

Spatial and Space-Time Correlations in Systems of Subpopulations With Genetic Drift and Migration

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ABSTRACT

The geographic distribution of genetic variation is an important theoretical and experimental component of population genetics. Previous characterizations of genetic structure of populations have used measures of spatial variance and spatial correlations. Yet a full understanding of the causes and consequences of spatial structure requires complete characterization of the underlying space-time system. This paper examines important interactions between processes and spatial structure in systems of subpopulations with migration and drift, by analyzing correlations of gene frequencies over space and time. We develop methods for studying important features of the complete set of space-time correlations of gene frequencies for the first time in population genetics. These methods also provide a new alternative for studying the purely spatial correlations and the variance, for models with general spatial dimensionalities and migration patterns. These results are obtained by employing theorems, previously unused in population genetics, for space-time autoregressive (STAR) stochastic spatial time series. We include results on systems with subpopulation interactions that have time delay lags (temporal orders) greater than one. We use the space-time correlation structure to develop novel estimators for migration rates that are based on space-time data (samples collected over space and time) rather than on purely spatial data, for real systems. We examine the space-time and spatial correlations for some specific stepping stone migration models. One focus is on the effects of anisotropic migration rates. Partial space-time correlation coefficients can be used for identifying migration patterns. Using STAR models, the spatial, space-time, and partial space-time correlations together provide a framework with an unprecedented level of detail for characterizing, predicting and contrasting space-time theoretical distributions of gene frequencies, and for identifying features such as the pattern of migration and estimating migration rates in experimental studies of genetic variation over space and time.

THE distribution of genetic variation over the space that a species occupies is an important part of population genetic processes. Spatial structure promotes formation of novel combinations of genes, and thus may interact over time with both local adaptiveness and the evolution of a species (WRIGHT 1978). Populations of species that share sufficiently low rates of migration become genetically isolated by distance, which affects levels of local inbreeding (WRIGHT 1943). Recently there have been increasing numbers of studies on spatial structure, and these generally indicate strongly spatially autocorrelated distributions of genetic variation (SOKAL and ODEN 1978; SOKAL 1979; SOKAL and MENOZZI 1982; SOKAL, SMOUSE and NEEL 1986; SOKAL, ODEN and BARKER 1987), in support of earlier studies [*e.g.*, reviews in ENDLER (1977) and EPPERSON (1990)]. To understand the theoretical causes and consequences of spatial structure, it will usually be necessary to fully describe the underlying processes in both space and time. This is also necessary simply for interpreting the form of spatial structure in real systems, because of complex-

ities that arise in choosing among various spatial processes generated by different underlying space-time processes [*e.g.*, BENNETT (1979)]. Moreover, natural selection can create sharp spatial patterns, and many studies have sought also to detect evidence of natural selection in spatial patterns of gene frequencies among subpopulations. However, many of the interactions of selection with spatial structure are confounded with those of isolation by distance (ENDLER 1977; EPPERSON 1990). Thus for both theoretical and experimental purposes it is important to develop and use in the fullest possible detail the space-time structures of processes for neutral loci.

There is a long tradition of mathematical analyses of the spatial variance and correlation (in addition to studies of spatial patterns of homozygosity and kinship coefficients) [*e.g.*, review by NAGYLAKI (1986)]. This work led to the advanced migration matrix methods of ROGERS and HARPENDING (1986) and ROGERS (1988), which are generally applicable to many theoretical and real systems. The present work uses a new method, and presents some new results on spatial

correlations. However, we also present the first analyses of complete sets of space-time correlations of gene frequencies, analyses for space-time data, and analyses of systems with subpopulation interactions that have time delay lags (temporal order) greater than one. The models studied here are the important stepping stone type models (KIMURA 1953; KIMURA and WEISS 1964; WEISS and KIMURA 1965; MALÉCOT 1948). These models feature discrete subpopulations, with discrete generations, genetic drift within each subpopulation, and migration between adjacent or spatially proximal subpopulations.

Results of studies on spatial correlations indicate that spatial distributions of genetic variation will bear simple characterizations only for some systems with one spatial dimension (where subpopulations such as riparian plants are distributed effectively on a line) and with simple patterns of migration [cf. FELSENSTEIN (1975), SAWYER and FELSENSTEIN (1981) and NAGYLAKI (1986)]. For systems with two spatial dimensions the spatial correlation structure generally does not bear a form that can be expressed simply [e.g., FLEMING and SU (1974) and NAGYLAKI (1974, 1978, 1986)]. Nonetheless, with the migration matrix approach, the variance and spatial correlations can be calculated for virtually any migration pattern in systems with finite numbers of subpopulations (BODMER and CAVALLI-SFORZA 1968; SMITH 1969; MARUYAMA 1974). However, even the general features of relationships of the spatial correlations to the migration rates are not clear. For example, the effects of the degree of anisotropy in migration rates has not been fully characterized (SOKAL 1979). In the further developments by ROGERS and HARPENDING (1986) and ROGERS (1988), models of finite systems are built to study various types of life cycles, some of which are clearly more appropriate for some species [see also FIX (1978)]. These studies do not include systems with temporal order one greater than one.

The space-time "structure" of migration drift processes has not been characterized. There are important process interactions between the spatial structure of genetic variation and the genetic changes caused by migration over time, and these warrant study. Genetic change in a subpopulation depends on both the amount of immigration from other subpopulations and the correlations of genetic variation between the source subpopulations and the recipient subpopulation. In addition, methods are not available for making full use of space-time genetic data for interpreting the underlying migrational processes. Methods such as SLATKIN's (1985) are based solely on spatial data for a single fixed point in time. It is becoming increasingly feasible to obtain substantial space-time genetic data. Analyses of space-time correlations use the additional information in space-time data sets for esti-

imating migration rates. Moreover, it is often possible to obtain space-time data for multiple loci, which for all neutral loci should show similar space-time structures and contrasts. Finally, there is a lack of studies of both theoretical and experimental population genetic processes with effects (interactions) that have time lags greater than one generation.

The present paper analyzes the complete space-time correlation structure of migration drift systems. It uses a new approach by employing theoretical results for a class of stochastic space-time models known as space-time autoregressive (STAR) models [e.g., BENNETT (1979), TANEJA and AROIAN (1980) and AROIAN (1985)]. In fact, the results using STAR methods extend to transformed space-time systems with effects with temporal lags greater than one, which systems (to the author's knowledge) have not been characterized in population genetics. Several other directions that the basic systems studied here can be extended, including extension to finite systems, are noted in the RESULTS and DISCUSSION. We simultaneously study new mathematical results and calculation formulae for *spatial correlations*, and these use different approximations and assumptions than do other methods of computing spatial correlations. The present methods simultaneously compute the entire space-time correlation structure along with the spatial correlations. Even when used just for spatial correlations, they are quite efficient, and they have some advantages in some cases arising from the fact that correlations are computed directly with spatial lags. However, in part because relative efficiency also may depend complexly on all aspects of a system, only a brief comparison of methods for calculating spatial correlations is made in the DISCUSSION.

We characterize a number of important properties and methods for finding the *space-time* correlations of gene frequencies. New results are developed for more general transformed space-time systems and then more specific properties are revealed for the correlations for specific models with one and two spatial dimensions. These features include how the decay of space-time correlations with time and the decay of spatial correlations over distance depend on the systematic force and migration parameters. Another aspect that is studied in some detail is the effect of anisotropic (directionally asymmetric) migration rates on the degree of directionality in space-time and spatial correlations. The effects of anisotropy on the directionality of spatial correlations have been important experimental issues (e.g., SOKAL, ODEN and BARKER 1987). We also find some cases with anisotropy which are counterexamples to the paradigm of strictly monotonic decrease of the (spatial) isolation function on distance (NAGYLAKI 1986). Non-monotonicity in real systems is sometimes interpreted as being due to

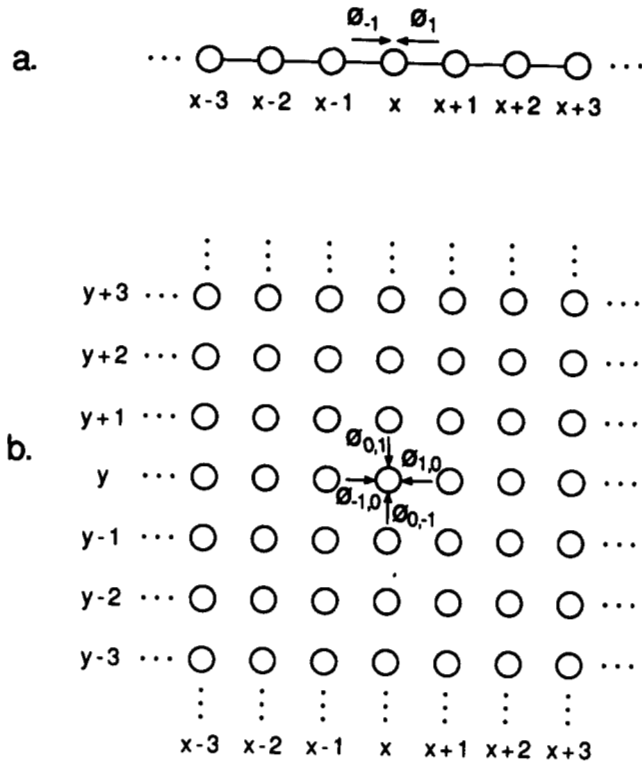


FIGURE 1.—Schematic representation of subpopulations (○), in strict stepping stone migration models, located on: (a) a line and (b) a two-dimensional lattice. (a) x represents the absolute location of subpopulation x ; ϕ_{-1} and ϕ_1 are the migration rates in the directions of the arrows. (b) x and y represent the coordinates for subpopulation (x, y) ; $\phi_{-1,0}$, $\phi_{1,0}$, $\phi_{0,-1}$, $\phi_{0,1}$ are the migration rates from each of the four nearest neighbors to subpopulation (x, y) .

rare long distance migration events or to deviations from neutrality assumptions. It is also shown how space-time correlations of gene frequencies in real systems can be used to develop estimators of migration rates that are based on space-time rather than purely spatial genetic data. Also described for the first time are the properties of the space-time partial correlation coefficients, which provide a unique framework for identifying migration patterns from genetic data in nature. In total, the results in this paper, by viewing transformed migration drift systems as STAR processes, provide frameworks both for studying theoretical space-time distributions and for characterizing experimental systems with space-time genetic data.

RESULTS

General features, life cycles, and recursion equations for gene frequencies in stepping stone type models: For the migration drift models of the type of KIMURA (1953), discrete subpopulations are arranged on a lattice (Figure 1) with uniform distances separating nearest neighbor subpopulations in each spatial dimension, and here all subpopulations are assumed to have equal numbers of individuals, N . The subpopulations are assumed to extend to infinity in every

direction, which simplifies the analyses by avoiding complications arising from boundary subpopulations (FELSENSTEIN 1975). Migration to and from any given subpopulation occurs only with a finite number of other subpopulations. In addition, there is an outside systematic pressure with constant rate, m_∞ , which may represent immigration from a population with fixed allele frequency, q_∞ . This may also be translated into terms of a constant rate of long distance migration, which is the same between all subpopulations, and q_∞ is simply the mean allele frequency, \bar{q} , among all subpopulations. In some contexts, the outside systematic pressure can also be translated into terms of rates of reversible mutation, or certain forms of selection (KIMURA and WEISS 1964).

