Geographical Variation in a Quantitative Character

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ABSTRACT

A model for the evolution of the local averages of a quantitative character under migration, selection, and random genetic drift in a subdivided population is formulated and investigated. Generations are discrete and nonoverlapping; the monoecious, diploid population mates at random in each deme. All three evolutionary forces are weak, but the migration pattern and the local population numbers are otherwise arbitrary. The character is determined by purely additive gene action and a stochastically independent environment; its distribution is Gaussian with a constant variance; and it is under Gaussian stabilizing selection with the same parameters in every deme. Linkage disequilibrium is neglected. Most of the results concern the covariances of the local averages. For a finite number of demes, explicit formulas are derived for (*i*) the asymptotic rate and pattern of convergence to equilibrium, (*ii*) the variance of a suitably weighted average of the local averages, and (*iii*) the equilibrium covariances when selection and random drift are much weaker than migration. Essentially complete analyses of equilibrium and convergence are presented for random outbreeding and site homing, the Levene and island models, the circular habitat and the unbounded linear stepping-stone model in the diffusion approximation, and the exact unbounded stepping-stone model in one and two dimensions.

DESPITE the prevalence of geographical variation in quantitative traits, the theoretical literature in this important area addresses only a small fraction of the biologically interesting questions (BULMER 1971a,b; 1980, pp. 180–184; FELSENSTEIN 1977; SLATKIN 1978; LANDE 1982, 1991, 1992; BARTON 1983; ROUHANI and BARTON 1987; LYNCH 1988). The reason is that the subject fuses two mathematically difficult topics: geographical variation and quantitative genetics. The former has been rather thoroughly investigated at the single-locus level (see NAGYLAKI 1989a,b; 1992a, Ch. 6; and references therein), but many fundamental open problems remain in the biologically rigorous analysis of the latter (see NAGYLAKI 1993 and references therein).

LANDE (1991) proposed a model for the evolution of the local averages of a quantitative trait under isotropic migration, weak Gaussian stabilizing selection, and random genetic drift in a population distributed homogeneously and continuously in one or two dimensions. For the covariances of these local averages at equilibrium, he obtained an integral, which he approximated for weak selection.

A reformulation and generalization of LANDE's (1991) model for a discretely subdivided population with arbitrary migration is desirable for several reasons.

First, random drift can be introduced into a discrete model through population regulation, without the use of an *ad hoc* spatial autocorrelation.

Second, LANDE's model is very similar to the continuous MALÉCOT (1948, 1955, 1959, 1967, 1969) model for migration, mutation, and random drift, and neither model takes into account the fact that if individuals reproduce and migrate independently of each other, then there are random fluctuations in the population density. Whereas in a discrete model this difficulty can be obviated by population regulation, this has not been accomplished for any biologically reasonable continuous model (FELSENSTEIN 1975; KINGMAN 1977; SUDBURY 1977; SAWYER and FELSENSTEIN 1981). In the continuous MALÉCOT model, biologically sensible initial conditions can lead (at least for low population densities) to probabilities of identity that are negative or greater than one (NAGYLAKI 1976). In LANDE's model, it is not clear whether initial nonnegative definiteness of the covariance matrix is always preserved, as required for acceptability.

Finally, our formulation will enable us to derive several illuminating results for an arbitrary migration pattern and to obtain essentially complete analyses of equilibrium and convergence for many particular, biologically interesting migration schemes.

We shall formulate our model in the next section. In the succeeding section, we shall establish our general results. We shall devote the following sections to random outbreeding and site homing, the Levene and island models, the circular habitat and the unbounded linear stepping-stone model in the diffusion approximation, and the exact unbounded stepping-stone model in one and two dimensions. We shall summarize and discuss our results in the final section.

FORMULATION

Generations are discrete and nonoverlapping; the monoecious, diploid population mates at random in each deme. The genotypic and environmental contributions to the character are additive and mutually stochastically independent; the latter is Gaussian with mean zero and variance V_E in each deme. The environmental values are mutually stochastically independent between individuals, demes, and generations. The genotypic value is determined purely additively, and we assume that its variance in each deme is approximately the same constant V_g (LANDE 1976, 1991). This approximation may be substantially less accurate than in a panmictic population if the variance of the mean phenotype among demes that are connected by appreciable gene flow is comparable to or greater than V_g. At least roughly, it might be possible to incorporate nonadditive genetic variation into V_E (LANDE 1976, 1991). We assume also that the distribution of the character is approximately Gaussian. We neglect linkage disequilibrium. This approximation requires that selection and random drift be weak. Moderate or strong migration might be permissible if the genetic variance V_g is sufficiently small; otherwise, we posit weak migration.

We now present a heuristic formulation of our model. A biologically and mathematically rigorous derivation from the basic principles of Mendelism, recombination, and gene action would be very difficult and has not been accomplished even for a single population (*cf.* FLEMING 1979; BARTON and TURELLI 1991; NAGYLAKI 1993).

The life cycle begins with a very large number, $\tilde{N}_j$, of zygotes in deme j; the mean of the character is the random variable $\bar{Z}_j$. The number of demes may be finite or infinite. We measure time, t (=0, 1, 2, . . .), in generations, and the prime denotes the next generation.

Migration changes $\tilde{N}_j$ and $\bar{Z}_j$ deterministically to N_j^* and $\bar{Z}_j^*$, respectively. To describe migration, we define the elements of the forward and backward migration matrices (MALÉCOT 1948, 1950; BODMER and CAVALLI-SFORZA 1968), $\tilde{m}_{jk}$ and m_{kj}, as follows. The probability that an adult in deme j migrates to deme k is the constant $\tilde{m}_{jk}$. Since we are positing that $\tilde{N}_j$ is very large, therefore $\tilde{m}_{jk}$ represents the fraction of adults that migrate from deme j to deme k in each generation. We signify by m_{kj} the probability that an adult in deme k migrated from deme j. The migration matrices satisfy the normalization conditions

$$\sum_k \tilde{m}_{jk} = 1, \quad \sum_j m_{kj} = 1 \tag{1}$$

and are connected by (MALÉCOT 1948; NAGYLAKI 1992a, p. 133)

$$m_{kj} = \tilde{N}_j \tilde{m}_{jk} \Big/ \sum_l \tilde{N}_l \tilde{m}_{lk}. \tag{2}$$

Clearly,

$$\bar{Z}_j^* = \sum_k m_{jk} \bar{Z}_k. \tag{3}$$

Deterministic Gaussian stabilizing selection with the same optimum value zero and parameter V_s in every deme follows migration:

$$w(z) = e^{-z^2/(2V_s)}. \tag{4}$$

Thus, interdemic divergence is due solely to random drift. We set

$$V_Z = V_g + V_E, \quad V = V_Z + V_s, \quad s = V_g/V, \tag{5}$$

where V_Z designates the phenotypic variance. Weak selection means that $0 < s \ll 1$.

