k+1, \ldots, p, \qquad k = 1, 2, \ldots, p \end{gathered} \qquad \text{(C.20)}$$

and

$$1 + a_{k+1,k} + a_{kk} \langle \mathbf{v}^{(k)}, A_k^{-1}\mathbf{u}^{(k)} \rangle = 0, \qquad k = 1, 2, \ldots, p \qquad \text{(C.21)}$$

Solving successively from the appropriate equations of (C.20), namely,

$$\begin{aligned} a_{k,k} &= -a_{k-1,k} \langle \mathbf{v}^{(k-1)}, A_{k-1}^{-1}\mathbf{u}^{(k-1)} \rangle \\ a_{k-1,k} &= -a_{k-2,k} \langle \mathbf{v}^{(k-2)}, A_{k-2}^{-1}\mathbf{u}^{(k-2)} \rangle \\ &\vdots \\ a_{1,k} &= -a_{p,k} \langle \mathbf{v}^{(p)}, A_p^{-1}\mathbf{u}^{(p)} \rangle \\ a_{p,k} &= -a_{p-1,k} \langle \mathbf{v}^{(p-1)}, A_{p-1}^{-1}\mathbf{u}^{(p-1)} \rangle \\ &\vdots \\ a_{k+2,k} &= -a_{k+1,k} \langle \mathbf{v}^{(k+1)}, A_{k+1}^{-1}\mathbf{u}^{(k+1)} \rangle \end{aligned} \qquad \text{(C.22)}$$

produces

$$a_{k,k} = a_{k+1,k}(-1)^{p-1}\frac{\prod_{j=1}^{p}\langle \mathbf{v}^{(j)}, A_j^{-1}\mathbf{u}^{(j)}\rangle}{\langle \mathbf{v}^{k}, A_k^{-1}\mathbf{u}^{(k)}\rangle} \qquad (C.23)$$

Substituting (C.23) into (C.21) gives

$$0 = 1 + a_{k+1,k}\left[1 + (-1)^{p-1}\prod_{j=1}^{p}\langle \mathbf{v}^{(j)}, A_j^{-1}\mathbf{u}^{(j)}\rangle\right] \qquad (C.24)$$

Observe that if

$$1 + (-1)^{p-1}\prod_{j=1}^{p}\langle \mathbf{v}^{(j)}, A_j^{-1}\mathbf{u}^{(j)}\rangle \neq 0 \qquad (C.25)$$

then we can solve for $a_{k+1,k}$ from (C.24) and subsequently ascertain successively all the $a_{\lambda,k}$ ($\lambda \neq k + 1$) by virtue of (C.22). The converse is also correct, affirming that an inverse X^{-1} exists if and only if (C.25) holds and then $X^{-1} = Y$ as displayed in (C.14) coupled to the determinations (C.18) and (C.19) and the calculation of the constants $\{a_{\lambda,\mu}\}$.

Next specialize (C.13) as follows. Let

$$A_k = E_k = \operatorname{diag}(e_1^{(k)}, \ldots, e_{n_k}^{(k)}), \qquad k = 1, 2, \ldots, p \qquad (C.26)$$

and assume $u_i^{(k+1)}v_j^{(k)} \geq 0$ and $e_i^{(k)} > 0$ throughout. The preceding calculations, adapting the analysis of subsection I, lead to

RESULT C.2.

$$\left.\begin{array}{l}\rho(X) > 1 \text{ if and only if (i) either } e_i^{(k)} \geq 1 \text{ for}\\ \text{some } i \text{ and } k \text{ or (ii) } e_i^{(k)} < 1 \text{ for all } i \text{ and } k\\ \\ \text{and}\\ \\ (-1)^p \displaystyle\prod_{k=1}^{p}\sum_{i=1}^{n_k}\frac{v_i^{(k)}u_i^{(k)}}{e_i^{(k)} - 1} > 1 \text{ prevails}\end{array}\right\} \qquad (C.27)$$

The finding of (C.27) with obvious identifications of the components is precisely the assertion of (12.5).

A further extension allows

$$A_k = E_k + Q_k \qquad (C.28)$$

having E_k the same as in (C.26) and Q_k is a rank-one matrix

$$Q_k = \| f_i^{(k)}g_j^{(k)} \|_{i,j=1}^{n_k} \qquad (C.29a)$$

having

$$f_i^{(k)}g_j^{(k)} \geq 0 \text{ for all } i \text{ and } j \qquad (C.29b)$$

while the $R_{k+1,k}$ are as previously. The version of (C.27) in this situation becomes

RESULT C.3. *Let X be nonnegative irreducible of the form (C.13) with A_k as in (C.28) and Q_k fulfilling (C.29). Suppose $e_i^{(k)} > 0$ for all i and k. Then $\rho(X) > 1$ if and only if one of the following conditions holds:*

(i) *$e_i^{(k)} \geq 1$ for some k and i;*

(ii) *$e_i^{(k)} < 1$ for all i and k and*

$$\sum_{i=1}^{n_k}\frac{f_i^{(k)}g_i^{(k)}}{1 - e_i^{(k)}} > 1 \textit{ for some } k = 1, 2, \ldots, p \qquad (C.30)$$

(iii) *$e_i^{(k)} < 1$ for all i and k, the inequalities of (C.30) are reversed for all k, and*

$$(-1)^p\prod_{k=1}^{p}\langle \mathbf{v}^{(k)}, (A_k - I)^{-1}\mathbf{u}^{(k)}\rangle > 1 \qquad (C.31)$$

It is possible to generalize further permitting A_k to have the structure (C.10). We will write out elsewhere the corresponding constructions and formulas.

APPENDIX D. EXPLICIT DETERMINATIONS OF PRINCIPAL EIGENVECTORS

In comparing and interpreting the sufficient conditions (1.18) and (1.19) for protection, an explicit evaluation of the left eigenvector ξ of the backward migration matrix is required. This calculation is accessible in analytic terms for a wide variety of migration matrices. The following elementary lemma serves well in this regard.

LEMMA D.1. Consider an $n \times n$ migration matrix admitting the representation

$$M = \Gamma^{-1}SC \tag{D.1}$$

where $S = \| s_{ij} \|$ is a symmetric irreducible nonnegative matrix, $C = \operatorname{diag}(c_1, c_2, \ldots, c_n)$, and $\Gamma = \operatorname{diag}(\gamma_1, \gamma_2, \ldots, \gamma_n)$ with $\gamma_i = \sum_{j=1}^{n} s_{ij}c_j$, $i = 1, 2, \ldots, n$. (The factor Γ^{-1} ensures that M is a stochastic matrix.)

The unique (normalized satisfying $\sum \xi_i = 1$) left eigenvector $\boldsymbol{\xi}$ of M ($\boldsymbol{\xi}M = \boldsymbol{\xi}$) with eigenvalue 1 has components $\boldsymbol{\xi} = (c_1\gamma_1/K, c_2\gamma_2/K, \ldots, c_n\gamma_n/K)$ where $K = \sum_{i=1}^{n} c_i\gamma_i$ is a normalizing constant.

PROOF. Direct verification. We have $(\boldsymbol{\xi}M)_j = (1/K)\sum_{i=1}^{n} c_i\gamma_i m_{ij} = (1/K)\sum_{i=1}^{n} c_i s_{ij} c_j = \gamma_j c_j/K = \xi_j$.

Recall that if M is the backward migration matrix for the soft selection model, then the corresponding hard selection migration matrix has the form

$$M^* = \tilde{\Gamma}^{-1}M\tilde{D} \tag{D.2}$$

where $\tilde{D} = \operatorname{diag}(1/d_1, 1/d_2, \ldots, 1/d_n)$ $\{d_i$ the usual selection values and $\tilde{\Gamma} = \operatorname{diag}([M(1/\mathbf{d})]_1, [M(1/\mathbf{d})]_2, \ldots, [\mathrm{M}(1/\mathbf{d})]_n)$, $[M(1/\mathbf{d})]_i = \sum_{j=1}^{n} m_{ij}(1/d_j)\}$. ☐

Under the conditions of Lemma D.1, we also have:

LEMMA D.2. *Let M fulfill the hypotheses of (D.1) and prescribe the associated hard selection migration matrix to be (D.2). Then the normalized left eigenvector $\boldsymbol{\xi}^*$ for M^* of eigenvalue 1 is $\boldsymbol{\xi}^* = (1/K^*)(c_1\gamma_1^*/d_1, c_2\gamma_2^*/d_2, \ldots, c_n\gamma_n^*/d_n)$ where $\gamma_i^* = \sum_{j=1}^{n} [s_{ij}(c_j/d_j)]$, $i = 1, 2, \ldots, n$, and $K^* = \sum_{k=1}^{n} c_k\gamma_k^*/d_k$.*

We record next the left eigenvector of eigenvalue 1 for a migration matrix involving a uniform homing propensity. Accordingly, consider

$$(1 - \alpha)I + \alpha M \tag{D.3}$$

with M of the form (D.1). Obviously, the left eigenvector $\boldsymbol{\xi}$ is independent of α. On the other hand, for the hard selection version of (D.3), the migration matrix becomes

$$M^*(\alpha) = \Gamma(\alpha)^{-1}[(1 - \alpha)I + \alpha M]\tilde{D} \tag{D.4}$$

with $\Gamma(\alpha)$ a diagonal matrix having nonzero elements $(1 - \alpha)(1/d_i) + \alpha[M(1/\mathbf{d})]_i$ down the diagonal and $\tilde{D}$ the same as in (D.2). A slight manipulation converts (D.4) into

$$M^*(\alpha) = \Gamma(\alpha)^{-1}\Gamma^{-1}[(1 - \alpha)\Gamma C^{-1} + \alpha S]C\tilde{D} \tag{D.5}$$

exhibiting a symmetric matrix in brackets while the other factors are all diagonal matrices. The method of Lemma D.1 verifies that the left eigenvector of eigenvalue 1 is

$$\boldsymbol{\xi}^*(\alpha) = [\xi_i^*(\alpha)]_{i=1}^{n} \tag{D.6}$$

with the components displayed as the weighted combinations

$$\begin{aligned} \xi_i^*(\alpha) &= \left[(1 - \alpha)\frac{\gamma_i}{d_i} + \alpha\delta_i\right]\frac{c_i}{d_i} \text{ with } \gamma_i = \sum_{j=1}^{n} s_{ij}c_j, \\ \delta_i &= \sum_{j=1}^{n} s_{ij}\frac{c_j}{d_j}, \; i = 1, 2, \ldots, n \end{aligned} \tag{D.7}$$

Many concrete classical and relevant migration forms admit the representation (D.1). We display a number of these cases. (We revert back to N components consistent with the notation of Section 2.)