In general, we let $q_{\mathbf{x},t}$ be the frequency of a gene in an adult subpopulation with spatial coordinates contained in the vector \mathbf{x} and at time generation t , after genetic drift, before migration.

The life cycle for each discrete generation is as in KIMURA and WEISS (1964) and BODMER and CAVALLI-SFORZA (1968). The genetic drift component in the system occurs only within each subpopulation as the gametes are randomly chosen to represent the adult generation. Then the gametes in the next generation are chosen deterministically, based on: 1) the gene frequencies in the adults of each subpopulation in the present generation; 2) the strength of the outside systematic pressure; and 3) the pattern and rates $(\phi_{\mathbf{x},\mathbf{b}})$ of migration between subpopulations. The gametes controlled by the outside systematic pressure have deterministic gene frequency q_∞ (as fixed in the outside population or as determined from mutation rates) or \bar{q} (the mean for all subpopulations in the case of "long distance migration"). The only stochastic component is random sampling during survival of adults from zygotes (genetic drift) within each subpopulation each generation. The gene frequency recursion equations for this life history, using notation similar to WEISS and KIMURA (1965), are:

$$q_{\mathbf{x},t+1} = (1 - \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{x},\mathbf{b}} - m_\infty)q_{\mathbf{x},t} + m_\infty q_\infty + \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{x},\mathbf{b}} q_{\mathbf{x}+\mathbf{b},t} + \xi_{\mathbf{x},t+1}. \tag{1}$$

Here the $\xi_{\mathbf{x},t+1}$ are the "sampling errors" associated with binomial sampling of genes during genetic drift each generation. Each $\phi_{\mathbf{x},\mathbf{b}}$ (for $\mathbf{b} \neq \mathbf{0}$) is the migration rate from all appropriately defined subpopulations to population \mathbf{x} , where \mathbf{x} is a vector of coordinates and \mathbf{b} is a vector of integer values for the spatial lags or relative location of a subpopulation (at $\mathbf{x} + \mathbf{b}$) from \mathbf{x} in each dimension. Thus the pattern of migration is the set of non-zero $\phi_{\mathbf{x},\mathbf{b}}$. As an example, consider the case of one spatial dimension, with isotropic migration between nearest neighbor subpopulations. The non-zero rates are $\phi_{x,-1} = \phi_{x,1} = m_1/2$ and:

$$q_{x,t+1} = (1 - m_1 - m_\infty)q_{x,t} + m_\infty q_\infty + \frac{m_1}{2} (q_{x-1,t} + q_{x+1,t}) + \xi_{x,t+1}.$$

In general, the random variable $\xi_{x,t+1}$ in Equation 1 has conditional mean zero and variance:

$$\text{Var}(\xi_{x,t+1}) = \frac{(1 - q''_{x,t+1})q''_{x,t+1}}{2N} \quad (2)$$

where $q''_{x,t+1}$ = expected value of $q_{x,t+1}$ (conditioned on $q_{x,t}$ for all \mathbf{x}), which equals the right hand side of Equation 1 without the term $\xi_{x,t+1}$.

Let $\tilde{q}_{x,t} = q_{x,t} - \bar{q}$, where \bar{q} is the expected allele frequency in any subpopulation in the system. Thus if the system is at allele frequency equilibrium as determined by the outside systematic pressure (*i.e.*, $E q = q_\infty$), the term $m_\infty q_\infty$ drops out. For the example of isotropic strict stepping stone in one dimension the equation simplifies to:

$$\tilde{q}_{x,t+1} = (1 - m_1 - m_\infty)\tilde{q}_{x,t} + \frac{m_1}{2} (\tilde{q}_{x-1,t} + \tilde{q}_{x+1,t}) + \xi_{x,t+1}.$$

The expected values and variances of the $\xi_{x,t+1}$ are unchanged.

STAR representations of migration drift models:

In order to use the STAR approach, which require homoscedasticity of error terms, the arcsine square root variance stabilizing transformation is applied to the gene frequencies in the general Equation 1. Details are presented in APPENDIX 1. Briefly, if $\tilde{z}_{x,t} = \arcsine(q_{x,t}^{1/2})$ and $z_\infty = \arcsine(q_\infty^{1/2})$ in radians, then the conditional variance of $\tilde{z}_{x,t}$ is the variance σ_a^2 of the new stochastic error $a_{x,t}$, $\sigma_a^2 = 1/8N + O(1/N^2)$, and the conditional expected value of $\tilde{z}_{x,t}$ is approximately:

$$\tilde{z}_{x,t} = \left(1 - \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{x},\mathbf{b}} - m_\infty\right) \tilde{z}_{\mathbf{x},t-1} + m_\infty z_\infty + \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{x},\mathbf{b}} \tilde{z}_{\mathbf{x}+\mathbf{b},t-1} + a_{\mathbf{x},t}. \quad (3)$$

This is true as long as the $q_{x,t}$ are not less than about 0.1 or greater than about 0.9 (see APPENDIX 1). The stochastic, genetic drift component is contained in the variable $a_{x,t}$. The expected value of $a_{x,t}$ is zero, and the important feature is that σ_a^2 is approximately constant at $1/8N$ for all $a_{x,t}$. The correlations between the $\tilde{z}_{x,t}$ are the same as those for $q_{x,t}$ (see APPENDIX 1). The variance of $\tilde{z}_{x,t}$ differs from that of $q_{x,t}$ because of the difference in the variance of the stochastic inputs, and at equilibrium,

$$\text{Var}(q) = 4\bar{q}(1 - \bar{q})\text{Var}(z) \quad (4)$$

where \bar{q} is the mean (equilibrium) gene frequency, q_∞ (BODMER and CAVALLI-SFORZA 1968).

Because we consider only cases in which the system has reached equilibrium (*i.e.*, $\bar{z} = E \tilde{z}_{x,t} = z_\infty$), we

subtract z_∞ from the $\tilde{z}_{x,t}$ to form a new set of (mean adjusted) $z_{x,t}$. Then at equilibrium,

$$z_{x,t} = \left(1 - \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{x},\mathbf{b}} - m_\infty\right) z_{\mathbf{x},t-1} + \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{x},\mathbf{b}} z_{\mathbf{x}+\mathbf{b},t-1} + a_{\mathbf{x},t}. \quad (5)$$

This is a STAR process. With the assumption that migration rates depend only on relative rather than absolute locations in space (see APPENDIX 1), we can write $\phi_{\mathbf{b}}$ instead of $\phi_{\mathbf{x},\mathbf{b}}$:

$$z_{x,t} = \left(1 - \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} - m_\infty\right) z_{\mathbf{x},t-1} + \sum_{\mathbf{b} \neq \mathbf{0}} \phi_{\mathbf{b}} z_{\mathbf{x}+\mathbf{b},t-1} + a_{\mathbf{x},t}. \quad (6)$$

In the specific cases of one and two spatial dimensions outlined below, we will not always use vector notations \mathbf{x} and \mathbf{b} . If we let ϕ_0 equal 1 minus the sum of the $\phi_{\mathbf{b}}$ for \mathbf{b} not equal $(0,0,\dots,0)$, minus m_∞ , then:

$$z_{x,t} = \sum \dots \sum \phi_{(b_1, b_2, \dots, b_k)} z_{(x_1+b_1, x_2+b_2, \dots, x_k+b_k), t-1} + a_{x,t}. \quad (7)$$

Note that the summations in Equation 7 include the vector $\mathbf{0} = (0,0,\dots,0)$, and they are taken over a certain range of spatial lags for each spatial dimension k , *i.e.*, b_k ranges from $-l_{1k}$ to l_{2k} .

In systems where both spatial and temporal stationarity obtain we can define the space-time covariances ($\sigma_{\mathbf{b},n}$) and correlations ($p_{\mathbf{b},n}$), and the spatial covariances ($\sigma_{\mathbf{b},0}$) and correlations ($p_{\mathbf{b},0}$), solely in terms of the spatial (\mathbf{b}) and temporal (n) lags separating pairs of subpopulation gene frequencies in space and time (HOOPER and HEWINGS 1981): $\sigma_{\mathbf{b},n} = E(z_{\mathbf{x},t} z_{\mathbf{x}-\mathbf{b},t-n})$ for $n = 0, \dots, \infty$ and all spatial lag vectors \mathbf{b} ; $p_{\mathbf{b},n} = \sigma_{\mathbf{b},n} / \sigma_z^2$, where $\sigma_z^2 = E(z_{\mathbf{x},t}^2)$ for any \mathbf{x} and t . It is noteworthy that for all weakly stationary processes: $p_{\mathbf{b},n} = p_{-\mathbf{b},-n}$; $p_{0,n} = p_{0,-n}$; and $p_{\mathbf{b},0} = p_{-\mathbf{b},0}$; but for some processes $p_{\mathbf{b},n}$ may not equal $p_{-\mathbf{b},n}$ (for $n \neq 0$) (TANEJA and AROIAN 1980).

Spatial and space-time correlations for general migration patterns: A detailed description of how a stationary migration drift (STAR) process can be inverted into what is known as an infinite parameter space-time moving average (STMA) process is presented in APPENDIX 2. The process Equation 7 is inverted to:

$$z_{x,t} = \Psi(B_{\mathbf{x}}, B_t) a_{\mathbf{x},t} \quad (8)$$

(Equation A11). In other words, each $z_{x,t}$ is a sum of fractions of random inputs from the past. $\Psi(B_{\mathbf{x}}, B_t)$ is known as the generating function for the coefficients for different spatial and temporal lags of the infinite moving average (MA) representation of the process (BENNETT 1979), and it is used for finding the individ-

ual moving average coefficients, the $\psi_{b,n}$ (APPENDIX 2). Each $\psi_{b,n}$ represents the component influence of the subpopulation with spatial lags \mathbf{b} away from \mathbf{x} and temporal lag n away from t , on the value of $z_{x,t}$. In APPENDIX 2, it is shown how this is done in general, and for specific systems as examples. Algorithms are provided below for these specific cases, and FORTRAN programs are available from the author. Finite sums of MA coefficients provide close approximations of $z_{x,t}$, and the space-time variance, σ_z^2 , and the correlations, $p_{b,n}$, can be closely approximated by summing the products of the coefficients $\psi_{b,n}$, times σ_a^2 (APPENDIX 2):

$$\sigma_z^2 = \sigma_a^2 \sum_{\mathbf{m}} \sum_{k=0}^{\infty} \psi_{\mathbf{m},k}^2 \tag{9}$$

$$p_{b,n} = \frac{\sum_{\mathbf{m}} \sum_{k=0}^{\infty} \psi_{\mathbf{m},k} \psi_{\mathbf{m}+\mathbf{b},k+n}}{\sum_{\mathbf{m}} \sum_{k=0}^{\infty} \psi_{\mathbf{m},k}^2} \tag{10}$$

Closely approximate values of σ_z^2 and $p_{b,n}$ can be computed, in many cases with quite moderate summation limits, once the forms of the $\psi_{b,n}$ are known and computed. This formulation (*i.e.*, infinite STMA) can also be used to show that transformed migration drift processes are generally stationary under minimal and realistic assumptions about the ϕ_b , when $m_{\infty} > 0$ (APPENDIX 2).