Random drift operates through population regulation, which reduces the large number of adults in deme j to N_j. In the $\tilde{N}_j$ zygotes of the next generation, we have, at least approximately (LANDE 1976, 1991; KIMURA and CROW 1978; NAGYLAKI 1984; 1992a, pp. 315–320; 1992b; 1993; HASTINGS 1990),

$$\bar{Z}_j' = \bar{Z}_j^{**} + \zeta_j, \tag{6}$$

where

$$\bar{Z}_j^{**} = p\bar{Z}_j^*, \quad p = 1 - s, \tag{7a}$$

$$\mathscr{E}(\zeta_j) = 0, \tag{7b}$$

$$\mathrm{Var}(\zeta_j) = \Gamma_j, \quad \Gamma_j = V_g/N_j. \tag{7c}$$

For each t, the random vector $\zeta(t)$ is stochastically independent of the random vector $\bar{Z}(t)$; for j = 1, 2, 3, . . . and t = 0, 1, 2, . . . , the random variables $\zeta_j(t)$ are mutually stochastically independent. Note that only the genic variance contributes to the increase in variance between lines of zygotes.

Even in the absence of selection and migration, the applicability of the statistical formula (7c) for sampling a mean is far from obvious. In this neutral, panmictic case, with the method in NAGYLAKI (1992a, p. 255) one can prove that (7c) is exact for a single multiallelic locus in a haploid population. For a diploid population without dominance, one can deduce from the results in NAGYLAKI (1992a, p. 255) that (7c) holds approximately for large population number. If there is dominance, we appeal to the diallelic analysis of the variance within and between lines by CROW and KIMURA (1970, p. 343), who neglect stochastic deviations from Hardy-Weinberg proportions. Their approximations should be accurate for large population number. Even then, however, (7c) holds only initially, when additive effects control the variance components. As the population evolves, fixations cause increasing departures from Hardy-Weinberg proportions in the entire population, and therefore the contribution of dominance becomes more important (*cf.* NAGYLAKI 1992a, Eq. 4.192). A constant supply of mutations may obviate this difficulty. For purely additive gene action, the work of KIMURA (1963, pp. 6–8) enables us to extend the single-locus diploid result to multiple loci in linkage equilibrium.

It is reasonable to suppose that $\tilde{N}_j$ is proportional to N_j. Then (2) becomes

$$m_{kj} = N_j\tilde{m}_{jk}\Big/\sum_l N_l\tilde{m}_{lk}, \tag{8}$$

which is constant.

From (6), (7a), and (3) we obtain our model,

$$\bar{Z}_j' = p\sum_k m_{jk}\bar{Z}_k + \zeta_j. \tag{9}$$

The same model applies if soft selection (DEMPSTER 1955; WALLACE 1968; NAGYLAKI 1992a, p. 134) precedes migration, and this observation holds approximately for any type of weak selection.

The model (9) is mathematically valid for arbitrary intensities of the evolutionary forces. Without additional difficulty, we shall derive many of our results in this general case and then simplify them for weak selection.

GENERAL RESULTS

In the following subsections, we shall establish sundry general properties of the model (9). We shall obtain bounds on the rates of convergence of the means

$$\mu_j(t) = \mathscr{E}[\bar{Z}_j(t)] \tag{10}$$

and of the covariances

$$\rho_{jk}(t) = \mathrm{Cov}[\bar{Z}_j(t), \bar{Z}_k(t)]. \tag{11}$$

For a finite number of demes, we shall derive formulas for the random vector of local averages $\bar{Z}(t)$, its characteristic function, the means $\mu_j(t)$, and the covariances $\rho_{jk}(t)$. We shall also deduce simple formulas for (*i*) the variance of a suitably weighted average of the local averages and (*ii*) the equilibrium covariances when selection and random drift are much weaker than migration.

Random variables: We set $A = pM$, where M denotes the backward migration matrix, and rewrite (9) in matrix form as

$$\bar{Z}' = A\bar{Z} + \zeta, \tag{12}$$

which has the unique solution

$$\bar{Z}(t) = A^t\bar{Z}(0) + \sum_{\tau=0}^{t-1} A^{t-1-\tau}\zeta(\tau). \tag{13}$$

In (13), the sum is absent if $t = 0$; the first term is absent if the initial means are at the optimum: $\bar{Z}(0) = \mathbf{0}$. At least for finitely many demes, since the spectral radius of A is $p < 1$, the first term in (13) converges to $\mathbf{0}$ as $t \to \infty$. From (13) we conclude also that if $\zeta_j(t)$ is normally distributed for every j and t and if $\bar{Z}(0)$ has a multivariate normal distribution, then $\bar{Z}(t)$ has a multivariate normal distribution for every t.

Suppose now that not only is the number of demes finite, but also that the backward migration matrix M is irreducible (GANTMACHER 1959, p. 50). This means that the descendants of individuals in every deme are able eventually to reach every other deme. Then Frobenius' theorem (GANTMACHER 1959, p. 53) informs us that to the simple maximal eigenvalue one of M corresponds a left eigenvector ν with positive components. Thus, the conditions

$$0 < \nu_j < 1, \quad \sum_j \nu_j = 1, \quad \nu^T M = \nu^T, \tag{14}$$

where the superscript T signifies transposition, determine ν uniquely.

If M is ergodic, *i.e.*, both irreducible and aperiodic (GANTMACHER 1959, pp. 80, 88), then ν is the unique stationary distribution of M. Given irreducibility, the biologically trivial condition that individuals have positive probability of remaining in some deme, *i.e.*, $m_{jj} > 0$ for some j, suffices for aperiodicity (FELLER 1968, p. 426).

The total population number N_T and the proportion of adults κ_j in deme j are given by

$$N_T = \sum_j N_j, \quad \kappa_j = N_j/N_T. \tag{15}$$

We have $\nu = \kappa$ if and only if migration is *conservative*, *i.e.*, it does not change the subpopulation numbers (NAGYLAKI 1980; 1992a, pp. 135–136).

We define the weighted grand mean of the local averages as

$$\bar{\bar{Z}} = \sum_j \nu_j\bar{Z}_j = \nu^T\bar{Z}. \tag{16}$$

From (16), (12), and (14) we obtain

$$\bar{\bar{Z}}' = p\bar{\bar{Z}} + \bar{\zeta}, \tag{17}$$

where $\bar{\zeta} = \nu^T\zeta$, which yields

$$\bar{\bar{Z}}(t) = \bar{\bar{Z}}(0)p^t + \sum_{\tau=0}^{t-1} p^{t-1-\tau}\bar{\zeta}(\tau). \tag{18}$$

This can also be derived from (13).

Characteristic function: The characteristic function of $\bar{Z}(t)$ is

$$\chi(\xi, t) = \mathscr{E}[e^{i\xi^T\bar{Z}(t)}], \tag{19}$$

where $i = \sqrt{-1}$. For simplicity, here we make the natural assumption that the distribution of $\zeta(t)$ is independent of t. Then (19) and (12) lead easily to the recursion relation

$$\chi(\xi, t+1) = \psi(\xi)\chi(B\xi, t), \tag{20}$$

where $B = A^T$ and

$$\psi(\xi) = \mathscr{E}[e^{i\xi^T\zeta(t)}] = \prod_j \mathscr{E}[e^{i\xi_j\zeta_j(t)}]. \tag{21}$$

Iterating (20), we find

$$\chi(\xi, t) = \chi(B^t\xi, 0) \prod_{\tau=0}^{t-1} \psi(B^\tau\xi), \tag{22}$$

which can also be proved by substituting (13) into (19).