Levene model. The backward migration matrix possesses the representation

$$M = UC \tag{D.8}$$

where $U = \| e_{ij} \|_1^N$, $e_{ij} \equiv 1$, and $C = \operatorname{diag}(c_1, c_2, \ldots, c_N)$ of the structure (D.1) where $\{c_i\}$ correspond to the array of the deme population sizes. In accordance with Lemmas D.1 and D.2, the appropriate soft selection left eigenvector of (D.8) is $\boldsymbol{\xi} = \mathbf{c}$ and for the corresponding hard selection model $\boldsymbol{\xi}^* = (1/K^*)(c_1/d_1, c_2/d_2, \ldots, c_N/d_N)$ where K^* is the normalizing constant $\sum_{i=1}^{N} c_i/d_i$.

Deakin model. The backward migration matrix possesses the representation $M = [(1 - \alpha)C^{-1} + \alpha U]C$ with U and C defined as above and $(1 - \alpha)C^{-1} + \alpha U = S$ manifestly symmetric. The left eigenvector is again $\boldsymbol{\xi} = \mathbf{c}$.

For the hard selection version [see (1.15)]

$$M^* = \Gamma^{-1}[(1 - \alpha)C^{-1} + \alpha U]CD^{-1}, \qquad D = \operatorname{diag}\left(\frac{1}{d_1}, \ldots, \frac{1}{d_N}\right),$$

$$\Gamma = \operatorname{diag}(\gamma_1^*, \gamma_2^*, \ldots, \gamma_N^*) \quad \text{with} \tag{D.9}$$

$$\gamma_i^* = (1 - \alpha)\frac{1}{d_i} + \alpha \sum_{k=1}^{N} \frac{c_k}{d_k}, \qquad i = 1, 2, \ldots, N$$

It follows that the left principal eigenvector of M^* for eigenvalue 1 is

$$\boldsymbol{\xi}^* = (\xi_1^*, \xi_2^*, \ldots, \xi_N^*), \qquad \xi_i^* = \frac{c_i\gamma_i^*}{d_i}\frac{1}{K^*}, \qquad K^* = \sum_{k=1}^{N} \frac{c_k\gamma_k^*}{d_k} \tag{D.10}$$

A nonhomogeneous homing pattern. Consider the migration mode of part III, (2.4), (2.5), having forward migration matrix $\Gamma^{-1}(I - A + AUC)$ with $A = \operatorname{diag}(\alpha_1, \alpha_2, \ldots, \alpha_N)$, $0 \le \alpha_i \le 1$, and $C = \operatorname{diag}(c_1, c_2, \ldots, c_N)$ and $U = \| e_{ij} \|$ as before. This encompasses a natural extension of the Deakin model allowing homing rates to vary with deme sites.

The backward migration matrix calculated in accordance with (1.7) becomes

$$M = \bar{\Gamma}^{-1}[(I - A)CA^{-1} + CUC]A \qquad \text{where } \bar{\Gamma} = \operatorname{diag}(\bar{\gamma}_1, \ldots, \bar{\gamma}_N),$$

$$\bar{\gamma}_i = c_i\left[(1 - \alpha_i) + \sum_{k=1}^{N} c_k\alpha_k\right] = c_i\gamma_i, \; i = 1, 2, \ldots, N \tag{D.11}$$

Application of Lemma D.2 yields the left principal eigenvector $\boldsymbol{\xi}$ for M of components

$$\xi_i = \frac{c_i\alpha_i\gamma_i}{\sum_{k=1}^{N} c_k\alpha_k\gamma_k}, \qquad i = 1, 2, \ldots, N \tag{D.12}$$

For the associated hard selection backward migration M^* matrix, we obtain $\xi_i^* = c_i\alpha_i\gamma_i^*/d_iK^*$, $\gamma_i^* = [(1 - \alpha_i)(1/d_i) + \sum_{k=1}^{N} c_k\alpha_k/d_k]$, $i = 1, 2, \ldots, N$, and K^* is a normalizing constant.

General stepping-stone model. Consider the backward migration matrix M of the form (2.17). It is useful to display the factorization

$$M = \Pi^{-1}S \tag{D.13}$$

where S is a symmetric tridiagonal matrix and $\Pi = \operatorname{diag}(\pi_1, \pi_2, \ldots, \pi_N)$ a positive diagonal matrix. Specifically, $\pi_1 = 1$, $\pi_i = p_1p_2\cdots p_{i-1}/q_2\cdots q_i$, $i = 2, 3, \ldots, N$, and observe that

$$S = \left\| \begin{matrix} \pi_1r_1 & \pi_1p_1 & 0 & 0 & \cdots \\ \pi_2q_2 & \pi_2r_2 & \pi_2p_2 & 0 & \cdots \\ 0 & \pi_3q_3 & \pi_3r_3 & \pi_3p_3 & \cdots \\ \vdots & \vdots & \vdots & \vdots & \end{matrix} \right\| \tag{D.14}$$

is symmetric owing to the identities $\pi_ip_i = \pi_{i+1}q_{i+1}$, $i = 1, 2, \ldots, N - 1$.

Invoking Lemma D.1 we ascertain the required left eigenvector $\boldsymbol{\xi}$ of M (eigenvalue 1) to be

$$\boldsymbol{\xi} = \left(\frac{\pi_1}{K}, \frac{\pi_2}{K}, \ldots, \frac{\pi_N}{K}\right), \qquad K = \sum_{i=1}^{N} \pi_i \tag{D.15}$$

With the corresponding hard selection migration matrix, $M^* = \Gamma^{*-1}MD^{-1} = \Gamma^{*-1}\Pi^{-1}SD^{-1}$ and $\pi_i\gamma_i^* = \sum_{j=1}^{N} s_{ij}(1/d_j) = \pi_i[q_i(1/d_{i-1}) + r_i(1/d_i) + p_i(1/d_{i+1})]$, $i = 2, \ldots, N - 1$, $\pi_1\gamma_1^* = \pi_1[(r_1/d_1) + (p_1/d_2)]$, $\pi_N\gamma_N^* = \pi_N[(q_N/d_{N-1}) + (r_N/d_N)]$, $i = 2, \ldots, N - 1$, the pertinent left eigenvector $\boldsymbol{\xi}^*$ has components

$$\xi_i^* = \frac{\pi_i\gamma_i^*}{d_i}\left(\sum_{k=1}^{N} \frac{\pi_k\gamma_k^*}{d_k}\right)^{-1}, \qquad i = 1, 2, \ldots, N \tag{D.16}$$

We record some specializations of interest. Consider the standard homogeneous stepping-stone migration mode having forward migration matrix F of (2.14). When the relative deme sizes premigration is given by $(c_1, c_2, \ldots, c_N)$, the backward migration matrix is

$$M = \Gamma^{-1}FC, \qquad \Gamma = \operatorname{diag}(\gamma_1, \gamma_2, \ldots, \gamma_N) \tag{D.17}$$

involving the elements γ_i defined in (2.16).

The left eigenvector $\boldsymbol{\xi}$ for (D.17) is composed of the components $\xi_i = c_i\gamma_i/\sum c_k\gamma_k$.

For a circular homogeneous stepping-stone flow pattern, the forward migration matrix has the expression

$$\tilde{F} = \begin{Vmatrix} 1-2m & 0 & 0 & \dots & 0 & m \\ m & 1-2m & m & \dots & 0 & 0 \\ \vdots & & & & & \vdots \\ 0 & 0 & 0 & \dots & 1-2m & m \\ m & 0 & 0 & \dots & m & 1-2m \end{Vmatrix}$$

and then the backward migration matrix is $\tilde{M} = \tilde{\Gamma}^{-1}\tilde{F}C$, with the left eigenvector again

$$\tilde{\xi}_i = \frac{\tilde{\gamma}_i c_i}{\sum \tilde{\gamma}_k c_k}, \qquad i = 1, 2, \dots, N$$

where $\tilde{\gamma}_k = \gamma_k$, $k = 2, 3, \dots, N-1$, as before but

$\tilde{\gamma}_1 = (1-2m)c_1 + mc_2 + mc_N$ and

$$\tilde{\gamma}_N = mc_1 + mc_{N-1} + (1-2m)c_N$$

A nonhomogeneous circular (with "friction") migration model. We consider the unidirectional circular stepping-stone model with backward migration matrix of the form

$$M = \begin{Vmatrix} a_1 & b_1 & 0 & \dots & 0 & 0 \\ 0 & a_2 & b_2 & \dots & 0 & 0 \\ & & & & & \vdots \\ \vdots & & & & a_{N-1} & b_{N-1} \\ b_N & 0 & 0 & \dots & 0 & a_N \end{Vmatrix}, \qquad \begin{array}{l} a_i + b_i = 1, 0 < b_i < 1, \\ i = 1, 2, \dots, N \end{array} \tag{D.18}$$

Thus, migration is "continuous discrete flow" proceeding in a clockwise direction through the deme locations. Another connotation for (D.18) is in terms of seasonal temporal variation in selection intensities (cf. Section 2, part V).