Important relationships between spatial and space-time correlation coefficients, and estimators for general migration models: In APPENDIX 2 (Equations A14) it is shown that:

$$p_{b,n} = \sum_{\mathbf{m}} \phi_{\mathbf{m}} p_{\mathbf{b}+\mathbf{m},n-1} \tag{11}$$

(except for $n = 0$, $\mathbf{b} = \mathbf{0}$). In general, the summation is taken over all spatial lags \mathbf{m} which exchange migrants, and including $\mathbf{m} = \mathbf{0}$. In addition,

$$\sigma_z^2 = \sigma_a^2 (1 - \sum_{\mathbf{b}} \phi_{\mathbf{b}} p_{\mathbf{b},1})^{-1} \tag{12}$$

(Recall that $\sigma_a^2 = 1/8N$.) These equations alone cannot be solved for the $p_{b,n}$ in terms of the ϕ_b (HOOPER and HEWINGS 1981). However, they are useful for checking sets of $p_{b,n}$ computed from MA coefficients.

One very important subset of the above equations, collectively known as the Yule-Walker equations, can be solved to find estimators for the ϕ_b for most systems (see below) (TANEJA and AROIAN 1980). Thus it is possible to estimate the ϕ_b from space-time data in real populations. Detailed examples of these estimators are provided below for the strict stepping stone models in one and two spatial dimensions.

STAR models for one spatial dimension and with temporal order one: Systems with one spatial dimension simplify to:

$$z_{x,t} = \sum_{b=-l_1}^{l_2} \phi_b z_{x+b,t-1} + a_{x,t} \tag{13}$$

ϕ_{-b} is the migration rate from population $x - b$ to x (Figure 1a). Equations for the spatial and space-time correlation coefficients are, by simplification of Equation 11:

$$p_{b,n} = \sum_{m=-l_1}^{l_2} \phi_m p_{b+m,n-1} \tag{14}$$

except for $b = n = 0$ (note that b is a scalar and the summation is over only one variable, unlike Equation 11).

The strict stepping stone model for one spatial dimension is one in which migration occurs only from the two adjacent neighbors, possibly with different rates, ϕ_{-1} from the left or negative direction, and ϕ_1 from the right or positive direction (see Figure 1a). In this case the process equation (Equation 13) becomes:

$$z_{x,t} = \phi_0 z_{x,t-1} + \phi_{-1} z_{x-1,t-1} + \phi_1 z_{x+1,t-1} + a_{x,t} \tag{15}$$

In APPENDIX 2 (Equation A20) it is shown that,

$$\psi_{b,n} = \phi_0 \psi_{b,n-1} + \phi_1 \psi_{b+1,n-1} + \phi_{-1} \psi_{b-1,n-1} \tag{16}$$

for $|b| < n$. Using this and noting that $\psi_{0,0} = 1$, and all other $\psi_{b,0} = 0$, provides a convenient algorithm for calculating the $\psi_{b,n}$. Equation 16 can be used iteratively starting with $n = 1$, and finding all nonzero coefficients, then with $n = 2$, etc.

An example of the MA coefficients is shown in Table 1 for a anisotropic case with $\phi_{-1} = 0.0405$, $\phi_1 = 0.0810$, $m_{\infty} = 0.01$ (thus $\phi_0 = 0.8685$). For this model there is greater migration from right to left than there is from left to right on the line shown in Figure 1a. Naturally the MA coefficients (random shocks) for $n > 1$ for the right side of x are larger (have more influence on $z_{x,t}$) than those for the left side (Table 1).

The ratio σ_z^2/σ_a^2 was calculated by,

$$\frac{\sigma_z^2}{\sigma_a^2} = \sum_{m=-s}^s \sum_{k=0}^L \psi_{m,k}^2 \tag{17}$$

and the spatial or space-time correlations for $|b| > 0$ or $n > 0$ by,

$$p_{b,n} = \frac{\sum_{m=-s}^s \sum_{k=0}^L \psi_{m,k} \psi_{m+b,k+n}}{\sum_{m=-s}^s \sum_{k=0}^L \psi_{m,k}^2} \tag{18}$$

In general, a reasonably small temporal limit L (*i.e.*, $k = 0, \dots, L$) and spatial limits $-s \leq m \leq s$ suffice for the variance ratio and the spatial correlations, if m_{∞} is not too small.

An example of the space-time correlations is shown

TABLE 1

Moving average coefficients for various generation lags for a one-dimensional case with $m_\infty = 0.01$, $\phi_{-1} = 0.0405$, and $\phi_1 = 0.081$

Lag	$\psi_{4,n}$	$\psi_{3,n}$	$\psi_{2,n}$	$\psi_{1,n}$	$\psi_{0,n}$	$\psi_{-1,n}$	$\psi_{-2,n}$	$\psi_{-3,n}$	$\psi_{-4,n}$
0	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
1	0.00	0.00	0.00	0.04	0.87	0.08	0.00	0.00	0.00
2	0.00	0.00	0.00	0.07	0.76	0.14	0.01	0.00	0.00
3	0.00	0.00	0.00	0.09	0.67	0.18	0.02	0.00	0.00
4	0.00	0.00	0.01	0.11	0.60	0.22	0.03	0.00	0.00
5	0.00	0.00	0.01	0.12	0.54	0.24	0.04	0.00	0.00
6	0.00	0.00	0.01	0.13	0.49	0.25	0.06	0.01	0.00
7	0.00	0.00	0.02	0.13	0.44	0.26	0.07	0.01	0.00
8	0.00	0.00	0.02	0.13	0.41	0.26	0.08	0.02	0.00
9	0.00	0.00	0.02	0.13	0.37	0.27	0.09	0.02	0.00
10	0.00	0.00	0.03	0.13	0.35	0.26	0.10	0.03	0.00
20	0.00	0.01	0.04	0.11	0.20	0.21	0.15	0.07	0.03
40	0.00	0.01	0.03	0.06	0.10	0.12	0.12	0.10	0.07
60	0.00	0.01	0.02	0.04	0.06	0.07	0.08	0.08	0.07
80	0.00	0.01	0.01	0.02	0.03	0.05	0.05	0.06	0.06
100	0.00	0.01	0.01	0.01	0.02	0.03	0.04	0.04	0.04
200	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01
300	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Computed by expanding Equation A19 for each d , and checked using Equation 16 (A20). Values listed after rounding off to two decimals.

TABLE 2

Spatial, $p_{s,0}$, and space-time, $p_{s,n}$, correlations for various generation lags, n , for a one-dimensional case with $m_\infty = 0.01$, $\phi_{-1} = 0.0405$, and $\phi_1 = 0.081$

Lag	$p_{5,n}$	$p_{4,n}$	$p_{3,n}$	$p_{2,n}$	$p_{1,n}$	$p_{0,n}$	$p_{-1,n}$	$p_{-2,n}$	$p_{-3,n}$	$p_{-4,n}$	$p_{-5,n}$
0	0.12	0.19	0.28	0.43	0.65	1.00	0.65	0.43	0.28	0.19	0.12
1	0.12	0.18	0.28	0.42	0.64	0.95	0.66	0.44	0.29	0.19	0.12
2	0.12	0.18	0.27	0.42	0.63	0.90	0.67	0.45	0.29	0.19	0.13
3	0.11	0.18	0.27	0.41	0.61	0.86	0.67	0.45	0.30	0.20	0.13
4	0.11	0.17	0.27	0.40	0.60	0.82	0.67	0.46	0.30	0.20	0.13
5	0.11	0.17	0.26	0.39	0.59	0.79	0.67	0.47	0.31	0.20	0.13
6	0.11	0.17	0.26	0.39	0.58	0.76	0.66	0.47	0.31	0.21	0.13
7	0.11	0.17	0.25	0.38	0.56	0.74	0.66	0.48	0.32	0.21	0.14
8	0.11	0.16	0.25	0.37	0.55	0.71	0.65	0.48	0.32	0.21	0.14
9	0.10	0.16	0.24	0.37	0.54	0.69	0.64	0.48	0.33	0.22	0.14
10	0.10	0.16	0.24	0.36	0.52	0.67	0.63	0.48	0.33	0.22	0.14
20	0.09	0.13	0.20	0.30	0.41	0.51	0.53	0.47	0.36	0.25	0.17

Computed using Equation 18 with temporal limit $L = 500$ and spatial limits $s = 20$. Correlations checked using Equation 19 (A21). Some of the moving average coefficients for this case are listed in Table 1.

in Table 2 for the MA coefficients represented in Table 1. Of course the purely spatial correlations ($n = 0$) are the same in each direction, but naturally the space-time correlations of $z_{s,t}$ with subpopulations to the right ($b < 0$) are greater than the correlations with those to the left ($b > 0$). Interestingly, the space-time correlations with some of the past subpopulations on the right side actually increase as the time lag increases for small time lags (again this reflects the effects of anisotropic migration), and then these decrease as time lag decreases further, as do all correlations for long time lags. In contrast, the space-time correlations for the left side all decrease monotonically with increasing time lag. Spatially symmetric space-time correlations occur if and only if the migra-

tion rates are isotropic (APPENDIX 2). In all examples studied the correlations calculated from the MA coefficients fit closely the specific forms of Equations 11 and 12:

$$p_{b,n} = \phi_0 p_{b,n-1} + \phi_1 p_{b+1,n-1} + \phi_{-1} p_{b-1,n-1} \quad (19)$$

and

$$\frac{\sigma_z^2}{\sigma_a^2} = (1 - \phi_0 p_{0,1} + \phi_1 p_{1,1} + \phi_{-1} p_{-1,1})^{-1}. \quad (20)$$

The spatial correlations for several other models with different migration rates and different values of m_∞ are shown in Figure 2. Briefly, the smaller the systematic pressure the greater the correlations, and

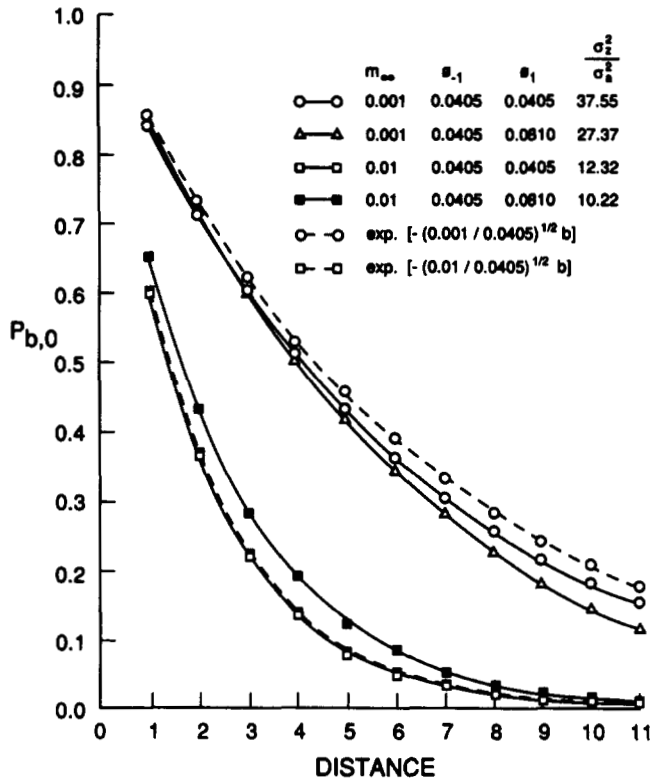


FIGURE 2.—Spatial correlations, $p_{b,0}$, between subpopulations separated by b spatial lags, for several one-dimensional strict stepping stone models with migration rates ϕ_{-1} , and ϕ_1 from nearest neighbors (see figure 1). Also shown are the spatial correlations between gene frequencies, as predicted by KIMURA and WEISS (1964) for the two isotropic cases: $p_{b,0} = \exp[-b\sqrt{m_\infty/\phi_1}]$.

the same is true for the space-time correlations. In the cases with anisotropy (along with greater total immigration, $\phi_{-1} + \phi_1$) the spatial correlations are only slightly greater than those for an isotropic model with migration rates equal to the lower rate of the anisotropic case. In addition, greater values of m_∞ result in smaller variance ratios (σ_z^2/σ_a^2), and the anisotropic cases, with greater total immigration rates, have lower variance ratios. The variance σ_z^2 can be obtained by multiplying the ratio by $\sigma_a^2 = 1/8N$.