In (22), the product is one if $t = 0$, and $\chi(B^t\xi, 0) = 1$ if $\bar{Z}(0) = \mathbf{0}$. Since $\chi(\mathbf{0}, t) = 1$ and the spectral radius of B is $p < 1$, for finitely many demes $\chi(B^t\xi, 0) \to 1$ as $t \to \infty$, and therefore

$$\chi(\xi, t) \to \prod_{\tau=0}^{\infty} \psi(B^\tau\xi) \tag{23}$$

as $t \to \infty$. This formula for the characteristic function of the stationary distribution of $\bar{Z}$ can also be established by inserting (13) into (19).

Note that (22) confirms the remark below (13) about the Gaussian case.

Means: Recalling (10) and (7b), from the expectation of (9) we get

$$\mu_j' = p \sum_k m_{jk}\mu_k. \tag{24}$$

We define $\|\mu\| = \sup_j|\mu_j|$, assume $\|\mu\| < \infty$, and let the vectors μ' and $\tilde{\mu}'$ represent the respective images of μ and $\tilde{\mu}$ under the mapping (24). Then (24) and (1) lead directly to

$$\|\mu' - \tilde{\mu}'\| \leq p\|\mu - \tilde{\mu}\|, \tag{25}$$

which demonstrates that (24) is a contraction. Therefore, $\mu(t) \to \mathbf{0}$ as $t \to \infty$ at least as fast as p^t, and the equilibrium $\mu = \mathbf{0}$ is unique. From (24) we obtain

$$\mu(t) = A^t\mu(0). \tag{26}$$

Thus, if $\mu(0) = \mathbf{0}$, then $\mu(t) = \mathbf{0}$ for every t.

If the number of demes is finite and M is irreducible, then (24) shows that the weighted grand mean

$$\bar{\mu} = \mathscr{E}(\bar{\bar{Z}}) = \nu^T\mu \tag{27}$$

satisfies $\bar{\mu}' = p\bar{\mu}$, whence

$$\bar{\mu}(t) = \bar{\mu}(0)p^t, \tag{28}$$

which follows also from (26). Observe that if $\bar{\mu}(0) = 0$, then $\bar{\mu}(t) = 0$ for every t.

If M is ergodic and $\bar{\mu}(0) \neq 0$, then (26) informs us that $\mu(t) \to \mathbf{0}$ at the asymptotic rate p^t as $t \to \infty$, and the asymptotic pattern of the means is uniform, corresponding to the right eigenvector of M with eigenvalue unity.

Covariances: The remainder of this paper is devoted to the study of the covariances (11). In this subsection, we shall derive the recursion relations they satisfy and then investigate their convergence, equilibrium, and strong-migration limit.

Recursion relations: We use a simple conditional decomposition of the covariances (NAGYLAKI 1992a, p. 253), (9), (7b), and (7c):

$$\begin{aligned}\rho_{jk}' &= \mathrm{Cov}[\mathscr{E}(\bar{Z}_j'|\bar{Z}), \mathscr{E}(\bar{Z}_k'|\bar{Z})] + \mathscr{E}[\mathrm{Cov}(\bar{Z}_j', \bar{Z}_k'|\bar{Z})]\\ &= \mathrm{Cov}[p\sum_l m_{jl}\bar{Z}_l, \quad p\sum_n m_{kn}\bar{Z}_n] + \mathscr{E}[\mathrm{Cov}(\zeta_j, \zeta_k)]\\ &= q\sum_{l,n} m_{jl}m_{kn}\rho_{ln} + \delta_{jk}\Gamma_j,\end{aligned} \tag{29}$$

where $q = p^2 = (1-s)^2 < 1$ and δ_{jk} designates the Kronecker delta, *i.e.*, $\delta_{jk} = 1$ if $j = k$ and $\delta_{jk} = 0$ if $j \neq k$. We now think of ρ and Γ as n^2-component vectors, where $(\Gamma)_{jk} = \delta_{jk}\Gamma_j$, and introduce the $n^2 \times n^2$ Kronecker-product matrix $K = M \otimes M$. Then we obtain the matrix form of (29):

$$\rho' = qK\rho + \Gamma. \tag{30}$$

The recursion relation (29) differs from the discrete MALÉCOT (1949, 1950, 1951, 1975) model for migration, mutation, and random drift only in its inhomogeneous term. Therefore, many of the ideas and methods used in the study of the MALÉCOT model can be applied to (29), though the results here will be different.

To make both mathematical and biological sense, the covariance matrix ρ must be symmetric, nonnegative, and nonnegative definite. We now prove that (29) preserves these three natural properties.

First, it is easy to check that if $\rho = \rho^T$, then $\rho' = (\rho')^T$. By induction, this demonstrates that if $\rho(0) = \rho^T(0)$, then $\rho(t) = \rho^T(t)$ for every t.

Second, if $\rho \geq 0$, then $\rho' \geq 0$, which establishes that if $\rho(0) \geq 0$, then $\rho(t) \geq 0$ for every t.

Third, ρ can be a covariance matrix if and only if it is nonnegative definite, *i.e.*, $b^T\rho b \geq 0$ for every vector b. Setting $c = M^Tb$, from (29) we deduce

$$b^T\rho' b = qc^T\rho c + \sum_j \Gamma_j b_j^2, \tag{31}$$

which implies that if ρ is nonnegative definite, then so is ρ'. Therefore, if $\rho(0)$ is nonnegative definite, then so is $\rho(t)$ for every t.

The correlation between $\bar{Z}_j$ and $\bar{Z}_k$ is given by

$$r_{jk} = \rho_{jk}/\sqrt{\rho_{jj}\rho_{kk}}. \tag{32}$$

If the number of demes is finite and M is irreducible, we express the variance of the grand mean as

$$\bar{\rho} = \mathrm{Var}(\bar{\bar{Z}}) = \sum_{j,k} \nu_j\nu_k\rho_{jk} = \nu^T \otimes \nu^T\rho. \tag{33}$$

Invoking (33), (30), and (14), we derive the recursion relation

$$\bar\rho' = q\bar\rho + \sum_j \Gamma_j\nu_j^2. \tag{34}$$

To simplify the sum, we define the *migration effective population number* as (NAGYLAKI 1980, 1982, 1983)

$$N_e = \beta N_T, \quad \beta = \Big(\sum_j \nu_j^2/\kappa_j\Big)^{-1}. \tag{35}$$