Obviously, where $b_N > 0$ and $N > 2$, it is not possible to represent M in the form E_1SE_2 with S symmetric and E_1 and E_2 positive diagonal matrices. It is elementary to verify the left eigenvector of M as

$$\xi_i = \frac{1/b_i}{\sum_{k=1}^{N} 1/b_k}, \qquad i = 1, 2, \dots, N \tag{D.19}$$

Unidirectional migration countered by gene flow from a distinguished deme. The backward migration matrix has the form (2.22). The components of the left eigenvector $\boldsymbol{\xi}$ for the eigenvalue 1 satisfy the recursion relations $\xi_k = \xi_{k-1}[p_{k-1}/(1-r_k)]$, $k = 2, 3, \dots, N$.

Setting $P_1 = 1$, $P_k = \prod_{i=2}^{k} [p_{i-1}/(1-r_i)]$, $k = 2, 3, \dots, N$, we obtain

$$\xi_k = \frac{P_k}{\sum_{i=1}^{N} P_i}, \qquad k = 1, 2, \dots, N \tag{D.20}$$

The reverse dispersal pattern [see (2.23)] is reflected by the backward migration matrix

$$M = \begin{Vmatrix} a_1 & a_2 & a_3 & \dots & a_n \\ b_2 & c_2 & 0 & \dots & 0 \\ 0 & b_3 & c_3 & \dots & 0 \\ \vdots & & & & \\ 0 & 0 & 0 & b_N & c_N \end{Vmatrix} \tag{D.21}$$

with $a_i > 0$ for all i and $b_i > 0$, $i = 2, \dots, N$, $\sum_{i=1}^{N} a_i = 1$, $b_i + c_i = 1$, $i = 2, \dots, N$, possesses the normalized left eigenvector for eigenvalue 1,

$$\xi_1 = \frac{1}{K}, \qquad \xi_k = \frac{\left(1 - \sum_{i=1}^{k-1} a_i\right)}{b_k} \frac{1}{K}, \qquad k = 2, 3, \dots, N \tag{D.22}$$

where K is a normalizing constant ensuring that $\sum_{i=1}^{N} \xi_i = 1$.

The star migration form and extensions. The backward migration matrix M under consideration is displayed in (3.25). Our objective is to calculate the normalized left eigenvector $\boldsymbol{\xi}$ corresponding to eigenvalue 1. A little reflection suggests we try for $\boldsymbol{\xi}$ the form

$$\begin{aligned} \boldsymbol{\xi} &= (\xi_0, \underbrace{x_1, \dots, x_1}_{n}, \underbrace{x_2, \dots, x_2}_{n}, \dots, \underbrace{x_m, \dots, x_m}_{n}) \\ &= (\xi_0, \mathbf{x} \otimes \mathbf{e}) \end{aligned} \tag{D.23}$$

so that apart from the first the remaining components are determined as a Kronecker product of $\mathbf{x}$ (with m components) and $\mathbf{e} = (1, \dots, 1)$ (of n components). Expressing the conditions $\boldsymbol{\xi} = \boldsymbol{\xi}M$ for the prescription

(D.23) leads to the relations

$$\mathbf{x} - \mathbf{x}\hat{L} = \mathbf{w} \tag{D.24}$$

where $\hat{L}$ is explicitly given in (D.26) and the specific vector $\mathbf{w} = (w_1, w_2, \ldots, w_m)$ has coordinates

$$w_i = \xi_0 \frac{c_i b_{i0}}{\gamma_0}, \qquad i = 1, 2, \ldots, m \tag{D.25}$$

Because at least one of the a_i $(i > 0)$ in (3.25) is positive, we know that $\hat{L}$ is definitely substochastic and irreducible implying $\rho(\hat{L}) < 1$. Therefore, $(I - \hat{L})^{-1} = \sum_{k=0}^{\infty} \hat{L}^k$ transforms nonnegative nonzero vectors into positive vectors yielding, in particular,

$$\mathbf{x}^* = \mathbf{w}(I - \hat{L})^{-1} \tag{D.26}$$

With this $\mathbf{x}^*$ determined, we obtain $\boldsymbol{\xi}$ of (D.23) by setting $\xi_0 = 1$ and normalizing the sum of components to 1 yielding

$$\boldsymbol{\xi} = \frac{1}{K}(\xi_0, \mathbf{x}^* \otimes \mathbf{e}), \qquad K = 1 + n \sum_{i=1}^{m} x_i^* \tag{D.27}$$

The fact that $\boldsymbol{\xi}$ of (D.27) is the appropriate left eigenvector of M corresponding to eigenvalue 1 is corroborated as follows. The eigenvalue equations

$$\xi_i = (\boldsymbol{\xi} M)_i, \qquad i = 1, 2, \ldots, nm$$

hold by the nature of the computation (D.26) (subject to $\xi_0 = 1$). The remaining identity (for $i = 0$) automatically ensues, that is, the equation $1 = \xi_0 = (\boldsymbol{\xi} M)_0$, as we know that 1 is an eigenvalue of M since $I - M$ carries rank $nm - 1$.

Example. Consider the case where $\hat{L}$ is a tridiagonal matrix engendered by a stepping-stone migration pattern along each ray as

$$\hat{L} = \left\| \begin{matrix} r_1 & \lambda_1 & 0 & \ldots & 0 & 0 \\ \mu_2 & r_2 & \lambda_2 & \ldots & 0 & 0 \\ 0 & \mu_3 & r_3 & \ldots & 0 & 0 \\ \vdots & & & & & \vdots \\ & & & & & \lambda_{m-1} \\ 0 & 0 & 0 & \ldots & \mu_m & r_m \end{matrix} \right\| \tag{D.28}$$

where

$$\mu_i + r_i + \lambda_i = 1 \text{ for } i = 2, 3, \ldots, m - 1, \ \lambda_i, \mu_i > 0$$
$$\text{but } r_1 + \lambda_1 < 1, \ \mu_m + r_m = 1$$

Assume also $a_0 > 0$, $a_1 > 0$ but $a_i \equiv 0$ for $i \geq 2$ signifying that population exchange per generation occurs only between neighboring demes. It follows that the relevant vector $\mathbf{w}$ of (D.25) in the case at hand is of the form $\mathbf{w} = (w_1, 0, 0, \ldots, 0)$.

Let $\pi_1 = 1$, $\pi_j = \lambda_1\lambda_2\cdots\lambda_{j-1}/\mu_2\mu_3\cdots\mu_j$, $j = 2, 3, \ldots$, and $\boldsymbol{\pi} = (\pi_1, \pi_2, \ldots, \pi_m)$. It is easy to verify that $(\delta\boldsymbol{\pi})(I - \hat{L}) = \mathbf{w}$ where the constant δ is a constant determined to guarantee the equation

$$\delta[\pi_1(1 - r_1) + \pi_2\mu_2] = 1$$

Example. For a "homogeneous" Deakin mixing model we find that $\hat{L} = \Delta^* + R^*$ where $\Delta^* = \operatorname{diag}(\delta_1, \ldots, \delta_m)$, $R^* = \| u_i v_j \|_1^m$. Then $(I - \hat{L})^{-1} = (I - \Delta^*)^{-1} - (1/\gamma)S^*$ where S^* is of rank one, viz., $\| r_i^* s_j^* \|$ with $\mathbf{r}^* = \{v_1/(1 - \delta_1), \ v_2/(1 - \delta_2), \ldots, v_m/(1 - \delta_m)\}$, $\mathbf{s}^* = \{u_1/(1 - \delta_1), u_2/(1 - \delta_2), \ldots, u_m/(1 - \delta_m)\}$ and $\gamma = 1 + \sum_{i=1}^{m} [v_i u_i/(1 - \delta_i)]$ [see (C.2b)].

More particularly, with n demes distributed at each distance from the hub and m demes along each ray (excluding the central deme) entailing a uniform migration flow with a constant homing rate, $1 - \alpha$, we obtain the forward migration matrix

$$\alpha \left\| \begin{array}{c|c} \frac{1}{nm+1} & \frac{1}{nm+1} \quad \cdots \\ \hline \frac{1}{m+1} & \\ \frac{1}{m+1} & \frac{1}{m+1} U \otimes I_n \\ \vdots & \end{array} \right\| + (1 - \alpha)\mathrm{I} \tag{D.29}$$

Let $(c_0, c_1, \ldots, c_m)$ be the vector of relative deme sizes at the various distances from the center. The associated backward migration matrix assumes the form

$$M = \alpha\Gamma^{-1}\left\|\begin{array}{llll} \dfrac{m+1}{(nm+1)^2} & \dfrac{1}{nm+1} & \dfrac{1}{nm+1} & \cdots \\ \dfrac{1}{nm+1} & & & \\ \cline{2-4} \vdots & \multicolumn{3}{|l}{\dfrac{1}{m+1}\, U \otimes I_n} \end{array}\right\| + (1-\alpha)\,\mathrm{diag}\left(\frac{m+1}{nm+1}, 1, 1, \ldots\right)\bar{C}$$

$$\bar{C} = \mathrm{diag}(c_0, \overbrace{c_1, \ldots, c_1}^{n}, \overbrace{c_2, \ldots, c_2}^{n}, \ldots, \overbrace{c_m, \ldots, c_m}^{n})$$

and Γ is a normalizing diagonal matrix, $\Gamma = \mathrm{diag}(\gamma_0, \gamma_1, \ldots, \gamma_1, \ldots, \gamma_m, \ldots, \gamma_m)$, whose explicit components are

$$\gamma_0 = c_0\left[\frac{m+1}{(nm+1)^2}\alpha + (1-\alpha)\frac{m+1}{nm+1}\right] + \alpha\sum_{k=1}^{m}\frac{n}{nm+1}c_k$$

$$\gamma_i = \alpha\left[\frac{c_0}{nm+1} + \frac{1}{m+1}\sum_{k=1}^{m}c_k\right] + (1-\alpha)c_i, \qquad i > 0$$

Following the delineations of Lemma D.1 we ascertain the left eigenvector $\boldsymbol{\xi}$ of the corresponding backward migration matrix to be

$$K\boldsymbol{\xi} = (c_0\gamma_0, \overbrace{c_1\gamma_1, \ldots, c_1\gamma_1}^{n}, \overbrace{c_2\gamma_2, \ldots, c_2\gamma_2}^{n}, \ldots, \overbrace{c_m\gamma_m, \ldots, c_m\gamma_m}^{n})$$

and K is a normalizing constant.