Two-dimensional models with temporal order 1: Finite parameter STAR models for two spatial dimensions, with temporal order one, have process equations of the form:

$$z_{x,y,t} = \sum_{a=-k_1}^{k_2} \sum_{b=-l_1}^{l_2} \phi_{b,a} z_{x+b,y+a,t-1} + a_{x,y,t} \quad (21)$$

Here $z_{x,y,t}$ is the transformed mean adjusted gene frequency in a subpopulation with coordinates x in the first spatial dimension and y in the second dimension (horizontal and vertical, respectively, in Figure 1b). Parameters l_1 and l_2 are as in the one dimensional case (*i.e.*, the minimum and maximum lags in the first spatial dimension for subpopulations exchanging migrants with $z_{x,y,t}$), and k_1 and k_2 are the analogous limits for the second spatial dimension.

For the strict stepping stone model, migration occurs only from the four nearest neighbors, thus:

$$z_{x,y,t} = \phi_{0,0} z_{x,y,t-1} + \phi_{-1,0} z_{x-1,y,t-1} + \phi_{1,0} z_{x+1,y,t-1} + \phi_{0,-1} z_{x,y-1,t-1} + \phi_{0,1} z_{x,y+1,t-1} + a_{x,y,t} \quad (22)$$

The MA coefficients can be easily calculated by iterating (FORTRAN program available from author) the formula (APPENDIX 2, Equation A28):

$$\begin{aligned} \psi_{b,a,n} = & \phi_{0,0} \psi_{b,a,n-1} + \phi_{-1,0} \psi_{b-1,a,n-1} \\ & + \phi_{1,0} \psi_{b+1,a,n-1} \\ & + \phi_{0,-1} \psi_{b,a-1,n-1} \\ & + \phi_{0,1} \psi_{b,a+1,n-1} \end{aligned} \quad (23)$$

and noting that $\psi_{0,0,0} = 1.0$ and, $\psi_{b,a,0} = 0$ for all other a and b . Table 3 shows the MA coefficients for generations 1, 10 and 100 for anisotropic migration rates $\phi_{-1,0} = 0.02$, $\phi_{1,0} = 0.01$, $\phi_{0,-1} = 0.01$, $\phi_{0,1} = 0.04$, and with systematic pressure $m_\infty = 0.01$. Thus there is more migration for left to right (negative to positive in x) and from top to bottom (positive to negative in y) than right to left and bottom to top. Values of $\psi_{b,a,n}$ are greater for $b > 0$, and for $a < 0$. As for the one-dimensional case the spatial gradient of $\psi_{b,a,n}$ becomes flatter as n becomes large.

The ratio of the variances, σ_z^2/σ_a^2 , is calculated by:

$$\frac{\sigma_z^2}{\sigma_a^2} = \frac{\sum_s \sum_t \sum_u \psi_{s,t,u}^2}{\sum_s \sum_t \sum_u \psi_{s,t,u}^2} \quad (24)$$

and the space-time correlations by:

$$p_{b,a,n} = \frac{\sum_s \sum_t \sum_u \psi_{s,t,u} \psi_{s-b,t-a,u-n}}{\sum_s \sum_t \sum_u \psi_{s,t,u}^2} \quad (25)$$

with appropriate temporal and spatial limits to the summations.

Values of $p_{b,a,0}$, and $p_{b,a,5}$ for the anisotropic case above are shown in Table 4. The space-time correlations are greater for past subpopulations that are to the left or "above" present subpopulations, as expected from the MA coefficients (Table 3). The spatial correlations differ between the two spatial dimensions, but are the same for opposite directions within a dimension. Spatial correlations for several other anisotropic migration models are shown in Table 5. Anisotropy in only one dimension causes asymmetry in the space-time correlations only in the same dimension (see example Table 4). Interestingly, in extreme cases, where there is migration only in one direction in each dimension, the MA coefficients in one direction (for each dimension) are zero, yet the correlations for short distances remain large. This reflects the shared history of local groups of subpopulations.

In general, nonequivalence of the migration rates for different dimensions causes nonequivalence of the

TABLE 3

Moving average coefficients, $\psi_{b,a,n}$, for generations $n = 1, 10$ and 100 for a case with $m_\infty = 0.01$, $\phi_{-1,0} = 0.02$, $\phi_{1,0} = 0.01$, $\phi_{0,-1} = 0.01$, $\phi_{1,1} = 0.04$

Generation	$\psi_{3,a,1}$	$\psi_{2,a,1}$	$\psi_{1,a,1}$	$\psi_{0,a,1}$	$\psi_{-1,a,1}$	$\psi_{-2,a,1}$	$\psi_{-3,a,1}$
Generation 1							
$\psi_{b,-3,1}$	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\psi_{b,-2,1}$	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\psi_{b,-1,1}$	0.00	0.00	0.00	0.04	0.00	0.00	0.00
$\psi_{b,0,1}$	0.00	0.00	0.02	0.91	0.01	0.00	0.00
$\psi_{b,1,1}$	0.00	0.00	0.00	0.01	0.00	0.00	0.00
$\psi_{b,2,1}$	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$\psi_{b,3,1}$	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Generation 10							
	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.01	0.04	0.00	0.00	0.00
	0.00	0.00	0.04	0.18	0.02	0.00	0.00
	0.00	0.01	0.09	0.42	0.05	0.00	0.00
	0.00	0.00	0.01	0.04	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Generation 100							
	0.01	0.01	0.02	0.01	0.01	0.00	0.00
	0.01	0.01	0.02	0.01	0.01	0.00	0.00
	0.01	0.01	0.01	0.01	0.01	0.00	0.00
	0.00	0.01	0.01	0.01	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Computed using Equation 23 (A28) and checked using Equation A27. Values listed after rounding off to two decimals.

TABLE 4

Spatial correlations, $p_{b,a,0}$, and space-time correlations for temporal lag five, $p_{b,a,5}$, for a two-dimensional case with $m_\infty = 0.01$, $\phi_{-1,0} = 0.02$, $\phi_{1,0} = 0.01$, $\phi_{0,-1} = 0.01$, $\phi_{0,1} = 0.04$

	$p_{4,a,0}$	$p_{3,a,0}$	$p_{2,a,0}$	$p_{1,a,0}$	$p_{0,a,0}$	$p_{-1,a,0}$	$p_{-2,a,0}$	$p_{-3,a,0}$	$p_{-4,a,0}$
$p_{b,-4,0}$	0.00	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.00
$p_{b,-3,0}$	0.01	0.01	0.02	0.04	0.06	0.04	0.02	0.01	0.01
$p_{b,-2,0}$	0.01	0.02	0.05	0.09	0.15	0.09	0.05	0.02	0.01
$p_{b,-1,0}$	0.01	0.03	0.07	0.17	0.37	0.17	0.07	0.03	0.01
$p_{b,0,0}$	0.01	0.03	0.09	0.27	1.00	0.27	0.09	0.03	0.01
$p_{b,1,0}$	0.01	0.03	0.07	0.17	0.37	0.17	0.07	0.03	0.01
$p_{b,2,0}$	0.01	0.02	0.05	0.09	0.15	0.09	0.05	0.02	0.01
$p_{b,3,0}$	0.01	0.01	0.02	0.04	0.06	0.04	0.02	0.01	0.01
$p_{b,4,0}$	0.00	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.00
	$p_{4,a,5}$	$p_{3,a,5}$	$p_{2,a,5}$	$p_{1,a,5}$	$p_{0,a,5}$	$p_{-1,a,5}$	$p_{-2,a,5}$	$p_{-3,a,5}$	$p_{-4,a,5}$
$p_{b,-4,5}$	0.00	0.01	0.01	0.02	0.03	0.02	0.01	0.01	0.00
$p_{b,-3,5}$	0.01	0.01	0.02	0.05	0.07	0.05	0.03	0.01	0.01
$p_{b,-2,5}$	0.01	0.02	0.05	0.10	0.17	0.10	0.05	0.02	0.01
$p_{b,-1,5}$	0.01	0.03	0.08	0.19	0.40	0.18	0.07	0.03	0.01
$p_{b,0,5}$	0.01	0.03	0.10	0.28	0.73	0.25	0.08	0.03	0.01
$p_{b,1,5}$	0.01	0.03	0.07	0.17	0.31	0.16	0.06	0.03	0.01
$p_{b,2,5}$	0.01	0.02	0.04	0.09	0.13	0.08	0.04	0.02	0.01
$p_{b,3,5}$	0.01	0.01	0.02	0.04	0.05	0.04	0.02	0.01	0.00
$p_{b,4,5}$	0.00	0.01	0.01	0.02	0.02	0.02	0.01	0.01	0.00

Computed using Equation 25 with temporal limit $L = 200$, and spatial limit ± 5 in each dimension. Some moving average coefficients for this case are listed in Table 3. Values listed after rounding off to two decimals.

spatial (Table 5) and space-time (not shown) correlations for the same distance, between the two dimensions. In the extreme case, where migration occurs exclusively in one dimension (results not shown), the spatial and space-time correlations are zero for spatial

lags in the dimension without migration, and the correlations for nonzero lags only in the other dimension, follow that of the one dimensional models discussed above. The reasons for these features can be seen in the relationships among the $p_{b,a,n}$, which come

TABLE 5

Spatial correlations, $\rho_{b,a,0}$, for different two-dimension models with anisotropic migration rates and different systematic pressures, m_∞ .