For a single multiallelic locus, this effective population number replaces the actual total population number in the strong-migration limit (NAGYLAKI 1980, 1983) and in some aspects of geographical invariance (NAGYLAKI 1982). We have $\beta \leqslant 1$ and hence $N_e \leqslant N_T$, with equality if and only if migration is conservative (NAGYLAKI 1980). From (7c), (15), and (35) we obtain

$$\sum_j \Gamma_j\nu_j^2 = V_g/N_e, \tag{36}$$

so (34) becomes

$$\bar\rho' = q\bar\rho + \frac{V_g}{N_e}. \tag{37}$$

Convergence: We define $\|\rho\| = \sup_{j,k}|\rho_{jk}|$, assume $\|\rho\| < \infty$, and let ρ' and $\tilde\rho'$ represent the respective images of ρ and $\tilde\rho$ under the mapping (29). Then (29) and (1) lead directly to

$$\|\rho' - \tilde\rho'\| \leqslant q\|\rho - \tilde\rho\|, \tag{38}$$

which demonstrates that (29) is a contraction. Therefore, $\rho(t) \longrightarrow \hat\rho$ as $t \longrightarrow \infty$ at least as fast as q^t, and the equilibrium $\hat\rho$ is the unique solution of

$$\hat\rho_{jk} = q\sum_{l,n} m_{jl}m_{kn}\hat\rho_{ln} + \delta_{jk}\Gamma_j. \tag{39}$$

We established below (30) that (29) preserves the symmetry, nonnegativity, and nonnegative definiteness of ρ. Consequently, the uniqueness of $\hat\rho$ implies that $\hat\rho$ also satisfies these three natural properties.

We set

$$\rho_{jk}(t) = \hat\rho_{jk} - q^t\varphi_{jk}(t) \tag{40}$$

and subtract (29) from (39) to deduce

$$\varphi_{jk}' = \sum_{l,n} m_{jl}m_{kn}\varphi_{ln}, \tag{41}$$

with the initial conditions

$$\varphi_{jk}(0) = \hat\rho_{jk} - \rho_{jk}(0). \tag{42}$$

If the initial local averages $\bar Z_j(0)$ are fixed, then $\rho_{jk}(0) = 0$ for every j and k and (42) reduces to $\varphi_{jk}(0) = \hat\rho_{jk}$.

For finitely many demes, the matrix form

$$\varphi' = K\varphi \tag{43}$$

of (41) has the solution

$$\varphi(t) = K^t\varphi(0). \tag{44}$$

Suppose now that M is ergodic, so that its simple eigenvalue one exceeds all other eigenvalues in absolute value. Since the eigenvalues of $K = M \otimes M$ are the products of the eigenvalues of M (LANCASTER 1969, pp. 259–260), therefore K has simple eigenvalue one, and this exceeds all other eigenvalues in absolute value; the corresponding eigenvector is the Kronecker product of the constant eigenvector of M with itself. Thus, we conclude from (40) and (44) that if $\bar\varphi(0) \neq 0$, then the asymptotic rate of convergence is q^t and the asymptotic transient pattern of the covariances is uniform. Substituting (40) into (32) reveals that the correlations also converge at the asymptotic rate q^t, but the transient part is not generically uniform as $t \longrightarrow \infty$.

From (43) we infer easily that the grand mean

$$\bar\varphi = \nu^T \otimes \nu^T\varphi \tag{45}$$

is constant: $\bar\varphi' = \bar\varphi$, and hence

$$\bar\varphi(t) = \bar\varphi(0) = \hat{\bar\rho} - \bar\rho(0), \tag{46}$$

which can be confirmed at once from (44).

Equilibrium: For a finite number of demes, the matrix form

$$\hat\rho = qK\hat\rho + \Gamma \tag{47}$$

of (39) has the solution

$$\hat\rho = (I - qK)^{-1}\Gamma, \tag{48}$$

where I signifies the $n^2 \times n^2$ identity matrix.

Suppose now that M is ergodic. Then, as noted above, K is also ergodic and its maximal eigenvalue is one. Therefore, the series expansion

$$\hat\rho = \sum_{n=0}^{\infty} q^nK^n\Gamma \tag{49}$$

of (48) converges. By the ergodicity of K, there exists a positive integer n_0 such that $K^n > 0$ for $n \geqslant n_0$ (GANTMACHER 1959, p. 80). Since $(\Gamma)_{jj} = \Gamma_j > 0$ for every j, we infer that $\hat\rho_{jk} > 0$ for every j and k. This conclusion is stronger than the general nonnegativity, $\hat\rho_{jk} \geqslant 0$, proved below (39).

For irreducible M, from (37) we obtain

$$\hat{\bar\rho} = \frac{V_g}{(1-q)N_e} = \frac{V_g}{s(2-s)N_e} \tag{50}$$

for the variance (33) of the grand mean $\bar{\bar Z}$. Since, as stated below (35), $N_e \leqslant N_T$, we see that

$$\hat{\bar\rho} \geqslant \frac{V_g}{s(2-s)N_T} = \rho_r, \tag{51}$$

with equality if and only if migration is conservative. Thus, $\hat{\bar\rho}$ exceeds LANDE's (1976) panmictic value ρ_r unless migration is conservative, in which case $\hat{\bar\rho} = \rho_r$.

Since the correlation $r_{jk} \leq 1$ for every j and k, we have

$$\rho_{jk} \leq \sqrt{\rho_{jj}\rho_{kk}} \leq \tfrac{1}{2}(\rho_{jj} + \rho_{kk}). \tag{52}$$

Defining the weighted mean variance

$$\bar{\rho}_0 = \sum_j \nu_j \rho_{jj}, \tag{53}$$

from (52), (33), (14), and (53) we derive

$$\bar{\rho} \leq \bar{\rho}_0. \tag{54}$$

At equilibrium, (51) and (54) yield

$$\rho_r \leq \hat{\bar{\rho}} \leq \hat{\bar{\rho}}_0. \tag{55}$$

For weak selection ($s \ll 1$), (50) simplifies to

$$\hat{\bar{\rho}} \approx \frac{V_g}{2sN_e} = \frac{V}{2N_e}. \tag{56}$$

The strong-migration limit: We consider finitely many demes with a fixed, ergodic backward migration matrix M. Selection and random drift will be comparable to each other and much weaker than migration if we put $\Gamma_j = s\gamma_j$ and let $s \rightarrow 0$ with γ_j fixed. To approximate the equilibrium covariances $\hat{\rho}_{jk}$, we set

$$\hat{\rho}_{jk} = \rho_{jk}^{(0)} + s\rho_{jk}^{(1)} + O(s^2) \tag{57}$$

as $s \rightarrow 0$, where $\rho_{jk}^{(0)}$ and $\rho_{jk}^{(1)}$ are independent of s, and substitute into (39). Equating powers of s leads to

$$\rho_{jk}^{(0)} = \sum_{l,n} m_{jl} m_{kn} \rho_{ln}^{(0)}, \tag{58a}$$

$$\rho_{jk}^{(1)} = \sum_{l,n} m_{jl} m_{kn} (\rho_{ln}^{(1)} - 2\rho_{ln}^{(0)}) + \delta_{jk}\gamma_j. \tag{58b}$$

As we saw below (44), the constant vector is the unique eigenvector of K with eigenvalue one, and hence (58a) implies that $\rho_{jk}^{(0)} = \rho^{(0)}$ for some constant $\rho^{(0)}$. This reduces (58b) to

$$\rho_{jk}^{(1)} = -2\rho^{(0)} + \sum_{l,n} m_{jl} m_{kn} \rho_{ln}^{(1)} + \delta_{jk}\gamma_j. \tag{59}$$

Averaging (59) as in (33) and invoking (14), we find

$$\rho^{(0)} = \tfrac{1}{2} \sum_j \gamma_j \nu_j^2; \tag{60}$$

in view of (36) and (57), this establishes the strong-migration (or quasi-panmictic) limit

$$\hat{\rho}_{jk} = \frac{V_g}{2sN_e} + O(s) \tag{61}$$

as $s \rightarrow 0$.