Mixing multiuniform cluster structure. (i) It is instructive to deal first with the simpler cluster model corresponding to the backward migration matrix (3.5)–(3.7). Scrutiny of (3.10) reveals the form

$$M = H \otimes F + nR \otimes \frac{1}{n}U_n \tag{D.30}$$

with $F = I$ and $(1/n)U_n$ both doubly stochastic, the latter composed of all equal elements. It is easy to ascertain that a left eigenvector $\boldsymbol{\xi}$ of (D.30) for eigenvalue 1 admits the Kronecker product form $\boldsymbol{\xi} = (\hat{\mathbf{x}} \otimes \mathbf{e})$, $\mathbf{e} = (1, 1, \ldots, 1)$ with n components where $\hat{\mathbf{x}} = (\hat{x}_1, \hat{x}_2, \ldots, \hat{x}_m)$ satisfies $\hat{\mathbf{x}}(H + nR) = \hat{\mathbf{x}}$. But

$$\begin{aligned} H + nR &= [a + (n-1)\beta_1 - n\beta_2]\bar{C}C + n\beta_2\bar{C}U_mC \\ &= \bar{C}[(a + (n-1)\beta_1 - n\beta_2)I + n\beta_2U_m]C = \bar{C}SC \end{aligned}$$

exhibiting the representation of type (D.1). By Lemma D.1 we deduce that

$$\hat{x}_i = \frac{c_i\gamma_i}{\sum_{k=1}^{m}c_k\gamma_k}, \qquad i = 1, 2, \ldots, m \tag{D.31}$$

where

$$\gamma_i = ac_i + \beta_1c_i(n-1) + n\beta_2\sum_{\substack{j=1 \\ j\neq i}}^{m}c_j \qquad \text{as in (3.6)}$$

(ii) We generalize next to the more varied cluster migration structure of (3.18) by putting superscripts on a and β_1 and attain a backward migration matrix of the form $\hat{M} = \bar{C}[\mathrm{diag}(a^i - \beta_1^i)]C \otimes I_n + \bar{C}[\mathrm{diag}(\beta_1^i - \beta_2)]C \otimes U_n + \bar{C}\beta_2U_mC \otimes U_n$. If $\boldsymbol{\xi}$ is the left eigenvector for $C[(1/n)\,\mathrm{diag}(a^i - \beta_1^i) + \mathrm{diag}(\beta_1^i - \beta_2) + \beta_2U_m]C$, we deduce readily that $\boldsymbol{\xi} \otimes \mathbf{e}_n$ is the left eigenvalue of $\hat{M}$.

The left eigenvector of $\hat{M}$ where the component matrices are defined in (3.18), $\hat{C}LC \otimes I + \hat{C}(K + R)C \otimes U$, generalizing (D.30) becomes $\boldsymbol{\xi} = \mathbf{x}^* \otimes \mathbf{e}$ and now

$$x_i^* = \frac{c_i\gamma_i^*}{n\sum_{i=1}^{m}c_i\gamma_i^*}, \qquad i = 1, 2, \ldots, m \tag{D.32}$$

with

$$\gamma_i^* = (n-1)b_ic_i + a_ic_i + nu_i\textstyle\sum_{j=1;j\neq i}^{m}c_jv_j.$$

The cluster circulant model. The backward migration matrix has the form (4.5) where each $M^{(i)}$ is an $N \times N$ stochastic matrix. It is convenient to segment the left eigenvector $\boldsymbol{\xi}$ to the form

$$\begin{aligned}\boldsymbol{\xi} &= (\xi_1^{(1)}, \ldots, \xi_N^{(1)}, \xi_1^{(2)}, \ldots, \xi_N^{(2)}, \ldots, \xi_1^{(p)}, \ldots, \xi_N^{(p)}) \\ &= (\boldsymbol{\xi}^{(1)}, \boldsymbol{\xi}^{(2)}, \ldots \boldsymbol{\xi}^{(p)}) \qquad \text{(D.33)}\end{aligned}$$

where the component vectors satisfy

$$\boldsymbol{\xi}^{(1)}M^{(p)} = \boldsymbol{\xi}^{(p)}, \ \boldsymbol{\xi}^{(k+1)}M^{(k)} = \boldsymbol{\xi}^{(k)}, \qquad k = 1, 2, \ldots, p-1 \qquad \text{(D.34)}$$

which in totality are equivalent to $\boldsymbol{\xi}\tilde{M} = \boldsymbol{\xi}$. Combining the equations of (D.34) we get

$$\boldsymbol{\xi}^{(1)} = \boldsymbol{\xi}^{(1)}M^{(p)}M^{(p-1)} \cdots M^{(1)} \qquad \text{(D.35)}$$

so that $\boldsymbol{\xi}^{(1)}$ is a left eigenvector of the stochastic matrix $T = M^{(p)}M^{(p-1)} \cdots M^{(1)}$. Once $\boldsymbol{\xi}^{(1)}$ is ascertained obeying (D.35), the components $\boldsymbol{\xi}^{(2)}, \ldots, \boldsymbol{\xi}^{(p)}$ are computed recursively from the relations (D.34).

The global vector $\boldsymbol{\xi}$, for our purposes, is normalized such that the sum of its coordinates equals 1.

The evaluation of $\boldsymbol{\xi}^{(1)}$ from (D.35) is readily tractable when

$$M^{(k)} = (1 - \alpha_k)I + \alpha_k R_k, \qquad R_k = \| u_i^{(k)} v_j^{(k)} \|_{i,j=1}^N \qquad \text{(D.36)}$$

where because R_k is a stochastic matrix of rank one we have $u_i^{(k)} \equiv 1$, $\sum_{j=1}^N v_j^{(k)} = 1$. The product T expanded becomes

$$T = \prod_{k=1}^{p} M^{(p-k+1)} = \sum_{\boldsymbol{\epsilon}} \left[\prod_{k=1}^{p} \alpha_k^{\epsilon_k}(1 - \alpha_k)^{1-\epsilon_k} \right] R_p^{\epsilon_p} \cdots R_2^{\epsilon_2} R_1^{\epsilon_1} \qquad \text{(D.37)}$$

where $\boldsymbol{\epsilon} = (\epsilon_1, \epsilon_2, \ldots, \epsilon_p)$ traverse the 2^p collection of all p-tuples with $\epsilon_k = 0$ or 1 independently specified; the interpretation of the powers conforms to

$$R_k^{\epsilon_k} = \begin{cases} R_k & \epsilon_k = 1 \\ I & \epsilon_k = 0 \end{cases}$$

Note that for each $\boldsymbol{\epsilon}$ with $|\boldsymbol{\epsilon}| = \sum \epsilon_k > 0$, the rank-one matrix $R_p^{\epsilon_p} \cdots R_2^{\epsilon_2} R_1^{\epsilon_1} = R_{i_0}$ where $i_0 = \min\{i\colon \epsilon_i > 0\}$ and therefore (D.37) reduces to

$$T = \sum_{k=1}^{p} \left[\alpha_k \prod_{j=1}^{k-1} (1 - \alpha_j) \right] R_k + \left[\prod_{k=1}^{p} (1 - \alpha_k) \right] I \qquad \text{(D.38)}$$

We readily check that the matrix

$$R = \sum_{k=1}^{p} \left[\alpha_k \prod_{j=1}^{k-1} (1 - \alpha_j) \right] R_k \text{ is of rank one, viz.,} \qquad \text{(D.39)}$$

$$R = \| u_i v_j \|_1^N \text{ with } u_i \equiv 1 \text{ and } \mathbf{v} = \sum_{k=1}^{p} \left[\alpha_k \prod_{j=1}^{k-1} (1 - \alpha_j) \right] \mathbf{v}^{(k)}$$

Thus, the left eigenvector (of eigenvalue 1) for T is $\mathbf{v}$ as displayed above so that $\boldsymbol{\xi}^{(1)} = K\mathbf{v}$ (K is a normalizing constant). By symmetry considerations we infer that the vector $\boldsymbol{\xi}^{(l)}$ possesses the expression

$$\boldsymbol{\xi}^{(l)} = \sum_{k=1}^{p} \left[\alpha_{l+k} \prod_{j=1}^{k-1} (1 - \alpha_{l+j}) \right] \mathbf{v}^{(l+k)} \qquad \text{(D.40)}$$

interpreting the indices by the convention that $l + k$ is diminished modulo p (thus, $p + 1$ means 1, $p + 2$ means 2, etc.).