Spatial lag a in y coordi- nate	Spatial lag b in x coordinate						
	0	1	2	3	4	5	6
a) $m_\infty = 0.001, \phi_{-1,0} = \phi_{1,0} = 0.03, \phi_{0,-1} = \phi_{0,1} = 0.01$							
0	1.00	0.58	0.37	0.24	0.16	0.10	0.07
1	0.40	0.34	0.26	0.19	0.14	0.09	0.06
2	0.20	0.19	0.16	0.13	0.10	0.07	0.05
3	0.11	0.11	0.09	0.08	0.06	0.05	0.03
4	0.06	0.06	0.05	0.05	0.04	0.03	0.02
5	0.04	0.03	0.03	0.03	0.02	0.02	0.01
6	0.02	0.02	0.02	0.01	0.01	0.01	0.01
b) $m_\infty = 0.01, \phi_{-1,0} = \phi_{1,0} = 0.03, \phi_{0,-1} = \phi_{0,1} = 0.01$							
0	1.00	0.42	0.19	0.09	0.04	0.02	0.01
1	0.22	0.16	0.10	0.05	0.03	0.01	0.01
2	0.06	0.05	0.04	0.03	0.01	0.01	0.00
3	0.02	0.02	0.01	0.01	0.01	0.00	0.00
4	0.01	0.01	0.00	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.00	0.00
c) $m_\infty = 0.01, \phi_{-1,0} = 0.03, \phi_{1,0} = 0.01, \phi_{0,-1} = 0.01, \phi_{0,1} = 0.03$							
0	1.00	0.32	0.12	0.05	0.02	0.01	0.00
1	0.32	0.18	0.09	0.04	0.02	0.01	0.00
2	0.12	0.09	0.05	0.02	0.01	0.00	0.00
3	0.05	0.04	0.02	0.01	0.01	0.00	0.00
4	0.02	0.02	0.01	0.01	0.00	0.00	0.00
5	0.01	0.01	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.00	0.00
d) $m_\infty = 0.01, \phi_{-1,0} = \phi_{1,0} = \phi_{0,-1} = 0.01, \phi_{0,1} = 0.05$							
0	1.00	0.22	0.06	0.02	0.00	0.00	0.00
1	0.42	0.15	0.05	0.01	0.00	0.00	0.00
2	0.18	0.09	0.03	0.01	0.00	0.00	0.00
3	0.08	0.04	0.02	0.01	0.00	0.00	0.00
4	0.03	0.02	0.01	0.00	0.00	0.00	0.00
5	0.01	0.01	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.00	0.00
e) $m_\infty = 0.01, \phi_{-1,0} = 0.015, \phi_{1,0} = 0.035, \phi_{0,-1} = 0.025, \phi_{0,1} = 0.005$							
0	1.00	0.37	0.15	0.06	0.03	0.01	0.00
1	0.27	0.17	0.09	0.05	0.02	0.01	0.00
2	0.09	0.07	0.05	0.03	0.01	0.01	0.00
3	0.03	0.03	0.02	0.01	0.01	0.00	0.00
4	0.01	0.01	0.01	0.00	0.00	0.00	0.00
5	0.00	0.00	0.00	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Only values for positive spatial lags are listed (as in all cases $\rho_{-b,a,0} = \rho_{b,-a,0} = \rho_{-b,-a,0} = \rho_{b,a,0}$).

from specific forms of Equations 11 and 12:

$$\frac{\sigma_z^2}{\sigma_a^2} = (1 - \phi_{0,0}\rho_{0,0,1} + \phi_{1,0}\rho_{1,0,1} + \phi_{-1,0}\rho_{-1,0,1} + \phi_{0,1}\rho_{0,1,1} + \phi_{0,-1}\rho_{0,-1,1})^{-1} \tag{26}$$

$$\begin{aligned} \rho_{b,a,n} = & \phi_{0,0}\rho_{b,a,n-1} + \phi_{1,0}\rho_{b+1,a,n-1} \\ & + \phi_{-1,0}\rho_{b-1,a,n-1} \\ & + \phi_{0,1}\rho_{b,a+1,n-1} \\ & + \phi_{0,-1}\rho_{b,a-1,n-1}. \end{aligned} \tag{27}$$

Spatial correlations for several isotropic migration models are shown in Figure 3. The spatial correlations are much smaller than for isotropic one dimensional cases with similar rates of overall immigration into a

subpopulation. It appears that migration is much more effective in spatially "spreading" the effects of local stochastic events in two spatial dimensions than in the one dimensional case. This, at least in part, is due to the fact that matrices of correlations are positive definite, which places more constraints on the values of the correlations for the two-dimensional cases [e.g., TANEJA and AROIAN (1980)]. In addition, greater systematic pressure has a strong effect of reducing spatial correlations and the spatial variance. The effects of parameters on the space-time correlations are similar to those on spatial correlations with the same spatial lag, and detailed results are not listed here. For a wide range of systematic pressures (m_∞ ranging from 0.0002 to 0.01) and migration rates, there are large spatial and space-time correlations for near neighbors,

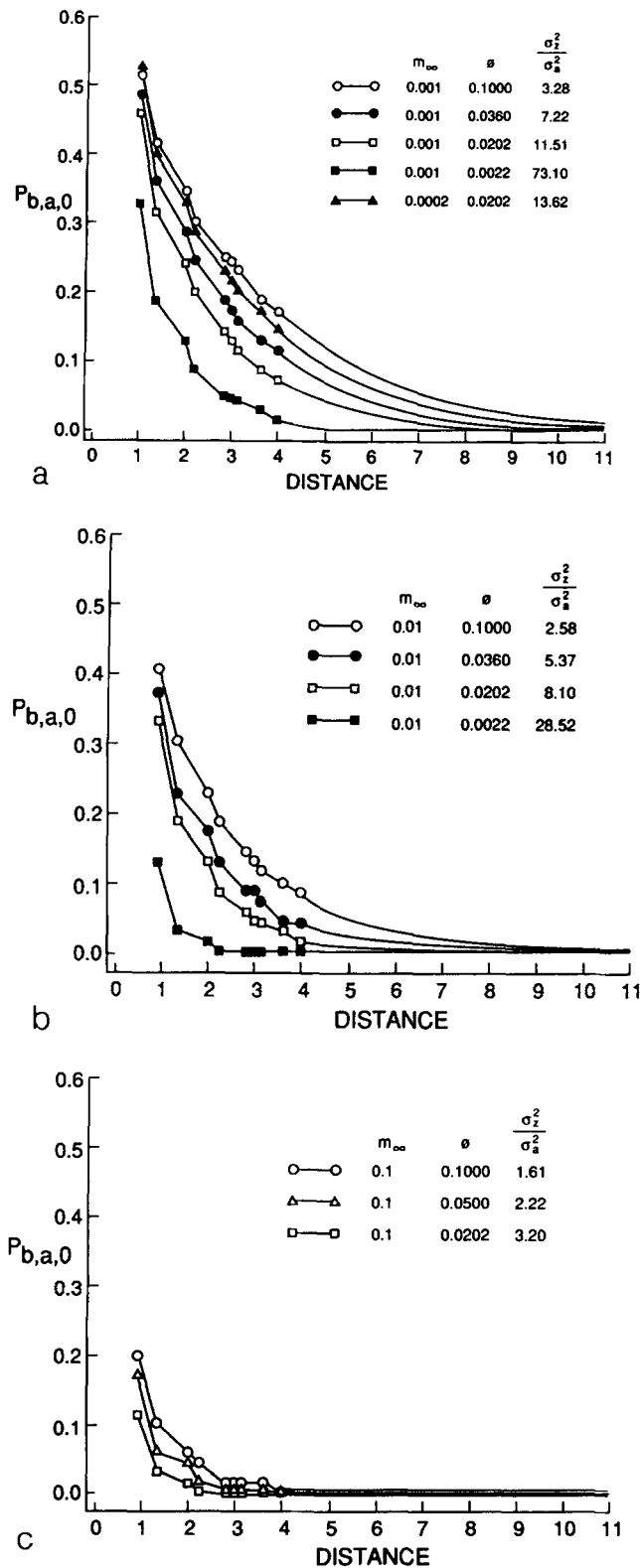


FIGURE 3.—Spatial correlations, $p_{b,a,0}$ as a function of distance, $d = (a^2 + b^2)^{1/2}$. In all cases $\phi = \phi_{-1,0} = \phi_{1,0} = \phi_{0,-1} = \phi_{0,1}$. (a) Four cases with $m_\infty = 0.001$, one case with $m_\infty = 0.0002$. (b) Four cases with $m_\infty = 0.01$. (c) Three cases with $m_\infty = 0.1$. In all cases, exact values are plotted for $d < 4.0$, and beyond 4.0 the graphs are “smoothed” (see text).

and correlations rapidly drop to near zero values for greater spatial lags. Spatial and space-time correlations are much smaller where $m_\infty = 0.1$. Greater migration rates result in greater spatial (and space-time) correlations. In all of the cases studied, the correlations decrease monotonically at least up to distances of four units. For greater distances the values sometimes did not decline *exactly* monotonically. The deviate correlations involved were always small, and always involved small increases (less than 0.005) above values for at most two, for always only slightly shorter distances.

Process identification and estimation of migration rates: Space-time genetic data can be used to identify features of the patterns of migration in a real system of subpopulations. It is assumed that the system is the usual case where migration occurs only between some finite set of spatially proximal subpopulations (up to some limits of spatial and temporal lags). Then identification can be effected by examination of the *partial correlations*. Partial correlation coefficients can be conveniently (but not necessarily) defined as the correlation between $z_{x,t}$ and $z_{x+b,t-k}$ *conditioned* on all of the spatially *and* temporally “intermediate” variables [e.g., HOOPER and HEWINGS (1981)]. For example, the intermediate variables for the one dimensional case with b and k positive are $\{z_{y,t-s}; y = x, x + 1, \dots, x + b, \text{ and } s = 1, \dots, k\}$; except for where $y = x + b$ and $s = k$. Under this definition, the *partial correlations* are zero for pairs of subpopulations separated by more than the greatest spatial lag between subpopulations exchanging migrants, or separated in time by more than one generation, for first order temporal models. The distance beyond which partial correlations are zero in real systems indicates roughly the spatial limits on migration, within the degree of statistical error.

Once the migration pattern for a real system has been identified or roughly delineated, or specified either by assumption or independent information, then estimators of the ϕ_b can be obtained from space-time data. This contrasts estimators [e.g., SLATKIN (1985)] which are based solely on spatial data. In many real systems, the pattern of migration may closely approximate and thus be treated as a strict stepping stone pattern. In general, limits on the spatial lags must be contained in the vectors \mathbf{l}_1 and \mathbf{l}_2 , or in the dimensional case the scalars l_1 and l_2 . If we form a set of equations of the type of Equations 11, by multiplying Equation 7 by the coefficient of each ϕ_b in Equation 7 and taking the expected values, then we will have a (usually nonsingular) set of k equations (linear in the ϕ_b) with k unknowns, that can be solved using standard methods. For example, in the general one-dimensional system (Equation 13), there are $k = l_1 + l_2 + 1$ equations and unknowns. These equations are

known as the Yule-Walker equations, and their solutions after replacing the space-time correlations with their estimates, give the Yule-Walker estimators of the migration parameters. Estimators of m_∞ can be obtained by subtracting the sum of the migration rates from 1.0. Also, in general it is possible to find the variances and covariances between the estimators (AROIAN 1985). The expressions for the estimators are usually very complex, and although it is preferable to simply use matrix algebraic operations, solutions are provided below for the one dimensional stepping stone model.