Thus, the limiting covariances are uniform, of $O(1)$ as $s \rightarrow 0$, and in agreement with the weighted mean covariance (56). Inserting (61) into (32) produces the correlations

$$\hat{r}_{jk} = 1 + O(s) \tag{62}$$

as $s \rightarrow 0$.

RANDOM OUTBREEDING AND SITE HOMING

The number of demes (n) is finite, and the backward migration matrix is given by (DEAKIN 1966; MAYNARD SMITH 1966, 1970a; CHRISTIANSEN 1974, 1975)

$$\begin{aligned} m_{jj} &= 1 - \gamma + \gamma\kappa_j, \\ m_{jk} &= \gamma\kappa_k, \quad j \neq k, \end{aligned} \tag{63}$$

where the rate of immigration is proportional to γ, and κ_j denotes the fraction of adults in deme j, as in (15). This model incorporates population subdivision, but not isolation by distance. It is easy to verify that the migration pattern (63) is conservative (NAGYLAKI 1992a, pp. 136, 149), and therefore $\nu = \kappa$. The proportion of immigrants in deme j is $1 - m_{jj} = \gamma(1 - \kappa_j)$, so we may take

$$0 \leq \gamma \leq 1/(1 - \kappa_{\min}) \tag{64}$$

instead of the customary, tighter restriction $0 \leq \gamma \leq 1$, which would preclude preferential outbreeding.

If $\gamma = 0$, there is no outbreeding; $\gamma = 1$ corresponds to the Levene model; the choices $\kappa_j = 1/n$ and $\gamma = nm/(n - 1)$ simplify (63) to the island model. In the next two sections, the Levene and island models will be treated as special cases of random outbreeding and site homing.

After deriving our recursion relations, we shall investigate equilibrium and convergence.

Recursion relations: Substituting (63) into (29) leads to

$$\begin{aligned} \rho_{jk}' = {} & q[(1 - \gamma)^2\rho_{jk} + \gamma(1 - \gamma)(\bar{\rho}_j + \bar{\rho}_k) + \gamma^2\bar{\rho}] \\ & + \delta_{jk}\left(\frac{\Gamma_T}{\kappa_j}\right), \end{aligned} \tag{65}$$

where

$$\bar{\rho}_j = \sum_k \rho_{jk}\kappa_k, \tag{66a}$$

$$\bar{\rho} = \sum_j \bar{\rho}_j\kappa_j = \sum_{j,k} \rho_{jk}\kappa_j\kappa_k, \tag{66b}$$

and $\Gamma_T = V_g/N_T$. It is natural to average (65) as in (66):

$$\bar{\rho}_j' = q[(1 - \gamma)\bar{\rho}_j + \gamma\bar{\rho}] + \Gamma_T, \tag{67}$$

$$\bar{\rho}' = q\bar{\rho} + \Gamma_T. \tag{68}$$

Since $N_e = N_T$ here, (68) is identical to (37).

Equilibrium: From (68) we obtain

$$\hat{\bar{\rho}} = \frac{\Gamma_T}{1 - q} = \frac{\Gamma_T}{s(2 - s)}, \tag{69}$$

in agreement with (50). Substituting (69) into (67) gives

$$\hat{\bar{\rho}}_j = \hat{\bar{\rho}}, \tag{70}$$

and inserting (69) and (70) into (65) yields the equilibrium covariances

$$\hat{\rho}_{jk} = \frac{\Gamma_T}{1 - q(1-\gamma)^2}\left[\frac{q\gamma(2-\gamma)}{1-q} + \frac{\delta_{jk}}{\kappa_j}\right]. \quad (71a)$$

From (32) and (71a) we obtain the correlations ($j \neq k$)

$$\hat{r}_{jk} = \left\{\left[1 + \frac{1-q}{q\gamma(2-\gamma)\kappa_j}\right]\left[1 + \frac{1-q}{q\gamma(2-\gamma)\kappa_k}\right]\right\}^{-1/2}. \quad (71b)$$

Our solution has some interesting properties. The covariances $\hat{\rho}_{jk}$ are independent of the demic proportions κ for $j \neq k$. The variance $\hat{\rho}_{jj}$ depends only on the component κ_j of κ and decreases as κ_j (or N_j) increases with the other parameters fixed. Clearly, $\hat{\rho}_{jk}$ increases as Γ_T or q increases; the former corresponds to greater variance V_g or more random drift (smaller N_T), whereas the latter corresponds to weaker selection (smaller s). It is easy to demonstrate that if $\gamma < 1$, then increasing migration (greater γ) increases $\hat{\rho}_{jk}$ for $j \neq k$ and decreases $\hat{\rho}_{jj}$. Thus, the dependence of $\hat{\rho}_{jk}$ on the evolutionary forces is intuitively reasonable.

The correlation $\hat{r}_{jk}$ is independent of Γ_T and increases as κ_j, κ_k, q, or γ (for $\gamma < 1$) increases.

By the above remarks, we can obtain lower and upper bounds on the variances $\hat{\rho}_{jj}$ by letting $q \longrightarrow 0$ ($s \longrightarrow 1$) and $\gamma \longrightarrow 0$, respectively, in (71a):

$$\Gamma_j \leq \hat{\rho}_{jj} \leq \frac{\Gamma_j}{1-q}. \quad (72)$$

The right-hand side agrees with (51) for an isolated deme and shows that migration decreases the variances $\hat{\rho}_{jj}$. In the usual case $\gamma \leq 1$, the limit $\gamma \longrightarrow 1$ reveals ($j \neq k$)

$$\hat{\rho}_{jk} \leq \frac{\Gamma_T q}{1-q}, \quad (73)$$

strengthens the lower bound in (72) to

$$\hat{\rho}_{jj} \geq \Gamma_T\left(\frac{q}{1-q} + \frac{1}{\kappa_j}\right) > \frac{\Gamma_T}{1-q}, \quad (74)$$

and informs us that ($j \neq k$)

$$\hat{r}_{jk} \leq \left[\left(1 + \frac{1-q}{q\kappa_j}\right)\left(1 + \frac{1-q}{q\kappa_k}\right)\right]^{-1/2}. \quad (75)$$

By (74) and (51), every local variance exceeds the panmictic variance ρ_r.