Protection for a seasonal and spatial selection regime. In line with Section 4, the backward migration matrix has the block form

$$M = \begin{Vmatrix} 0 & M_2 & 0 & & 0 \\ 0 & 0 & M_3 & & 0 \\ \vdots & & & \ddots & \vdots \\ 0 & 0 & 0 & & M_p \\ M_1 & 0 & 0 & \ldots & 0 \end{Vmatrix} \qquad \text{(D.41)}$$

where each M_i is a usual $N \times N$ migration matrix. The criterion for protection in the general context of (D.41) is given in (Section 12). The condition can be made explicit where each M_i has the special structure

$$M_i = E_i + R_i$$

such that E_i is nonnegative and invertible and

$$R_i = \| r_\lambda \rho_\mu \| \text{ is of rank one}$$

(see Result C.3 in Appendix C). The large matrix $\tilde{M} = MD$ ($D = \operatorname{diag}(d_1, d_2, \ldots, d_{Np})$) maintains the form (D.41) having also $\tilde{M}_i = \tilde{E}_i + \tilde{R}_i$, $\tilde{E}_i$ nonnegative invertible, and $\tilde{R}_i$ of rank one. The spectral radius of $\tilde{M}$ coincides with that of

$$T = (E_1 + R_1)D_1(E_2 + R_2)D_2 \cdots (E_p + R_p)D_p \tag{D.42}$$

$D_1 = \operatorname{diag}(d_1, \ldots, d_N)$, $D_2 = \operatorname{diag}(d_{N+1}, \ldots, d_{2N})$, $D_3 = \operatorname{diag}(d_{2N+1}, \ldots, d_{3N})$, etc. The matrix T can be expanded to

$$T = E_1D_1E_2D_2 \cdots E_pD_p + \sum_\alpha S_\alpha$$

where S_α are nonnegative matrices each of rank one. The explicit conditions equivalent to $\rho(T) > 1$ (assuring allele A-protection) are accessible by application of Result C.3 of Appendix C.

Consider an extended backward migration matrix of the form apart from zero blocks consisting of matrix entries A_i and B_j

$$M = \begin{Vmatrix} A_1 & 0 & 0 & \ldots & B_p \\ B_1 & A_2 & 0 & \ldots & 0 \\ 0 & B_2 & A_3 & & 0 \\ \vdots & & & & \end{Vmatrix} \tag{D.43}$$

When A_i, B_j are nonnegative irreducible $N \times N$ matrices, then the matrices $(I - A_k)^{-1}$ are all positive and

$$Q = B_p(I - A_p)^{-1}B_{p-1}(I - A_{p-1})^{-1} \cdots B_1(I - A_1)^{-1} \tag{D.44}$$

is a stochastic matrix. Let ξ_1 be a left principal eigenvector for Q and then calculate

$$\xi_p = \xi_1B_p(I - A_p)^{-1}, \qquad \xi_k = \xi_{k+1}B_k(I - A_k)^{-1}, \qquad k = p, p-1, \ldots, 1 \tag{D.45}$$

recursively.

It is easy to verify that

$$\xi^* = \frac{1}{p}(\xi_1, \xi_2, \ldots, \xi_p) \tag{D.46}$$

is the principal left frequency eigenvector for M of (D.43). Under further specializations, where B_k are of rank one (Levene migration form), $B_k = b_{k+1} \| e_i^{(k)} v_j^{(k)} \|$, $e_i^{(k)} \equiv 1$, and $\mathbf{v}_k = (v_1^{(k)}, v_2^{(k)}, \ldots, v_N^{(k)})$, $\sum_{j=1}^N v_j^{(k)} = 1$ with $A_k = (1 - a_k - b_k)I$, $0 < a_k, b_k$; $a_k + b_k < 1$. Then (D.46) becomes

$$\xi = \frac{1}{K}\left(\frac{1}{b_1}\mathbf{v}_1, \frac{1}{b_2}\mathbf{v}_2, \ldots, \frac{1}{b_p}\mathbf{v}_p\right) \tag{D.47}$$

which is normalized by $K = \sum_{i=1}^p 1/b_i$.

A slightly more general case of interest has $\mathbf{v}_k$ as the left principal eigenvector of A_k and $B_k = \| u_i^{(k)} v_j^{(k)} \|$, $u_i^{(k)}, v_j^{(k)} > 0$, where $\mathbf{v}_k = (v_1^{(k)}, \ldots, v_N^{(k)})$. The left principal eigenvector then becomes

$$\xi = \frac{1}{K}(\alpha_1\mathbf{v}_1, \alpha_2\mathbf{v}_2, \ldots, \alpha_p\mathbf{v}_p) \tag{D.48}$$

where α_i are determined by the recursive relation $\alpha_k[1 - \rho(A_k)] = \alpha_{k+1} \sum_{i=1}^N v_i^{(k)} u_i^{(k)}$, $\alpha_1 = 1$, and $\rho(A_k)$ is the spectral radius of A_k which is less than 1 as A_k is substochastic.

Migration pattern corresponding to a multideme spatial plant population involving seed pools. The backward migration matrix has the form (4.28). Determine, recursively (assuming for simplicity $A_1 = 0$)

$$\xi_2B_1 = \xi_1$$

$$\xi_3B_2 + \xi_1A_2 = \xi_2 \quad \text{or} \quad \xi_3B_2(I - B_1A_2)^{-1} = \xi_2$$

$$\xi_4B_3 + \xi_1A_3 = \xi_3 \quad \text{or} \quad \xi_4B_3[I - B_2(I - B_1A_2)^{-1}B_1A_3]^{-1} = \xi_3$$

etc., where ξ_p is the principal eigenvector of the equation $\xi_1A_p = \xi_p$ after substituting for ξ_1.

Circulant block migration structure. Consider a backward migration matrix M of the form (4.27) constructed as a circulant migration flow superimposed on a multideme structure. We verify the following fact.

PROPOSITION D.1. *Let ω be a pth root of unity. Form the nth-order matrix*

$$M_\omega = \sum_{k=1}^p \omega^{k-1}\gamma_kM_k \tag{D.49}$$

Let $\mathbf{x}M_\omega = \lambda\mathbf{x}$ *with eigenvalue* λ. *Then the np component vector*

$$\mathbf{z} = (\mathbf{x}, \omega\mathbf{x}, \omega^2\mathbf{x}, \ldots, \omega^{p-1}\mathbf{x}) \tag{D.50}$$

is a left eigenvector of M for the eigenvalue λ.

PROOF. Operating with M on (D.50) yields for the first row block

$$\mathbf{x}\sum_{k=1}^{p} \omega^{k-1}\gamma_k M_k = \mathbf{x}M_\omega = \lambda\mathbf{x} \tag{D.51}$$

the last equation resulting from the determination of $\mathbf{x}$; the outcome of the second row block is

$$\begin{aligned} &\mathbf{x}(\gamma_p M_p + \omega\gamma_1 M_1 + \omega^2\gamma_2 M_2 + \cdots + \omega^{p-1}\gamma_{p-1}M_{p-1}) \text{ (and as } \omega^p = 1) \\ &\quad = \omega\mathbf{x}(\omega^{p-1}\gamma_p M_p + \gamma_1 M_1 + \cdots + \omega^{p-2}\gamma_{p-1}M_{p-1}) \qquad \text{(D.52)} \\ &\quad = \omega\mathbf{x}M_\omega = \lambda\omega\mathbf{x} \end{aligned}$$

The other row blocks applied to $\mathbf{z}$ produce, by analogous manipulations, the required outcomes thereby validating the assertion of Proposition D.1. □

By letting ω traverse the collection of all pth roots of unity, we accumulate all eigenvalues (and eigenvectors) of M. Most important for us is the following corollary of Proposition D.1.

PROPOSITION D.2. *Let the stipulations of Proposition D.1 be in force. Then the left principal eigenvector for M is* $\boldsymbol{\xi} = (1/p)\ (\boldsymbol{\theta}, \boldsymbol{\theta}, \ldots, \boldsymbol{\theta})$ *where* $\boldsymbol{\theta}$ *is the stationary vector of the* $n \times n$ *stochastic matrix*

$$S = \sum_{k=1}^{p} \gamma_k M_k \tag{D.53}$$

APPENDIX E. ANALYSIS OF THEOREM 5.2

We restate it for convenience.

THEOREM 5.2. *Let M be a general nonnegative irreducible backward migration matrix. Consider the family of migration matrices*

$$M_\alpha = (1 - \alpha)I + \alpha M \tag{E.1}$$

Then for any set of positive fitness values $D = \operatorname{diag}(d_1, d_2, \ldots, d_n)$

$$\rho(\alpha) = \rho(M_\alpha D) \tag{E.2}$$

is decreasing as α *increases* (strictly provided $D \neq dI$).

We use the notation $\langle \mathbf{z}, \mathbf{w} \rangle = \sum z_i w_i$ to denote the inner product of the indicated vectors. Log $\mathbf{d}$ stands for the vector of components $\log d_i$.

PROOF. For the demonstration of (E.2) we exploit the Donsker–Varadhan variational formula (1975) (see also Friedland and Karlin, 1975) exhibited in (E.4) below. Let

$$\varphi(\mathbf{p}, \alpha) = \varphi(p_1, \ldots, p_n, \alpha) = \sup_{x>0} \sum_{i=1}^{n} p_i \log \left[\frac{x_i}{(M_\alpha \mathbf{x})_i}\right] \tag{E.3}$$

displaying the dependence on the homing parameter α. Knowing that $\varphi(\mathbf{p}, \alpha)$ is strictly convex (and of continuity class C^2) over $\mathbf{p} = (p_1, p_2, \ldots, p_n) > \mathbf{0}$, we have that the supremum of

$$\log \rho(\alpha) = \log \rho(M_\alpha D) = \sup_{\mathbf{p}>0} [\langle \mathbf{p}, \log \mathbf{d} \rangle - \varphi(\mathbf{p}, \alpha)] \tag{E.4}$$

is uniquely achieved at the vector $\mathbf{p}(\alpha) = [p_1(\alpha), \ldots, p_n(\alpha)]$ that is continuously differentiable as α traverses the unit interval. Therefore

$$\begin{aligned} \frac{d\rho}{d\alpha} &= \langle \frac{d\mathbf{p}(\alpha)}{d\alpha}, \log \mathbf{d} \rangle - \sum_{i=1}^{n} \frac{\partial \varphi}{\partial \mathbf{p}_i} \frac{dp_i(\alpha)}{d\alpha} - \frac{\partial}{\partial \alpha} \varphi(\mathbf{p}_0 \alpha) \\ &= -\frac{\partial}{\partial \alpha} \varphi[\mathbf{p}(\alpha), \alpha] \end{aligned} \tag{E.5}$$

as $\mathbf{p}(\alpha)$ is the unique critical point of the right-hand quantity in (E.4). Let $\mathbf{x}(\alpha)$ be the unique positive vector (normalized by the condition $[\mathbf{x}\langle\alpha\rangle, \mathbf{e}] = 1$) yielding $\varphi(\mathbf{p}, \alpha)$ in (E.3). A calculation paralleling (E.5) applied to (E.3) with $\mathbf{p}$ fixed produces

$$\begin{aligned} \frac{\partial \varphi}{\partial \alpha}(\mathbf{p}, \alpha) &= -\sum_{i=1}^{n} \frac{p_i}{[M_\alpha \mathbf{x}(\alpha)]_i} \sum_{j=1}^{n} m_{ij}(\alpha) \frac{dx_j(\alpha)}{d\alpha} + \sum_{i=1}^{n} \frac{p_i}{x_i(\alpha)} \frac{dx_i(\alpha)}{d\alpha} \\ &\quad + \sum_{i=1}^{n} \frac{p_i}{(M_\alpha \mathbf{x})_i} \{x_i(\alpha) - [M\mathbf{x}(\alpha)]_i\} \\ &= \langle \frac{\mathbf{p}}{M_\alpha \mathbf{x}(\alpha)}, (I - M)\mathbf{x}(\alpha) \rangle \end{aligned} \tag{E.6}$$