For the one-dimensional anisotropic strict stepping stone migration model, we can derive the Yule-Walker equations, which are (after substituting one for $p_{0,0}$ and $p_{b,0}$ for $p_{-b,0}$):

$$\begin{aligned} p_{0,1} &= \phi_0 + \phi_{-1}p_{1,0} + \phi_1p_{1,0} \\ p_{1,1} &= \phi_0p_{1,0} + \phi_{-1} + \phi_1p_{2,0} \\ p_{-1,1} &= \phi_0p_{1,0} + \phi_{-1}p_{2,0} + \phi_1 \end{aligned} \quad (28)$$

which have the solutions:

$$\begin{aligned} \phi_1 &= \frac{(1 - p_{1,0}^2)(p_{-1,1} - p_{0,1}p_{1,0}) - (p_{1,1} - p_{0,1}p_{1,0})(p_{2,0} - p_{1,0}^2)}{(1 - p_{1,0}^2)^2 - (p_{2,0} - p_{1,0}^2)^2} \\ \phi_{-1} &= \frac{(1 - p_{1,0}^2)(p_{1,1} - p_{0,1}p_{1,0}) - (p_{-1,1} - p_{0,1}p_{1,0})(p_{2,0} - p_{1,0}^2)}{(1 - p_{1,0}^2)^2 - (p_{2,0} - p_{1,0}^2)^2} \\ \phi_0 &= p_{0,1} - \frac{p_{1,0}(1 - p_{1,0}^2) - (p_{2,0} - p_{1,0}^2)}{(1 - p_{1,0}^2)^2 - (p_{2,0} - p_{1,0}^2)^2}. \end{aligned} \quad (29)$$

Estimates can be calculated by substituting estimates of $p_{b,n}$ for the $p_{b,n}$. In the isotropic case, the expressions for Yule-Walker estimators simplify considerably.

In the two dimension strict stepping stone model we find the equations:

$$\begin{aligned} p_{-1,0,1} &= \phi_{0,0}p_{1,0,0} + \phi_{1,0} + \phi_{-1,0}p_{2,0,0} \\ &\quad + \phi_{0,1}p_{1,1,0} + \phi_{0,-1}p_{1,1,0} \\ p_{1,0,1} &= \phi_{0,0}p_{1,0,0} + \phi_{1,0}p_{2,0,0} + \phi_{-1,0} \\ &\quad + \phi_{0,1}p_{1,1,0} + \phi_{0,-1}p_{1,1,0} \\ p_{0,0,1} &= \phi_{0,0} + \phi_{1,0}p_{1,0,0} + \phi_{-1,0}p_{1,0,0} \\ &\quad + \phi_{0,1}p_{0,1,0} + \phi_{0,-1}p_{0,1,0} \\ p_{0,-1,1} &= \phi_{0,0}p_{0,1,0} + \phi_{1,0}p_{1,1,0} + \phi_{-1,0}p_{1,1,0} \\ &\quad + \phi_{0,1} + \phi_{0,-1}p_{0,2,0} \\ p_{0,1,1} &= \phi_{0,0}p_{0,1,0} + \phi_{1,0}p_{1,1,0} + \phi_{-1,0}p_{1,1,0} \\ &\quad + \phi_{0,1}p_{0,2,0} + \phi_{0,-1}. \end{aligned} \quad (30)$$

Because algebraic solutions for the $\phi_{b,a,n}$ are very com-

plex, they are not listed here; however, the above system of equations can be solved using standard methods.

DISCUSSION

In this paper it is shown how STAR models can be used to characterize with great detail the distribution of genetic variation over space and time in migration drift systems. STAR results developed include novel descriptions of the space-time correlations of gene frequencies in migration drift systems. Together with the variance, the space-time correlation structure constitutes a *complete* space-time specification for many theoretical genetic drift migration systems. Analyses of STAR process representations contribute new information to understanding the relations of space-time correlation structure and variance of gene frequencies to the patterns and rates of migration, the dimensionality of the system, and the strengths of systematic forces. This can also be viewed as representing information on the interactions of temporal changes with spatial structure of gene frequencies. In addition, STAR models form a detailed framework for studying real systems, for either spatial or space-time data [see also CLIFF and ORD (1981)]. Thus STAR processes can be used not only as theoretical models, but also in principle as statistical models for identifying, describing, and interpreting the processes underlying the history of real systems.

General theoretical systems: In the present paper, it was shown how space-time correlations, as well as spatial correlations and variances, can be found for most types of patterns of migration. Stationary distributions of the STAR process representations exist if there is a nonzero uniform systematic pressure, m_∞ , and there are some biologically reasonable constraints on the migration patterns. Spatial and space-time correlations can, in principle, be found for the stationary distributions of even very complex migration models. In the present paper this is done by using backshift operators and the individual coefficients, $\psi_{b,n}$, of the infinite parameter moving average (STMA) representation, which is found by inverting a (finite parameter) stationary STAR process. This is an extension of the BOX and JENKINS (1976) methods of analyzing time series. Here the methods of the present paper depart from previous methods of analysis [e.g., ROGERS and HARENDING (1986)]. The generality of the inversion method extends to systems in which subpopulations are not regularly spaced on a lattice. The only requirement is that fixed migration rates (and backshift operators) can be assigned to well-defined subsets of subpopulations (HOOPER and HEWINGS 1981). Although the present paper considers only systems with infinite sets of subpopulations, the same principles can be applied to systems with finite sets. The methods

extend also to space-time systems with temporal orders greater than one. For example, time delayed migration effects are expected in plant species with seed migration and seed dormancy. Thus the basic framework described here seems promising for expansion into several important theoretical areas.

Results for theoretical systems for complex migration patterns are not expressed in simple forms (ROGERS and HARPENDING 1986). As have others, we found that for any kind of isolation by distance migration pattern, the spatial correlations are generally largest among spatially proximal subpopulations, and to this we add the somewhat unsurprising result that this is also generally true for the space-time correlations. However, where migration rates are strongly anisotropic, the space-time correlations can be substantially *smaller* for the most spatially proximal subpopulations compared to less proximal subpopulations, for longer back time lags. In other words, with strongly anisotropic systems, spatial proximity per se is not very indicative of the relative amount of influence from an existing subpopulation on future subpopulations at other locations, even in strict stepping stone migration models. Moreover, in anisotropic systems the space-time correlations for a given spatial lag do not always decrease as the time lag between populations increases, even in one dimensional strict stepping stone migration models. Increasing the systematic pressure generally decreases the space-time correlations as well as the spatial correlations and the variance. Although general migration patterns rarely give rise to "explicit, general formulas" for the correlations or variance (ROGERS and HARPENDING 1986), one general theoretical result for the *partial* space-time correlations is very simple. Under the definition used in this work [HOOPER and HEWINGS (1981); cf. MARTIN and OEPFEN (1975)], the partial correlations must be zero for pairs of subpopulations separated by more than the greatest spatial lag between subpopulations exchanging migrants, or separated in time by more than one generation, for first order temporal models.

Limitations to the present methods include the assumption that the effects of migration are deterministic, as do many other methods [e.g., KIMURA and WEISS (1964), MALÉCOT (1948, 1973), HARPENDING (1973), SAWYER (1976), MORTON (1982), and NAGYLAKI (1986)]. Thus STAR results are strictly applicable to systems in which large numbers (relative to N) of propagules (not adults) migrate. The present paper does not consider other important models such as those of ROGERS (1988) and FIX (1978) which incorporate stochastic migration effects; however we have found that it is possible to incorporate many forms of stochastic migration effects into modified STAR systems (B. K. EPPERSON, unpublished results). In addition, the systematic force is assumed to be determin-

istic and uniform over all subpopulations [cf., e.g., BODMER and CAVALLI-SFORZA (1968)]. Finally, in formulating migration drift systems as STAR stochastic processes, the original spatial time series of gene frequency evolution $\{q_{x,t}\}$ was transformed to the process $\{z_{x,t}\}$ using the arcsine square root transformation (FISHER and FORD 1947; BODMER and CAVALLI-SFORZA 1968). The transformed process $\{z_{x,t}\}$ is an acceptable approximate representation of the process $\{q_{x,t}\}$ as long as the gene frequencies are not close to zero or one (MOSTELLER and YOUTZ 1961; BODMER and CAVALLI-SFORZA 1968). Previous methods for finding gene frequency correlations [e.g., KIMURA and WEISS (1964) and NAGYLAKI (1986)] have often used different approximations. Under the conditions of approximation, the scales of the parameters in the recursions of the transformed process $\{z_{x,t}\}$ are the same as those in the untransformed process $\{q_{x,t}\}$, and the correlations for $\{z_{x,t}\}$ are the same as those for $\{q_{x,t}\}$; however the variance differs (BODMER and CAVALLI-SFORZA 1968).

One- and two-dimensional theoretical stepping stone systems: Several of the most important stepping stone type processes for one and two spatial dimensions were studied in some detail. Results on space-time correlations of gene frequencies are new to population genetics. FORTRAN programs that use the MA coefficients to compute the space-time correlations together with the spatial correlations and variance in either anisotropic or isotropic strict stepping stone systems are available from the author. Space-time correlations are generally larger in cases where m_{∞} is smaller or where migration rates are larger, and are generally smaller in the two dimensional models. Unlike spatial correlations, space-time correlations may differ substantially between directions within a spatial dimension as well as differ between dimensions, in anisotropic systems. Naturally, space-time correlations are greater for the past subpopulations that were located in the direction opposite the direction of greater migration flow. The differences can be substantial, even for time lags as small as five generations. Thus directional migration should be detectable in space-time data with similar spans of generations.

The results for partial correlations, as defined in the present paper, are simply stated. For strict stepping stone models (isotropic or anisotropic), the partials are zero for distances or time lags greater than one.

Some of our results on spatial correlations and variance are new and others are paralleled in previous studies, although the approximations, expressions, and computational methods are different. The spatial correlations were large for nearest neighbors and generally decrease smoothly as the distance of separation increases. However, it is interesting that we

were able to find some cases of anisotropic two-dimensional strict stepping stone processes in which the decrease was not exactly monotonic, contrary to generalized results on kinship coefficients (NAGYLAKI 1986). Some of the results which are directly comparable to previous studies for strict stepping stone systems in one and two dimensions are briefly: 1) greater systematic pressures cause greater homogenization of the surface, resulting in lower spatial auto-correlations and smaller spatial variances; 2) for isotropic cases, greater amounts of migration result in *greater* spatial correlations, but also result in lower variances in frequencies; 3) spatial correlations are much greater in the one-dimension models compared to two dimension models with similar total rates of immigration into each subpopulation and similar values of m_∞ . New features revealed include that anisotropic migration rates tend to produce spatial correlations similar to those of isotropic migration models with rates equal that of the lower rate, at least in the cases studied. In addition, for two spatial dimension cases, differences between the two dimensions in migration rates cause differences between the dimensions in spatial correlations for the same absolute value lag, but values of spatial correlations are the same for the two directions within a dimension. The differences can be substantial with as little as two to four fold differences in migration rates in different dimensions (Table 5). Thus this level of dimensional directionality of spatial correlations may exist in nature (SOKAL, ODEN and BARKER 1987).