The demes are strongly differentiated if $\hat{r}_{jk} \ll 1$ for every j and k such that $j \neq k$, for which (71b) yields the sufficient condition

$$1 - q \gg q\gamma(2-\gamma)\kappa_{\max}. \quad (76)$$

In this case,

$$\hat{\rho}_{jj} \approx \frac{\Gamma_j}{1 - q(1-\gamma)^2}, \quad (77a)$$

$$\hat{r}_{jk} \approx \left[\frac{q\gamma(2-\gamma)}{1-q}\right]\sqrt{\kappa_j\kappa_k}, \quad j \neq k. \quad (77b)$$

If (76) is strengthened to

$$1 - q \gg q\gamma(2-\gamma), \quad (78)$$

then (77a) and (71a) simplify to

$$\hat{\rho}_{jj} \approx \frac{\Gamma_j}{1-q}, \quad (79a)$$

$$\hat{\rho}_{jk} \approx \frac{\Gamma_T q\gamma(2-\gamma)}{(1-q)^2}, \quad j \neq k; \quad (79b)$$

(79a) is the variance for an isolated deme.

Interdeme differentiation is weak if $\hat{r}_{jk} \approx 1$ for every j and k, for which the condition

$$1 - q \ll q\gamma(2-\gamma)\kappa_{\min} \quad (80)$$

suffices. Then we obtain the panmictic formula

$$\hat{\rho}_{jk} \approx \frac{\Gamma_T}{1-q}. \quad (81)$$

Since our formulation posits weak selection, little is lost biologically by approximating our results for $s \ll 1$. Then (71) becomes

$$\hat{\rho}_{jk} \approx \frac{\Gamma_T}{\gamma(2-\gamma) + 2s(1-\gamma)^2}\left[\frac{\gamma(2-\gamma)}{2s} + \frac{\delta_{jk}}{\kappa_j}\right] \quad (82a)$$

and ($j \neq k$)

$$\hat{r}_{jk} \approx \left\{\left[1 + \frac{2s}{\gamma(2-\gamma)\kappa_j}\right]\left[1 + \frac{2s}{\gamma(2-\gamma)\kappa_k}\right]\right\}^{-1/2}. \quad (82b)$$

From (76) and (77) we see that differentiation is strong if

$$2s \gg \gamma(2-\gamma)\kappa_{\max}, \quad (83)$$

in which case

$$\hat{\rho}_{jj} \approx \frac{\Gamma_j}{\gamma(2-\gamma) + 2s(1-\gamma)^2}, \quad (84a)$$

$$\hat{r}_{jk} \approx \left[\frac{\gamma(2-\gamma)}{2s}\right]\sqrt{\kappa_j\kappa_k}, \quad j \neq k. \quad (84b)$$

A glance at (78) and (79) tells us that if (83) is strengthened to

$$2s \gg \gamma(2-\gamma), \tag{85}$$

then (79) becomes ($j \neq k$)

$$\hat{\rho}_{jj} \approx \frac{\Gamma_j}{2s}, \quad \hat{\rho}_{jk} \approx \frac{\Gamma_T\gamma(2-\gamma)}{4s^2}. \tag{86}$$

By contrast, (80) and (81) reveal that differentiation is weak if

$$2s \ll \gamma(2-\gamma)\kappa_{\min}, \tag{87}$$

in which case

$$\hat{\rho}_{jk} \approx \frac{\Gamma_T}{2s}. \tag{88}$$

These results simplify further if migration is also weak: $\gamma \ll 1$. Then (82) reduces to

$$\hat{\rho}_{jk} \approx \frac{\Gamma_T}{2(\gamma+s)}\left(\frac{\gamma}{s} + \frac{\delta_{jk}}{\kappa_j}\right), \tag{89a}$$

$$\hat{r}_{jk} \approx \left[\left(1+\frac{s}{\gamma\kappa_j}\right)\left(1+\frac{s}{\gamma\kappa_k}\right)\right]^{-1/2}, \quad j \neq k. \tag{89b}$$

According to (83) and (84), differentiation is strong if

$$s \gg \gamma\kappa_{\max}, \tag{90}$$

in which case

$$\hat{\rho}_{jj} \approx \frac{\Gamma_j}{2(\gamma+s)}, \tag{91a}$$

$$\hat{r}_{jk} \approx \frac{\gamma}{s}\sqrt{\kappa_j\kappa_k}, \quad j \neq k. \tag{91b}$$

If (90) is strengthened to $s \gg \gamma$, then (86) becomes

$$\hat{\rho}_{jj} \approx \frac{\Gamma_j}{2s}; \quad \hat{\rho}_{jk} \approx \frac{\Gamma_T\gamma}{2s^2}, \quad j \neq k.$$

By contrast, (87) informs us that differentiation is weak if

$$s \ll \gamma\kappa_{\min}; \tag{92}$$

of course, (88) does not simplify.

Convergence: With the substitution (40), it will suffice to solve for $\varphi_{jk}(t)$ with the initial condition (42). Inserting (40) into (65), (67), and (68), we find

$$\varphi'_{jk} = (1-\gamma)^2\varphi_{jk} + \gamma(1-\gamma)(\bar{\varphi}_j + \bar{\varphi}_k) + \gamma^2\bar{\varphi}, \tag{93a}$$

$$\bar{\varphi}'_j = (1-\gamma)\bar{\varphi}_j + \gamma\bar{\varphi}, \tag{93b}$$

$$\bar{\varphi}' = \bar{\varphi}, \tag{93c}$$

the last of which is a special case of (46). The averages in (93) are defined as in (66). Hence, the solution of (93b) reads

$$\bar{\varphi}_j(t) = \bar{\varphi}(0) + [\bar{\varphi}_j(0) - \bar{\varphi}(0)](1-\gamma)^t, \tag{94}$$

and this enables us to solve (93a):

$$\begin{aligned}\varphi_{jk}(t) = {} & \bar{\varphi}(0) + [\bar{\varphi}_j(0) + \bar{\varphi}_k(0) - 2\bar{\varphi}(0)](1-\gamma)^t \\ & + [\varphi_{jk}(0) - \bar{\varphi}_j(0) - \bar{\varphi}_k(0) + \bar{\varphi}(0)](1-\gamma)^{2t}.\end{aligned} \tag{95}$$

Thus, $\varphi_{jk}(t) \to \bar{\varphi}(0)$ at the generic asymptotic rate $(1-\gamma)^t$. In view of (40), this exemplifies our general result that the transient part of $\rho_{jk}(t)$ decays at the asymptotic rate q^t and is asymptotically uniform. Observe that the homing tendency γ is the sole parameter that enters the time-dependence of $\varphi_{jk}(t)$.

THE LEVENE MODEL

Taking $\gamma = 1$ in (63) yields $m_{jk} = \kappa_k$, the backward migration matrix for the LEVENE (1953) model (see NAGYLAKI 1992a, pp. 144–148). Then (65) reduces to

$$\rho'_{jk} = q\bar{\rho} + \delta_{jk}\left(\frac{\Gamma_T}{\kappa_j}\right). \tag{96}$$

It is easy to verify that in the MALÉCOT model with $m_{jk} = \kappa_k$, the probabilities of identity are uniform after one generation of panmixia. By contrast, the inhomogeneous term in (96) produces interdemic differentiation.