Noting that $(I - M_\alpha)\mathbf{x}(\alpha) = \alpha(I - M)\mathbf{x}(\alpha)$, the final expression in (E.6) reduces to

$$\alpha \sum_{i=1}^{n} \frac{p_i}{[M_\alpha \mathbf{x}(\alpha)]_i}\{x_i(\alpha) - [M_\alpha \mathbf{x}(\alpha)]_i\} = \alpha\left(\sum_{i=1}^{n} \frac{p_i x_i(\alpha)}{[M_\alpha \mathbf{x}(\alpha)]_i} - 1\right) \tag{E.7}$$

The concavity of the log function entails

$$\log\left(\sum_{i=1}^{n} p_i \frac{x_i(\alpha)}{[M_\alpha \mathbf{x}(\alpha)]_i}\right) \geq \sum_{i=1}^{n} p_i \log\left(\frac{x_i(\alpha)}{[M_\alpha \mathbf{x}(\alpha)]_i}\right) \tag{E.8}$$

On account of $\varphi(\mathbf{p}) \geq 0$ and the definition of $\mathbf{x}(\alpha)$, we deduce that

$$\varphi(\mathbf{p}) = \sum_{i=1}^{n} p_i \log\left(\frac{x_i(\alpha)}{[M_\alpha \mathbf{x}(\alpha)]_i}\right) \geq 0$$

Therefore $\sum_{i=1}^{n} p_i \frac{x_i(\alpha)}{[M_\alpha \mathbf{x}(\alpha)]_i} \geq 1$ and this fact in conjunction with (E.6) and (E.7) verifies $d\varphi[p(\alpha), \alpha]/d\alpha \geq 0$. The foregoing conclusion combined with the relation (E.5) implies the assertion that $\rho(\alpha)$ is nonincreasing. □

Slightly more care with the details of the analysis establishes strict inequality $\partial\varphi[\mathbf{p}(\alpha), \alpha]/\partial\alpha > 0$, $0 < \alpha < 1$, unless $\mathbf{p}(\alpha)$, the left eigenvector of $M_\alpha D$, is independent of α, a property precluded when $D \neq cI$.

Remark. It is tempting to conjecture an extension of Theorem 5.2 such that the (more mixing) ordering relationship

$$M^{(1)} > M^{(2)} \tag{E.9}$$

in the sense that

$$m_{ij}^{(1)} \geq m_{ij}^{(2)} \qquad \text{for all } i \neq j \tag{E.10}$$

implies the inequality

$$\rho(M^{(1)}D) \leq \rho(M^{(2)}D) \tag{E.11}$$

Such a conclusion is generally *not* valid. Indeed, if (E.11) prevails for all fitness regimes D, then necessarily

$$\begin{aligned} \varphi^{(1)}(\mathbf{p}) &= \sup_{x>0} \sum_{i=1}^{n} p_i \log\left[\frac{x_i}{(M^{(1)}\mathbf{x})_i}\right] \geq \varphi^{(2)}(\mathbf{p}) \\ &= \sup_{x>0} \sum_{i=1}^{n} p_i \log\left[\frac{x_i}{(M^{(2)}\mathbf{x})_i}\right] \end{aligned} \tag{E.12}$$

applies for all $\mathbf{p}$. However, the relation (E.12) for all $\mathbf{p}$ entails that the stochastic matrices $M^{(1)}$ and $M^{(2)}$ share an identical stationary frequency state (the same left eigenvector for eigenvalue 1). This requirement is usually not consistent with the stipulation (E.9).

In particular, the version of (E.2) with variable homing rates (Section 2, part III) generally does not hold. Specifically, increasing a local homing rate does not ipso facto increase the likelihood of a protected polymorphism. In contrast, Theorem 5.2 asserts that a *uniform* increase in homing rates (effective throughout the population range) does facilitate the expression of a protected polymorphism.

APPENDIX F. PROOF OF THEOREM 5.1

We start with a matrix of the form

$$M = E_2 S E_1 \tag{F.1}$$

where E_1 and E_2 are positive diagonal matrices and S is real symmetric. Let D be a positive diagonal matrix.

The following known fact plays an essential role in our analysis.

Lemma F.1. *Let M have the form (F.1), then there exists an inner product with respect to which M is symmetric* (M is symmetrizable in an inner product determined by a diagonal matrix).

Proof. We may express M as KE with $K = E_2 S E_2$ symmetric and $E = E_2^{-1}E_1$ a positive diagonal matrix. Now define the new inner product

$$\langle\langle \mathbf{x}, \mathbf{y} \rangle\rangle = \sum_{i=1}^{n} \epsilon_i x_i y_i \tag{F.2}$$

where ϵ_i are the diagonal elements of E. The next string of equations are easily justified: [((,)) is the usual inner product]

$$\begin{aligned}\langle\langle M\mathbf{x}, \mathbf{y}\rangle\rangle &= ((M\mathbf{x}, E\mathbf{y})) = ((E_2SE_1\mathbf{x}, E\mathbf{y})) = ((E_1\mathbf{x}, SE_2E\mathbf{y}))\\ &= ((E_1\mathbf{x}, SE_1\mathbf{y})) = ((E_2^{-1}E_1\mathbf{x}, M\mathbf{y})) = ((E\mathbf{x}, M\mathbf{y}))\\ &= ((M\mathbf{y}, E\mathbf{x})) = \langle\langle M\mathbf{y}, \mathbf{x}\rangle\rangle = \langle\langle \mathbf{x}, M\mathbf{y}\rangle\rangle\end{aligned}$$

showing that M is symmetric in the inner product $\langle\langle\ ,\ \rangle\rangle$. □

Also, $D^{1/2}MD^{1/2}$ (D diagonal) is symmetric with respect to the inner product $\langle\langle\ ,\ \rangle\rangle$ as any two diagonal matrices, in particular D and E, commute.

We will avail ourselves of the classical variational characterization of the spectral radius for symmetric matrices $\rho(MD)$ yielding

$$\begin{aligned}\rho(MD) = \rho(D^{1/2}MD^{1/2}) &= \sup_{\mathbf{x}>0} \frac{\langle\langle D^{1/2}MD^{1/2}\mathbf{x}, \mathbf{x}\rangle\rangle}{\langle\langle \mathbf{x}, \mathbf{x}\rangle\rangle}\\ &= \sup_{\mathbf{y}>0} \frac{\langle\langle M\mathbf{y}, \mathbf{y}\rangle\rangle}{\langle\langle D^{-1}\mathbf{y}, \mathbf{y}\rangle\rangle}\end{aligned} \tag{F.3}$$

using the substitution $\mathbf{y} = D^{1/2}\mathbf{x}$ in the last equation.

Proof of Theorem 5.1. As M_1 and M_2 are symmetrizable and commute, there exists an appropriate inner product $\langle\langle\ ,\ \rangle\rangle$ determined by a positive diagonal matrix as described in Lemma F.1, leading to the representation

$$\begin{aligned}\rho(M_1M_2D) &= \rho(M_2^{1/2}M_1^{1/2}DM_1^{1/2}M_2^{1/2})\\ &= \sup_{\mathbf{x}\neq 0} \frac{\langle\langle M_2^{1/2}M_1^{1/2}DM_1^{1/2}M_2^{1/2}\mathbf{x}, \mathbf{x}\rangle\rangle}{\langle\langle \mathbf{x}, \mathbf{x}\rangle\rangle}\\ &= \sup_{\mathbf{y}\neq 0} \frac{\langle\langle M_1^{1/2}DM_1^{1/2}\mathbf{y}, \mathbf{y}\rangle\rangle}{\langle\langle M_2^{-1}\mathbf{y}, \mathbf{y}\rangle\rangle}\end{aligned} \tag{F.4}$$

But M_2 is stochastic positive definite in $\langle\langle\ ,\ \rangle\rangle$ and therefore

$$\langle\langle M_2^{-1}\mathbf{y}, \mathbf{y}\rangle\rangle \geq \langle\langle \mathbf{y}, \mathbf{y}\rangle\rangle \text{ for all } \mathbf{y} \tag{F.5}$$

As M_1 is also positive definite, (F.5) implies that the quantity in (F.4) is estimated above by $\sup_{\mathbf{y}\neq 0}\langle\langle M_1^{1/2}DM_1^{1/2}\mathbf{y}, \mathbf{y}\rangle\rangle/\langle\langle \mathbf{y}, \mathbf{y}\rangle\rangle$. But this equals $\rho(M_1D)$. The proof of Theorem 5.1 is complete. □

As a consequence of Theorem 5.1 with $M_1 = M$, $M_2 = M^k$ (the kth power of M), we obtain:

Corollary F.1. *If M is a stochastic matrix symmetrizable to a positive definite matrix of the form (F.1), then*

$$\rho(M^kD) \geq \rho(M^{k+1}D), \qquad k = 1, 2, \ldots \tag{F.6}$$

Corollary F.2. *If M is symmetrizable to a positive semidefinite matrix, then*

$$\rho(MD) \geq \sum_{i=1}^{n} \xi_i d_i \tag{F.7}$$

where $\boldsymbol{\xi}M = \boldsymbol{\xi}$ and $\boldsymbol{\xi}$ obeys the normalization $(\boldsymbol{\xi}, \mathbf{u}) = \sum_{i=1}^{n} \xi_i = 1$, $\mathbf{u} = (1, 1, \ldots, 1)$.