For specific cases of isotropic one dimensional models, the correlations and variances computed from the formulas of KIMURA and WEISS (1964):

$$p_{b,0} = e^{-b} \sqrt{\frac{m_\infty}{\phi_1}}$$

$$V(q_{x,t}) = \frac{\bar{q}(1 - \bar{q})}{1 + 8N\sqrt{\phi_1 m_\infty}}$$

and the formula $\sigma_q^2 = 4\bar{q}(1 - \bar{q}) \sigma_z^2 + O(1/N^2)$ from BODMER (1960), fit very closely those calculated using STAR methods (Figure 2). For the variance ratios, with $\phi_1 = 0.0405$, for $m_\infty = 0.01$, the predicted value is 12.42, and for $m_\infty = 0.001$ the value is 39.28. The values calculated are similar, 12.32 and 37.55, respectively (Figure 2). It is worth noting that the spatial correlations for the several isotropic two dimensional models reported here, with chosen parameters similar to some recent simulations by SLATKIN and ARTER (1991), fit fairly closely (after spatial rescaling), the values of Moran's I -statistics calculated on the gene frequencies in these simulations.

Applications to real systems: STAR models also form a general framework for statistical models for a broad range of space-time systems. Good discussions

of the multifaceted statistical "structure" of STAR models can be found in BENNETT (1979), CLIFF and ORD (1981), and UPTON and FINGLETON (1985). Moreover, there are well established statistical procedures and some computer programs for analyzing space-time data in the STAR framework (UPTON and FINGLETON 1985). Briefly stated, this complex structure can be used to analyze space-time data (or spatial data) alone or together with different forms of adjunct information, and information may enter in at different levels. STAR processes can be used as statistical models to identify, describe, and interpret the processes underlying the history of a real system. Theoretical analyses are useful for forecasting a real system, if the parameters and the distributions at present are known (BENNETT 1979). For example, if independent information on migration rates, even for quite complex migration patterns in real populations is known, expected values of $\{z_{x,t}\}$ as well as the spatial and space-time correlations for neutral loci can be calculated. We can also compare statistically observed space-time correlations for data to the theoretical correlations calculated from STAR results. Thus the STAR framework provides a degree of generality that seems unique in population genetics. Moreover, although in order to use the STAR methods, the arcsine square root transformation must be applied to space-time gene frequency data, arguably this transformation should be applied for many other situations in population genetics (for example in ANOVA treatments of gene frequency data), for improved statistical properties.

In the present paper, the foci were on estimation of the migration rates and systematic force, and also on the partial correlation coefficients because of the simplicity of presentation for the use of partials in process identification. Once a migration pattern (*i.e.*, the set of non zero ϕ_b) is estimated, approximated or assumed, it is possible in general to obtain equations relating the space-time correlations to the migration parameters, the ϕ_b . These equations can be used to find Yule-Walker estimates of the rates ϕ_b , after substituting sample estimates for the $p_{b,n}$. These estimators can be expressed explicitly (as was done in the Results for a special case), although it is more practical to use matrix operations in computerized calculations of estimates of ϕ_b from data. AROIAN (1985) investigated the statistical properties of the estimators, and their variances and relationships to least squares and maximum likelihood estimators. It appears that these are the first published estimators of migration rates based on space-time rather than spatial sets of genetic data. The relative efficiency of the different types of estimators awaits thorough analysis.

It is worth noting that Moran's I -statistic (CLIFF and

ORD 1981), a popular measure of spatial correlation, will differ slightly from the theoretical correlations, which are always positive. Moran's *I*-statistic is based on the mean for a finite set of subpopulations (not the grand mean of an infinite, stationary process), and may be negative for large spatial lags (BARBUJANI 1987). The differences between the two sets of correlation measures, especially for short distances, presumably become trivial when large numbers of subpopulations are sampled.

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APPENDIX 1

Transformation of migration-drift models into STAR representations: Homoscedasticity of stochastic error terms is obtained by using the arcsine square root transformation on the gene frequencies (BODMER and CAVALLI-SFORZA 1968). Let $\tilde{z}_{\mathbf{x},t} = \arcsine(q_{\mathbf{x},t}^{1/2})$, $y_{\mathbf{x},t} = \arcsine(q_{\mathbf{x},t}''^{1/2})$, and $z_{\infty} = \arcsine(q_{\infty}^{1/2})$. Then, in radians, the conditional variance of $\tilde{z}_{\mathbf{x},t} = 1/8N + O(1/N^2)$, and the conditional expected value of $\tilde{z}_{\mathbf{x},t} = y_{\mathbf{x},t} + O(1/N)$. The approximations are close, and the variances independent of $y_{\mathbf{x},t}$ for a region around $q_{\mathbf{x},t}'' = 0.5$, which region extends close to 1.0 and 0 as N becomes large (MOSTELLER and YOUTZ 1961). After substituting for $q_{\mathbf{x},t}''$ in text Equation 1, we have

$$\sin^2 y_{\mathbf{x},t} = \left(1 - \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} - m_{\infty}\right) \sin^2 \tilde{z}_{\mathbf{x},t-1} + m_{\infty} \sin^2 z_{\infty} + \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} \sin^2 \tilde{z}_{\mathbf{x}+\mathbf{b},t-1} \quad (\text{A1})$$

Using a Taylor series expansion about $\pi/4$, it can be shown that

$$\sin^2 \tilde{z} = \tilde{z} + 1/2 - \pi/4 - O(\tilde{z} - \pi/4)^3 \quad (\text{A2})$$

which provides a close approximation as long as the gene frequencies are not less than about 0.1 or greater than about 0.9. Thus the expectation of $\tilde{z}_{\mathbf{x},t}$ (conditioned on $\tilde{z}_{\mathbf{x},t-1}$ for all \mathbf{x}), is,

$$y_{\mathbf{x},t} = \left(1 - \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} - m_{\infty}\right) \tilde{z}_{\mathbf{x},t-1} + m_{\infty} z_{\infty} + \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} \tilde{z}_{\mathbf{x}+\mathbf{b},t-1} + O(\tilde{z} - \pi/4)^3 \quad (\text{A3})$$

and the conditional variance is approximately $1/8N$. As long as the stochastic variation is such that the gene frequencies in subpopulations are not less than about 0.1 or greater than 0.9, then the approximation errors in the above equations do not accumulate significantly (BODMER and CAVALLI-SFORZA 1968). Further studies are required to better characterize the approximation near these bounds. The transformed process can also be expressed (dropping the O approximation) in the form:

$$\tilde{z}_{\mathbf{x},t} = \left(1 - \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} - m_{\infty}\right) \tilde{z}_{\mathbf{x},t-1} + m_{\infty} z_{\infty} + \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} \tilde{z}_{\mathbf{x}+\mathbf{b},t-1} + a_{\mathbf{x},t} \quad (\text{A4})$$

The random variable $a_{\mathbf{x},t}$ replaces the $\xi_{\mathbf{x},t}$ of KIMURA and WEISS (1964), and the expected value of $a_{\mathbf{x},t}$ is zero; however $\sigma_a^2 = 1/8N$ for all $a_{\mathbf{x},t}$. The variance of the stochastic input or error terms no longer depends on the gene frequency for the previous generation in a location in time and space. The scale of migration rates and systematic pressure are unchanged, and the correlations between the $\tilde{z}_{\mathbf{x},t}$ are the same as those for

$q_{\mathbf{x},t}$ by KIMURA and WEISS (BODMER and CAVALLI-SFORZA 1968). The variance of $\tilde{z}_{\mathbf{x},t}$ differs from that of $q_{\mathbf{x},t}$ because of the difference in the variance of the stochastic inputs. BODMER and CAVALLI-SFORZA (1968) showed that:

$$\text{Var}(q) \cong 4\bar{q}(1 - \bar{q})\text{Var}(z) \quad (\text{A5})$$

where \bar{q} is the mean (equilibrium) gene frequency.

We will consider cases in which the system has reached frequency equilibrium (*i.e.*, $\tilde{z} = E \tilde{z}_{\mathbf{x},t} = z_{\infty}$). Thus if we subtract z_{∞} from the $\tilde{z}_{\mathbf{x},t}$ to form a new set of (mean adjusted) $z_{\mathbf{x},t}$, then at equilibrium,

$$z_{\mathbf{x},t} = \left(1 - \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} - m_{\infty}\right) z_{\mathbf{x},t-1} + \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{x},\mathbf{b}} z_{\mathbf{x}+\mathbf{b},t-1} + a_{\mathbf{x},t}. \quad (\text{A6})$$

This process is immediately identifiable as a STAR process.

Another advantage of the transformation is that for large enough N , $z_{\mathbf{x},t}$ is approximately *normal*. For *normal* STAR processes, stationarity of the variance-covariances (and thus weak stationarity because the mean is constant zero by assumption in equation A6) implies strict stationarity (BENNETT 1979). The variance covariance structure completely specifies the probability density of $z_{\mathbf{x},t}$ for arbitrary \mathbf{x} and t . Conditions for weak stationarity are presented in the text.

We consider in detail here only cases where the interactions (migration rates), $\phi_{\mathbf{x},\mathbf{b}}$, depend only on \mathbf{b} , the set of spatial lags or integers of separation in each dimension, not on \mathbf{x} itself: *i.e.*, absolute location is arbitrary. Thus under the assumption of spatially homogeneous migration we can write $\phi_{\mathbf{b}}$ instead of $\phi_{\mathbf{x},\mathbf{b}}$ (HOOPER and HEWINGS 1981). The present paper is concerned only with models in which the only time lag is that for one generation increments, and it is simply noted that STAR models may have arbitrary numbers of temporal lags [see, *e.g.*, HOOPER and HEWINGS (1981)]. With the assumptions that migration rates are constant over time and absolute space, the STAR representations are of the form:

$$z_{\mathbf{x},t} = \left(1 - \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{b}} - m_{\infty}\right) z_{\mathbf{x},t-1} + \sum_{\mathbf{b} \neq 0} \phi_{\mathbf{b}} z_{\mathbf{x}+\mathbf{b},t-1} + a_{\mathbf{x},t}. \quad (\text{A7})$$