Equilibrium: Setting $\gamma = 1$ in (71) gives

$$\hat{\rho}_{jk} = \Gamma_T\left(\frac{q}{1-q} + \frac{\delta_{jk}}{\kappa_j}\right), \tag{97a}$$

$$\hat{r}_{jk} = \left[\left(1+\frac{1-q}{q\kappa_j}\right)\left(1+\frac{1-q}{q\kappa_k}\right)\right]^{-1/2}, \quad j \neq k. \tag{97b}$$

The discussion and results between (71) and (75) apply with $\gamma = 1$.

From (76) and (77) we see that interdeme differentiation is strong if

$$1 - q \gg q\kappa_{\max}, \tag{98}$$

in which case $\hat{\rho}_{jj} \approx \Gamma_j$ and ($j \neq k$)

$$\hat{r}_{jk} \approx \left(\frac{q}{1-q}\right)\sqrt{\kappa_j\kappa_k}. \tag{99}$$

Since our model is biologically invalid (though mathematically well defined) for $q \ll 1$ ($s \approx 1$), therefore (98) requires $\kappa_{\max} \ll 1$, *i.e.*, that there be many demes.

According to (80) and (81), differentiation is weak if

$$1 - q \ll q\kappa_{\min}, \tag{100}$$

and this again produces (81).

For weak selection ($s \ll 1$), (97) simplifies to

$$\hat{\rho}_{jk} \approx \Gamma_T\left(\frac{1}{2s} + \frac{\delta_{jk}}{\kappa_j}\right), \tag{101a}$$

$$\hat{r}_{jk} \approx \left[\left(1 + \frac{2s}{\kappa_j}\right)\left(1 + \frac{2s}{\kappa_k}\right)\right]^{-1/2}, \quad j \neq k. \tag{101b}$$

By (98) and (99), differentiation is strong if $2s \gg \kappa_{\max}$, in which case ($j \neq k$)

$$\hat{r}_{jk} \approx \frac{\sqrt{\kappa_j \kappa_k}}{2s}. \tag{102}$$

Differentiation is weak if $2s \ll \kappa_{\min}$, in which case (88) holds.

Convergence: Setting $\gamma = 1$ in (93a) yields $\varphi'_{jk} = \bar{\varphi}$, so (93c) informs us that $\varphi_{jk}(t) = \bar{\varphi}(0)$ for $t \geq 1$. Thus, after one generation, the transient part of (40) decays at the generic rate q^t and is uniform.

THE ISLAND MODEL

The choices

$$\kappa_j = \frac{1}{n}, \quad \gamma = \frac{nm}{n-1} \tag{103}$$

in (63) give the backward migration matrix

$$\begin{aligned} m_{jj} &= 1 - m, \\ m_{jk} &= \frac{m}{n-1}, \quad j \neq k, \end{aligned} \tag{104}$$

for the island model (MORAN 1959; MARUYAMA 1970; MAYNARD SMITH 1970b; NAGYLAKI 1983, 1986) with n (≥ 2) demes and migration rate $m (0 < m < 1)$.

Recursion relations: Although we shall deduce our results for equilibrium and convergence by substituting (103) into the corresponding results for random outbreeding and site homing, it is also of interest to derive the symmetrized recursion relations for the island model. Since $\kappa_j = 1/n$, the last term in (65) becomes $\delta_{jk}\Gamma$, where $\Gamma = n\Gamma_T = V_g/N$ and N is the number of adults in each deme. Suppose that $\rho_{jj} = \rho_0$ and $\rho_{jk} = \rho_1$ for every j and k such that $j \neq k$. Then (65) implies that these relations hold for the next generation. Therefore, by induction, if we posit

$$\rho_{jj}(0) = \rho_0(0), \quad \rho_{jk}(0) = \rho_1(0) \tag{105}$$

for every j and k such that $j \neq k$, then

$$\rho_{jj}(t) = \rho_0(t), \quad \rho_{jk}(t) = \rho_1(t) \tag{106}$$

for every j, k, and t such that $j \neq k$. Substituting (106) and (103) into (65) leads to

$$\rho_0' = q[a\rho_0 + (1-a)\rho_1] + \Gamma, \tag{107a}$$

$$\rho_1' = q[b\rho_0 + (1-b)\rho_1], \tag{107b}$$

where

$$a = (1-m)^2 + \frac{m^2}{n-1}, \tag{108a}$$

$$b = \frac{m}{n-1}\left(2 - \frac{nm}{n-1}\right) = \frac{1-a}{n-1}. \tag{108b}$$

These parameters satisfy

$$0 < b \leq 1/n \leq a < 1; \tag{109}$$

both equalities in (109) are attained for random mating in the entire population, when $m = (n-1)/n$.

Since the equilibrium (71a) of (65) is unique, it is obtained correctly from the symmetrized system (107). Furthermore, since (65) preserves the symmetrization (105), a result of BOUCHER and NAGYLAKI (1988) implies that (107) correctly yields the asymptotic rate q^t and the asymptotically uniform pattern of convergence.

Equilibrium: Substituting (106), (103), and (108b) into (71), we get

$$\hat{\rho}_0 = \Gamma B/D, \quad \hat{\rho}_1 = \Gamma q b/D, \tag{110a}$$

$$\hat{r} = \hat{\rho}_1/\hat{\rho}_0 = qb/B, \tag{110b}$$

where

$$B = 1 - q(1-b), \tag{110c}$$

$$D = (1-q)[1 - q(1-nb)]. \tag{110d}$$

The remarks below (71) inform us that the covariances increase as Γ increases and they decrease as s increases; the correlation is independent of Γ and decreases as s increases; for $m < (n-1)/n$, $\hat{\rho}_0$ decreases and $\hat{\rho}_1$ and $\hat{r}$ increase as m increases. The bounds (72) to (75) reduce to

$$\Gamma \leq \hat{\rho}_0 \leq \frac{\Gamma}{1-q}, \tag{111}$$

and for $m < (n-1)/n$

$$\hat{\rho}_0 \geq \frac{\Gamma}{n}\left(\frac{q}{1-q} + n\right) > \frac{\Gamma}{n(1-q)}, \tag{112a}$$

$$\hat{\rho}_1 \leq \frac{\Gamma q}{n(1-q)}, \tag{112b}$$

$$\hat{r} \leq \frac{q}{q + n(1-q)}. \tag{112c}$$

From (76) and (77) we see that interdeme differentiation is strong if

$$1 - q \gg qb, \tag{113}$$

which implies

$$\hat{\rho}_0 \approx \frac{\Gamma}{1 - q(1 - nb)}, \quad \hat{r} \approx \frac{qb}{1 - q}. \tag{114}$$

If (113) is strengthened to

$$1 - q \gg nqb, \tag{115}$$

then (79) yields

$$\hat{\rho}_0 \approx \frac{\Gamma}{1 - q}, \quad \hat{\rho}_1 \approx \frac{\Gamma qb}{(1 - q)^2}. \tag{116}$$