Proof. Let $k \to \infty$ in (F.6) producing

$$\rho(MD) \geq \lim_{k\to\infty} \rho(M^kD) \tag{F.8}$$

But the classical matrix ergodic theorem affirms that $M^\infty = \lim_{k\to\infty} M^k$ coincides with the rank-one matrix $\| u_i\xi_i \|$, $u_i \equiv 1$, and manifestly $\rho(M^\infty D) = \sum_{i=1}^{n} \xi_i d_i$. □

Remark. Let A_1 and A_2 be symmetric positive definite stochastic matrices. We can paraphrase the argument of Theorem 5.1 to show that $\rho(A_1A_2) \leq \rho(A_1)$, and more generally, $\rho(A_1^{k+1}A_2) \leq \rho(A_1^kA_2)$. Letting $k \to \infty$ produces the lower bound

$$\rho(A_1A_2) \geq (A_2\mathbf{u}, \boldsymbol{\xi}) = \sum_{i=1}^{n} (A_2\mathbf{u})_i\xi_i$$

where $\boldsymbol{\xi}$ satisfies $\boldsymbol{\xi}A_1 = \boldsymbol{\xi}$ [$\boldsymbol{\xi}$ normalized to satisfy $(\mathbf{u}, \boldsymbol{\xi}) = 1$].

Using the representation (F.3) we can also prove:

Theorem F.1. *Assume that M is a symmetric (symmetrizable as in (F.1) suffices) positive definite stochastic matrix. Let $M^{(\alpha)} = (1 - \alpha)I + \alpha M$. Then*

$\varphi(\alpha) = \rho(M^{(\alpha)}D)$ is convex decreasing as α increases

This result extends Theorem 5.2 in that $\varphi(\alpha)$ is convex as well as decreasing.

ACKNOWLEDGMENTS

This work was supported in part by NIH Grant 5R01 GM10452-17 and NSF Grant MCS 79-24310.

REFERENCES

Antonovics, J., 1971, The effects of a heterogeneous environment on the genetics of natural populations, *Am. Sci* **59:**592–599.

Aston, J. L., and Bradshaw, A. D., 1966, Evolution in closely adjacent plant populations. 5. *Agrostis stolonifera* in maritime habitats, *Heredity* **21:**649–664.

Ayala, F. J., Valentine, J. W., Hedgecock, D., and Barr, L. G., 1975, Deep-sea asteroids: High genetic variability in a stable environment, *Evolution* **29:**203–212.

Berger, E., 1976, Heterosis and the maintenance of enzyme polymorphism, *Am. Nat.* **110:**823–839.

Bodmer, W. F., and Cavalli-Sforza, L. L., 1968, A migration matrix model for the study of random genetic drift, *Genetics* **59:**565–592.

Bradshaw, A. D., 1971, Plant evolution in extreme environments, in: *Ecological Genetics and Evolution*, Appleton–Century–Crofts, New York.

Bretsky, P. W., 1970, An essay on genetic adaptive strategies and mass extinctions, *Geol. Soc. Am. Bull.* **81:**2449–2456.

Bretsky, P. W., and Lorenz, D. M., 1969, Adaptive response to environmental stability: A unifying concept in paleoecology, *Proc. N. Am. Paleoecol. Conv. Pt. E* 522–550.

Brown, A. H. D., 1979, Enzyme polymorphism in plant populations, *Theor. Pop. Biol.* **15:**1–44.

Brown, A. H. D., Marshall, D. R., and Albrecht, L., 1974, The maintenance of alcohol dehydrogenase polymorphism in *Bromus mollis* L., *Aust. J. Biol. Sci.* **27:**545–559.

Bryant, E. H., 1974, On the adaptive significance of enzyme polymorphisms in relation to environmental variability, *Am. Nat.* **108:**1–19.

Bulmer, M. G., 1972, Multiple niche polymorphisms, *Am. Nat.* **106:**254–257.

Cain, A. S., and Sheppard, P. R., 1952, The effects of natural selection on body colour on the land snail *Cepaea nemoralis*, *Heredity* **6:**217–223.

Carmelli, D., and Cavalli-Sforza, L., 1976, Some models of population structure and evolution, *Theor. Pop. Biol.* **9:**329–359.

Carson, H. L., 1958, The population genetics of *Drosophila robusta*, *Adv. Genet.* **9:**1–40.

Christiansen, F. B., 1974, Sufficient conditions for protected polymorphism in a subdivided population, *Am. Nat.* **108:**157–166.

Christiansen, F. B., 1975, Hard and soft selection in a subdivided population, *Am. Nat.* **109:**11–16.

Christiansen, F. B., and Feldman, M. W., 1975, Subdivided populations: A review of the one- and two-locus deterministic theory, *Theor. Pop. Biol.* **7:**13–38.

Clarke, B. C., 1979, The evolution of genetic diversity, *Proc. R. Soc. London* **205:**543–574.

Cook, R. D., and Hartl, D. L., 1974, Uncorrelated random environments and their effects on gene frequency, *Evolution* **28:**265–274.

Deakin, M. A. B., 1966, Sufficient conditions for genetic polymorphism, *Am. Nat.* **100:**690–692.

Dempster, E. R., 1955, Maintenance of genetic heterogeneity, *Cold Spring Harbor Symp. Quant. Biol.* **20:**25–32.

Dobzhansky, Th., 1943, Genetics of natural populations. IX. Temporal changes in the composition of populations of *Drosophila pseudoobscura*, *Genetics* **28:**162–186.

Dobzhansky, Th., 1956, Genetics of natural populations. XXV. Genetic changes in populations of *Drosophila pseudoobscura* and *Drosophila persimilis* in some localities in California, *Evolution* **10:**82–93.

Dobzhansky, Th., 1967, Genetic diversity and diversity of environments, *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability*, Volume 4 (L. Lecam and J. Neyman, eds.), pp. 295–304, University of California Press, Berkeley.

Dobzhansky, Th., Spassky, B., and Sved, J., 1969, Effects of selection and migration on geotactic and phototactic behaviour of *Drosophila* II, *Proc. R. Soc. London Ser. B* **173:**191–207.

Donsker, M. D., and Varadhan, S. R. S., 1975, On a variational formula for the principal eigenvalue for operators with maximum principle, *Proc. Natl. Acad. Sci. USA* **72:**780–783.

Ehrlich, P., 1961, Intrinsic variables to disperal in checker-spot butterfly, *Science* **134:**108–109.

Ehrlich, P., Holm, R., and Parnell, D. R., 1974, *The Process of Evolution*, 2nd ed., McGraw–Hill, New York.

Endler, J. A., 1973, Gene flow and population differentiation, *Science* **179:**243–250.

Endler, J. A., 1977, *Geographic Variation, Speciation, and Clines*, Princeton University Press, Princeton, N.J.

Felsenstein, J., 1976, The theoretical population genetics of variable selection and migration, *Annu. Rev. Genet.* **10:**157–166.

Fleming, W. H., 1975, A selection migration model in population genetics, *J. Math. Biol.* **2:**219–233.

Ford, E. B., 1975, *Ecological Genetics*, Wiley, New York.

Friedland, S., and Karlin, S., 1975, Some inequalities for the spectral radius of nonnegative matrices and applications, *Duke Math. J.* **42:**459–490.

Gantmacher, F. R., 1959, *The Theory of Matrices*, Volume II, Chelsea, New York.

Gillespie, J. H., 1975, The role of migration in the genetic structure of populations in temporally and spatially varying environments. I. Conditions for polymorphism, *Am. Nat.* **109:**127–135.

Gillespie, J. H., 1976, A general model to account for enzyme variation in natural populations. II. Characterizations of the fitness functions, *Am. Nat.* **110:**809–821.

Gillespie, J. H., and Langley, C., 1976, Multilocus behavior in random environments. I. Random Levene models, *Genetics* **82:**123–137.

Glidden, C., and Strobeck, C., 1975, Necessary and sufficient conditions for multiple-niche polymorphism in haploids, *Am. Nat.* **109:**233–235.

Goodhart, C. B., 1963, 'Area effects' and nonadaptive variations between populations of *Cepaea* (Mollusca), *Heredity* **18:**459–465.

Gourley, R., and Lawrence, C., 1977, Stable population analysis in periodic environments, *Theor. Pop. Biol.* **11:**49–59.

Grassle, J. F., 1972, Species diversity, genetic variability, and environmental uncertainty, *Fifth European Marine Biological Symposium*, pp. 19–26, Piccin Editore, Padua.

Haldane, J. B. S., and Jayakar, S. D., 1963, Polymorphism due to selection of varying direction, *J. Genet.* **58:**237–242.

Hamrick, J. L., and Allard, R. W., 1972, Microgeographic variation in allozyme frequencies in *Avena barbata*, *Proc. Natl. Acad. Sci. USA* **69:**2100–2104.

Hanson, W. D., 1966, The effects of partial isolation (distance), migration, and different fitness requirements among environmental pockets upon steady state gene frequencies, *Biometrics* **22**:453–468.

Hedrick, P. J., Ginevan, M. E., and Ewing, E. P., 1976, Genetic polymorphism in heterogeneous environments, *Annu. Rev. Ecol. Syst.* **7**:1–33.