APPENDIX 2

Results on stationarity and correlations for general migration patterns: Results on conditions for stationarity and on correlation structure are readily developed through using backshift operators in time, B_t , and backshift operators, B_i , in the negative ("backward") direction for each spatial dimension X_i (*e.g.*, leftward and downward in Figure 1b). The power b_i

of each B_i acts to index the lag b_i of the coordinate of the X_i dimension from \mathbf{x} . Thus:

$$z_{\mathbf{x}-\mathbf{b},t-n} = B_1^{b_1} B_2^{b_2} \dots B_k^{b_k} B_i^n z_{\mathbf{x},t} \tag{A8}$$

where $\mathbf{b} = (b_1, b_2, \dots, b_k)$. Text Equation 7 is written:

$$z_{\mathbf{x},t} = \sum_{b_1=-l_{11}}^{l_{21}} \sum_{b_2=-l_{12}}^{l_{22}} \dots \sum_{b_k=-l_{1k}}^{l_{2k}} \phi_{\mathbf{b}} B_1^{-b_1} \dots B_k^{-b_k} B_i z_{\mathbf{x},t} + a_{\mathbf{x},t} \tag{A9}$$

where again for notational convenience the summation also includes the term ϕ_0 for the resident contribution. If we let

$$\Phi(B_{\mathbf{x}}, B_t) = 1 - \sum_{b_1=-l_{11}}^{l_{21}} \sum_{b_2=-l_{12}}^{l_{22}} \dots \sum_{b_k=-l_{1k}}^{l_{2k}} \phi_{\mathbf{b}} B_1^{-b_1} B_2^{-b_2} \dots B_k^{-b_k} B_t \tag{A10}$$

then

$$\Phi(B_{\mathbf{x}}, B_t) z_{\mathbf{x},t} = a_{\mathbf{x},t}$$

This is important because for any finite parameter (*i.e.*, finite number of subpopulations that exchange migrants with any given subpopulation) stationary STAR process the inverse, $\Phi^{-1}(B_{\mathbf{x}}, B_t)$, exists and equals $\Psi(B_{\mathbf{x}}, B_t)$, the generating function for the coefficients for different spatial and temporal lags of the infinite moving average (MA) representation of the process. Thus:

$$z_{\mathbf{x},t} = \Psi(B_{\mathbf{x}}, B_t) a_{\mathbf{x},t} \tag{A11}$$

The form of $\Psi(B_{\mathbf{x}}, B_t)$ can be found through long division of 1 by $\Phi(B_{\mathbf{x}}, B_t)$ in separate terms of powers of B_t (TANEJA and AROIAN 1980; HOOPER and HEWINGS 1981). The MA generating function can be used for finding the individual moving average coefficients, $\psi_{\mathbf{b},n}$, which represent the component influence of a subpopulation with spatial lags \mathbf{b} (toward the negative direction from \mathbf{x}) and temporal lag n , on the value of $z_{\mathbf{x},t}$. In general, this may be done by finding for each n , the functions of the $\phi_{\mathbf{b}}$ for each combination of B_i^k and $(B_i^{-1})^l$ such that $b_i = k - l$, and b_i is the i th element of \mathbf{b} . Details are shown below for some of the strict stepping stone models. The moving average representation is useful in several ways. Finite sums of MA coefficients provide close approximations of $z_{\mathbf{x},t}$, because the $\psi_{\mathbf{b},n}$ go to zero as $n \rightarrow \infty$ or as the spatial lag in any dimension goes to infinity. Space-time covariances, $\sigma_{\mathbf{b},n}$, can be closely approximated by multiplying the MA representation of $z_{\mathbf{x},t}$ with one of $z_{\mathbf{x}-\mathbf{b},t-n}$ and then taking expectations. For stationary processes we have:

$$\sigma_z^2 = \sigma_a^2 \sum_{\mathbf{m}} \sum_{k=0}^{\infty} \psi_{\mathbf{m},k}^2 \tag{A12}$$

$$p_{\mathbf{b},n} = \frac{\sum_{\mathbf{m}} \sum_{k=0}^{\infty} \psi_{\mathbf{m},k} \psi_{\mathbf{m}+\mathbf{b},k+n}}{\sum_{\mathbf{m}} \sum_{k=0}^{\infty} \psi_{\mathbf{m},k}^2} \tag{A13}$$

where the summations for \mathbf{m} , in every case, are infinite in every direction (AROIAN 1985).

Stationarity obtains whenever $\Psi(B_{\mathbf{x}}, B_t)$ converges for $|B_i| \leq 1$ for all coordinates (dimensions) X_i , and $|B_t| \leq 1$ (TANEJA and AROIAN 1980), and it can be shown that these conditions are generally met in migration drift models when $m_{\infty} > 0$ and all $\phi_{\mathbf{b}} \geq 0$.

Equations for the relationships between different space-time correlation coefficients can be obtained by multiplying equation 7 by $z_{\mathbf{x}-\mathbf{b},t-n}$, then taking expectations, and noting that for $n > 0$ $E z_{\mathbf{x}-\mathbf{b},t-n} a_{\mathbf{x},t} = 0$. Thus the equations:

$$p_{\mathbf{b},n} = \sum_{\mathbf{m}} \phi_{\mathbf{m}} p_{\mathbf{b}+\mathbf{m},n-1} \tag{A14}$$

(except for $n = 0, \mathbf{b} = \mathbf{0}$). The summation is taken over all spatial lags \mathbf{m} which exchange migrants, and including $\mathbf{m} = \mathbf{0}$ [Theorem 4.5 of AROIAN (1985)]. The set of above equations for all coefficients of the $\phi_{\mathbf{b}}$ in Equation 7 (see text) are known as the Yule-Walker equations and they provide the basis for the Yule-Walker estimators of the migration parameters ($\phi_{\mathbf{b}}$) from the space-time correlations from space-time data in real populations (see text). They also can be used for checking sets of theoretical $p_{\mathbf{b},n}$ obtained from the MA representations. Multiplying Equation 7 by $z_{\mathbf{x},t}$ and taking expectations leads to the equation:

$$\sigma_z^2 = \sigma_a^2 \left(1 - \sum_{\mathbf{b}} \phi_{\mathbf{b}} p_{\mathbf{b},1} \right)^{-1} \tag{A15}$$

(Recall that $\sigma_a^2 = 1/8N$). Notice that the $p_{\mathbf{b},1}$ depend on the ratio of the process variance to the error variance.

Finite parameter STAR models for one spatial dimension and with temporal order one of the form of text Equation 13 have the form in terms of backshift operators:

$$\Phi(B_{\mathbf{x}}, B_t) = 1 - \sum_{b=-l_1}^{l_2} \phi_b B_{\mathbf{x}}^{-b} B_t^1 \tag{A16}$$

where l_1 and l_2 are limits defined under Equation 13 in the text, and the moving average generating function is given by:

$$\Psi(B_{\mathbf{x}}, B_t) = \sum_{d=0}^{\infty} \left(\sum_{b=-l_1}^{l_2} \phi_b B_{\mathbf{x}}^{-b} \right)^d B_t^d \tag{A17}$$

For the strict stepping stone model for one spatial

dimension (see text Equation 15, and Figure 1a), we have:

$$\Phi(B_x, F_x, B_t) = 1 - (\phi_0 + \phi_{-1}B_x + \phi_1F_x)B_t \quad (A18)$$

where $F_x = B_x^{-1}$. The moving average generating function can be written:

$$\Psi(B_x, B_x^{-1}, B_t) = \sum_{d=0}^{\infty} (\phi_0 + \phi_{-1}B_x + \phi_1B_x^{-1})^d B_t^d. \quad (A19)$$

Approximations for calculating the spatial and space-time correlations require finding the individual contributions, $\psi_{b,n}$, to $z_{x,t}$ from subpopulations b units to the left (or negative direction) and n generations ago. One way of calculating the $\psi_{b,n}$ by computer is to simply go through all possible trinomic combinations of all possible l and k for a given $d = n$, and add the contributions to $\psi_{b,n}$, where $b = k - l$. Alternatively, using Equation A19 it can be shown that,

$$\psi_{b,n} = \phi_0\psi_{b,n-1} + \phi_1\psi_{b+1,n-1} + \phi_{-1}\psi_{b-1,n-1} \quad (A20)$$

for $|b| < n$. Using this and noting that $\psi_{0,0} = 1$, and all other $\psi_{b,0} = 0$, provides a convenient algorithm for calculating the $\psi_{b,n}$. Using the equations,

$$p_{b,1} = \phi_0p_{b,0} + \phi_1p_{b+1,0} + \phi_{-1}p_{b-1,0} \quad (A21)$$

$$p_{-b,1} = \phi_0p_{b,0} + \phi_1p_{b-1,0} + \phi_{-1}p_{b+1,0}$$

it can be shown that in general $p_{b,n} = p_{-b,n}$ when $\phi_1 = \phi_{-1}$.

Two-dimensional models with temporal order 1:

Finite parameter STAR models for two spatial dimensions, with temporal order one are of the form in Equation 21 in the text:

$$z_{x,y,t} = \sum_{a=-k_1}^{k_2} \sum_{b=-l_1}^{l_2} \phi_{b,a} z_{x+b,y+a,t-1} + a_{x,y,t}. \quad (A22)$$

Let B_x and B_y be the spatial backshift operators, then

$$\Phi(B_x, B_y, B_t) = 1 - \sum_{a=-k_1}^{k_2} \sum_{b=-l_1}^{l_2} \phi_{b,a} B_x^{-b} B_y^{-a} B_t. \quad (A23)$$

The moving average generating function is

$$\Psi(B_x, B_y, B_t) = \sum_{d=0}^{\infty} \left(\sum_{a=-k_1}^{k_2} \sum_{b=-l_1}^{l_2} \phi_{b,a} B_x^{-b} B_y^{-a} \right)^d B_t^d \quad (A24)$$

and $z_{x,y,t} = \Psi(B_x, B_y, B_t) a_{x,y,t}$.

For the strict stepping stone model migration occurs only from the four nearest neighbors, thus (text Equation 22):

$$z_{x,y,t} = \phi_{0,0}z_{x,y,t-1} + \phi_{-1,0}z_{x-1,y,t-1} + \phi_{1,0}z_{x+1,y,t-1} + \phi_{0,-1}z_{x,y-1,t-1} + \phi_{0,1}z_{x,y+1,t-1} + a_{x,y,t}. \quad (A25)$$

The MA generating function can be written:

$$\Psi(B_x, B_y, B_t) = \sum_{d=0}^{\infty} (\phi_{0,0} + \phi_{-1,0}B_x + \phi_{1,0}B_x^{-1} + \phi_{0,-1}B_y + \phi_{0,1}B_y^{-1})^d B_t^d \quad (A26)$$

$$= \sum_{d=0}^{\infty} \sum_{l+k=d} \sum_{s+u=d} \sum_{t+v=d} \left(\frac{d!}{l!k!s!u!v!} \right) \cdot \phi_{0,0}^l \phi_{-1,0}^k \phi_{1,0}^s B_x^{k-s} \phi_{0,-1}^u \phi_{0,1}^v B_y^{u-v} B_t^d \quad (A27)$$

Individual $\psi_{b,a,n}$ (the relative effect on $z_{x,y,t}$ of the subpopulation at $x - b, y - a, t - n$) can be found by first fixing $n = d$ in Equation A27, and then summing up all multinomial increments for which $b = k - s$, and $a = u - v$. (Note that $\psi_{b,a,n} = 0$ for $|b| + |a| > n$.) The MA coefficients can also be more easily calculated by iterating the formula:

$$\begin{aligned} \psi_{b,a,n} &= \phi_{0,0}\psi_{b,a,n-1} + \phi_{-1,0}\psi_{b-1,a,n-1} \\ &+ \phi_{1,0}\psi_{b+1,a,n-1} \\ &+ \phi_{0,-1}\psi_{b,a-1,n-1} \\ &+ \phi_{0,1}\psi_{b,a+1,n-1} \end{aligned} \quad (A28)$$

and noting that $\psi_{0,0,0} = 1.0$ and, $\psi_{b,a,0} = 0$ for all other a and b .

Using the text Equations 27 and the identities $p_{b,a,n} = p_{-b,-a,-n}$, $p_{0,0,n} = p_{0,0,-n}$, and $p_{b,a,0} = p_{-b,-a,0}$ (TANEYA and AROIAN 1980; AROIAN 1985), it can be shown that if $\phi_{-1,0} = \phi_{1,0}$ and $\phi_{0,-1} = \phi_{0,1}$ then $p_{b,a,1} = p_{-b,-a,1}$, and finally that $p_{b,a,n} = p_{b,-a,n} = p_{-b,a,n} = p_{-b,-a,n}$. Thus the observations on the $p_{b,a,n}$ in the various anisotropic models described above are as expected.