Jain, S. K., and Bradshaw, A. D., 1966, Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis, *Heredity* **20**:407–411.

Jones, J. S., and Yamazaki, T., 1974, Genetic background and the fitness of allozymes, *Genetics* **78**:1185–1189.

Jones, J. S., Leith, B. H., and Rawlings, P., 1977, Polymorphism in *Cepaea*, *Annu. Rev. Ecol. Syst.* **8**:109–143.

Karlin, S., 1968, Equilibrium behaviour of population genetic models with non-random mating, *J. Appl. Prob.* **5**:231–313, 487–566.

Karlin, S., 1976, Population subdivision and selection migration interactions, in: *Population Genetics and Ecology* (S. Karlin and E. Nevo, eds.), pp. 617–657, Academic Press, New York.

Karlin, S., 1977*a*, Gene frequency patterns in the Levene subdivided population model, *Theor. Pop. Biol.* **11**:356–385.

Karlin, S., 1977*b*, Protection of recessive and dominant traits in a subdivided population with general migration structure, *Am. Nat.* **11**:1145–1162.

Karlin, S., and Campbell, R. B., 1978, Analysis of central equilibrium configurations for certain multilocus systems in subdivided populations, *Genet. Res.* **32**:151–168.

Karlin, S., and Campbell, R. B., 1979, Selection-migration regimes characterized by a globally stable equilibrium, *Genetics* **94**:1064–1084.

Karlin, S., and Campbell, R. B., 1980, Polymorphism in subdivided populations characterized by a major and subordinate demes, *Heredity* **44**:151–168.

Karlin, S., and Campbell, R. B., 1981, The existence of a protected polymorphism under conditions of soft as against hard selection in a multi-population system, *Am. Nat.* **117**:262–275.

Karlin, S., and Kenett, R. S., 1977, Variable spatial selection with two stages of migration and comparisons between different timings, *Theor. Pop. Biol.* **11**:386–409.

Karlin, S., and McGregor, J., 1972*a*, Polymorphisms for genetic and ecological systems with weak coupling, *Theor. Pop. Biol.* **3**:210–238.

Karlin, S., and McGregor, J., 1972*b*, Applications of method of small parameters to multiniche population genetic models, *Theor. Pop. Biol.* **3**:186–209.

Karlin, S., and Richter-Dyn, N., 1976, Some theoretical analyses of migration selection interaction in a cline: A generalized two range environment, in: *Population Genetics and Ecology* (S. Karlin and E. Nevo, eds.), pp. 659–706, Academic Press, New York.

Kimura, M., and Weiss, G. H., 1964, The stepping stone model of population structure and the decrease of genetic correlation with distance, *Genetics* **49**:561–576.

Koehn, R. K., 1969, Esterase heterogeneity: Dynamics of a polymorphism, *Science* **163**:943–944.

Levene, H., 1953, Genetic equilibrium when more than one ecological niche is available, *Am. Nat.* **87**:331–333.

Lewontin, R. C., 1974, *The Genetic Basis of Evolutionary Change*, Columbia University Press, New York.

Li, W. T., 1976, Effect of migration on genetic distance, *Am. Nat.* **110**:841–847.

McDonald, J. F., and Ayala, F. J., 1974, Genetic response to environmental heterogeneity, *Nature (London)* **250**:572–574.

Malécot, G., 1948, *Les Mathématiques de L'Hérédité*, Masson, Paris; revised English translation, 1970, Freeman, San Francisco.

Malécot, G., 1951, Some probabilistic schemes for the variability of natural populations, *Univ. Lyon Sci. Sect.* **13**:37–60.

Malécot, G., 1959, Stochastic models in population genetics, *Publ. Inst. Stat. Univ. Paris* **8**(F3):173–210.

Malécot, G., 1967, Identical loci and relationship, in: *Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability*, Volume 4 (L. Lecam and J. Neyman, eds.), pp. 317–332, University of California Press, Berkeley.

Malécot, G., 1975, Heterozygosity and relationship and regularly subdivided populations, *Theor. Pop. Biol.* **8**:212–241.

Maruyama, T., 1970, Stepping stone models of finite length, *Adv. Appl. Probab.* **2**:229–258.

Maynard Smith, J., 1970, Genetic polymorphism in a varied environment, *Am. Nat.* **104**:487–490.

Merritt, R. B., 1972, Geographic distribution and enzymatic properties of lactate dehydrogenase allozymes in the fathead minnow, *Pimephales promelas*, *Am. Nat.* **196**:173–184.

Mitton, J. B., and Koehn, R. K., 1975, Genetic organization and adaptive response of allozymes to ecological variables in *Fundulus heteroclitus*, *Genetics* **79**:97–111.

Nagylaki, T., 1974, The decay of genetic variability in geographically structured populations, *Proc. Natl. Acad. Sci. USA* **71**:2932–2936.

Nagylaki, T., 1975, Polymorphisms in cyclically-varying environments, *Heredity* **35**:67–74.

Nagylaki, T., 1976*a*, Dispersion-selection balance in localized plant populations, *Heredity* **35**:59–67.

Nagylaki, T., 1976*b*, Clines with variable migration, *Genetics* **83**:867–886.

Nagylaki, T., 1978, The relation between distant individuals in geographically structured populations, in: *Studies in Mathematical Biology*, Volume 15 (S. A. Levin, ed.), pp. 588–624, Mathematical Association of America, Providence, R.I.

Nagylaki, T., 1979, The island model with stochastic migration, *Genetics* **91**:163–176.

Nagylaki, T., and Lucier, B., 1980, Numerical analysis of random drift in a cline, *Genetics* **94**:497–517.

Nei, M., and Chakravarti, T., 1977, Mean and variance of F_{ST} in a finite number of incompletely isolated populations, *Theor. Pop. Biol.* **11**:291–306.

Nevo, E., 1978, Genetic variation in natural populations: Patterns and theory, *Theor. Pop. Biol.* **13**:121–177.

Powell, J. R., 1971, Genetic polymorphism in varied environments, *Science* **174**:1035–1036.

Powell, J. R., 1975, Protein variation in natural populations of animals, *Evol. Biol.* **8**:79–119.

Prout, T., 1968, Sufficient conditions for multiple niche polymorphism, *Am. Nat.* **102**:493–496.

Scott, J. A., and McClelland, G. A. H., 1977, A model of polymorphism with several seasons and several habitats, and its application to the mosquito *Aedes aegypti*, *Theor. Pop. Biol.* **11**:342–355.

Slatkin, M., 1973, Gene flow and selection in a cline, *Genetics* **75**:733–756.

Slatkin, M., and Charlesworth, B., 1978, The spatial distribution of transient alleles in a subdivided population: A simulation study, *Genetics* **87**:793–810.

Smith, C. A. B., 1969, Local fluctuations in gene frequencies, *Ann. Hum. Genet.* **32**:251–260.

Soule, M., 1976, Allozyme variation: Its determinants in space and time, in: *Molecular Evolution* (F. J. Ayala, ed.), pp. 60–77, Sinauer, Sunderland, Mass.

Spieth, P. T., 1974, Gene flow and genetic differentiation, *Genetics* **78**:961–965.

Strobeck, C., 1974, Sufficient conditions for polymorphism with *N* niches and *M* matings groups, *Am. Nat.* **108**:152–156.

Sved, J. A., 1976, The relationship between genotype and fitness for heterotic models, in: *Population Genetics and Ecology* (S. Karlin and E. Nevo, eds.), pp. 441–465, Academic Press, New York.

Sved, J. A., and Latter, B. D. H., 1977, Migration and mutation in stochastic models of gene frequency changes, *J. Math. Biol.* **5**:61–73.
Templeton, A., 1977, Survival probabilities of mutant alleles in fine-grained environments, *Am. Nat.* **111**:951–966.
Templeton, A. R., and Levin, S. A., 1979, Evolutionary consequences of seed pools, *Am. Nat.* **114**:232–249.
Templeton, A. R., and Rothman, E. D., 1974, Evolution in heterogeneous environments, *Am. Nat.* **108**:409–428.
Templeton, A. R., and Rothman, E. D., 1978, Evolution in fine-grained environments. I. Environmental runs and the evolution of homeostasis, *Theor. Pop. Biol.* **13**:340–355.
Valentine, J., 1976, Genetic strategies of adaptation, in: *Molecular Evolution* (F. J. Ayala, ed.), pp. 78–94, Sinauer, Sunderland, Mass.
Wallace, B., 1968, *Topics in Population Genetics*, Norton, New York.
Wallace, B., 1975, Hard and soft selection revisited, *Evolution* **29**:465–473.
Wright, S., 1943, Isolation by distance, *Genetics* **28**:114–138.
Wright, S., 1951, The genetical structure of populations, *Ann. Eugenics* **15**:323–354.
Wright, S., 1969, *Evolution and the Genetics of Populations, Volume 2*, Chicago University Press, Chicago.

3

Regulatory Mutations and the Development of New Metabolic Pathways by Bacteria

R. P. MORTLOCK

Department of Microbiology
College of Agriculture and Life Sciences
Cornell University
Ithaca, New York 14853

INTRODUCTION

It is generally assumed that the earliest living microorganisms were relatively simple in their metabolic capabilities and were provided by their environment with a great abundance of organic molecules for incorporation into their structure of utilization for energy. As such substrates began to become depleted, these primitive microorganisms were forced to acquire new enzymatic abilities to permit them to utilize a wider range of compounds as metabolites. It is normally assumed that the genetic material of bacteria has increased in its amount during the course of evolution.

In 1945, Horowitz proposed that metabolic pathways might have arisen by a process of "retrograde evolution." He suggested that when an essential metabolite of primitive microorganisms became limiting, the cells were forced to evolve the enzymatic ability to convert a previously unused compound into the needed metabolite. As the new substrate would not differ greatly in structure from the old metabolite, the newly evolved enzyme could originate from the enzyme that formerly used the older