By (80) and (81), differentiation is weak if

$$1 - q \ll qb, \tag{117}$$

which gives the panmictic result

$$\hat{\rho}_0 \approx \hat{\rho}_1 \approx \frac{\Gamma}{n(1 - q)}. \tag{118}$$

For weak selection ($s \ll 1$), (110) simplifies to

$$\hat{\rho}_0 \approx \frac{\Gamma(2s + b)}{2s(2s + nb)}, \quad \hat{\rho}_1 \approx \frac{\Gamma b}{2s(2s + nb)}, \tag{119a}$$

$$\hat{r} \approx \frac{b}{2s + b}. \tag{119b}$$

By (113) and (119), differentiation is strong if $2s \gg b$, which implies

$$\hat{\rho}_0 \approx \frac{\Gamma}{2s + nb}, \quad \hat{\rho}_1 \approx \frac{\Gamma b}{2s(2s + nb)}, \tag{120}$$

and $\hat{r} \approx b/(2s)$. Under the stronger condition $2s \gg nb$, (120) reduces to

$$\hat{\rho}_0 \approx \frac{\Gamma}{2s}, \quad \hat{\rho}_1 \approx \frac{\Gamma b}{4s^2}. \tag{121}$$

Differentiation is weak if $2s \ll b$, in which case

$$\hat{\rho}_0 \approx \hat{\rho}_1 \approx \frac{\Gamma}{2ns}. \tag{122}$$

If migration is also weak ($m \ll 1$), we may substitute $b \approx 2m/(n - 1)$ throughout.

Finally, we note that letting $n \to \infty$ in (110) leads to

$$\hat{\rho}_0 \to \frac{\Gamma}{1 - q(1 - m)^2}, \quad \hat{\rho}_1 \to 0, \quad \hat{r} \to 0.$$

Now we can let $s \to 0$ to deduce

$$\hat{\rho}_0 \to \frac{\Gamma}{m(2 - m)},$$

which simplifies to $\Gamma/(2m)$, a result of LANDE (LOFSVOLD 1988), for $m \ll 1$.

Convergence: We impose (106) and rewrite (40) in our present notation for $l = 1, 2$:

$$\rho_l(t) = \hat{\rho}_l - q^t\varphi_l(t). \tag{123}$$

Then (66) and (103) demonstrate that for each deme, *i.e.*, $j = 1, 2, \ldots, n$,

$$\bar{\varphi}_j(t) = \bar{\varphi}(t) = \left(\frac{1}{n}\right)\varphi_0(t) + \left(\frac{n - 1}{n}\right)\varphi_1(t), \tag{124}$$

and inserting (124) and (103) into (95), we find for $l = 1, 2$

$$\varphi_l(t) = \bar{\varphi}(0) + [\varphi_l(0) - \bar{\varphi}(0)]\left(1 - \frac{nm}{n - 1}\right)^{2t}, \tag{125}$$

in which the initial conditions may be evaluated from (123) and (124).

THE CIRCULAR HABITAT IN THE DIFFUSION APPROXIMATION

This is the simplest model of a finite population that incorporates isolation by distance. We shall formulate the model discretely, take the diffusion limit, and derive explicit formulas for its stationary and transient states.

Recursion relations: We suppose that n colonies, each of which comprises N individuals, form a closed loop (MALÉCOT, 1951). This arrangement might be a mathematical idealization of an atoll; demes around a mountain, lake, or shore of an island; or colonies of amphibious or shallow-water organisms in a large, deep lake or around an island. Starting at an arbitrary colony, we circle the loop repeatedly and number the colonies without limit 0, 1, 2, . . . counterclockwise and 0, −1, −2, . . . clockwise. Dispersion is homogeneous: $m_{jk} = m_{j-k}$; thus, m_j signifies the probability of displacement by j demes, where $j = 0, \pm 1, \pm 2, \ldots$. The probability that the separation between two individuals changes by j demes reads (MARUYAMA, 1971; NAGYLAKI, 1974a)

$$\omega_j = \sum_{k=-\infty}^{\infty} m_k m_{j+k}. \tag{126}$$

Observe that ω_j is even (NAGYLAKI, 1974a, 1978a): $\omega_{-j} = \omega_j$.

The recursion relations (29) now have the form

$$\rho'_{jk} = q \sum_{l,p=-\infty}^{\infty} m_{j-l} m_{k-p} \rho_{lp} + \Gamma \sum_{l=-\infty}^{\infty} \delta_{j-k,ln}, \tag{127}$$

where $\Gamma = V_g/N$. The homogeneity of dispersion suggests homogeneity of the covariances: $\rho_{jk} = \tilde{\rho}_{j-k}$ for every j and k. Then (127) implies that $\rho'_{jk} = \tilde{\rho}'_{j-k}$ for every j and k. Therefore, by induction, if we posit that $\rho_{jk}(0) = \tilde{\rho}_{j-k}(0)$ for every j and k, then $\rho_{jk}(t) = \tilde{\rho}_{j-k}(t)$ for every j, k, and t. This simplifies (127) to

$$\tilde{\rho}_j' = q \sum_{k=-\infty}^{\infty} \omega_k \tilde{\rho}_{j-k} + \Gamma \sum_{k=-\infty}^{\infty} \delta_{j,kn}. \tag{128}$$

Acceptable solutions of (128) must be even and periodic: for $j, k = 0, \pm1, \pm2, \ldots,$

$$\tilde{\rho}_{-j} = \tilde{\rho}_j, \quad \tilde{\rho}_{j+kn} = \tilde{\rho}_j. \tag{129}$$

Indeed, since (128) preserves (129), it suffices to define $\tilde{\rho}_j(0)$ so that (129) holds.

Since the equilibrium of (127) is unique, it is obtained correctly from (128). Furthermore, since (127) preserves homogeneity, a result of BOUCHER and NAGYLAKI (1988) establishes that (128) correctly gives the asymptotic rate q^t and the asymptotically uniform pattern of convergence.

Discrete Fourier analysis (MALÉCOT 1951, 1965, 1975; NAGYLAKI 1983) enables us to express the equilibrium solution of (128) as an explicit finite sum. Nevertheless, since our model requires weak selection and random drift, we proceed at once to the more tractable and illuminating diffusion approximation.

The diffusion approximation: We scale space and time according to

$$x = j\epsilon, \quad T = \lambda t, \quad \rho(x, T) = \tilde{\rho}_j(t). \tag{130}$$

In the new units, ϵ represents the distance between adjacent colonies and λ corresponds to one generation. The scaled circumference of the habitat, selection intensity, and random-drift parameter are

$$L = n\epsilon, \quad s_0 = s/\lambda, \quad \Gamma_0 = \epsilon\Gamma/\lambda. \tag{131}$$

We can interpret Γ_0 naturally by fixing V_g and scaling the population density d:

$$d = N/\epsilon, \quad d_0 = \lambda d, \tag{132}$$

$$\Gamma_1 = \epsilon\Gamma = V_g/d, \quad \Gamma_0 = \Gamma_1/\lambda = V_g/d_0. \tag{133}$$

We let $\epsilon \to 0$, $\lambda \to 0$, $n \to \infty$, $s \to 0$, and $N \to \infty$ so that λ/ϵ^2, L, s_0, and Γ_0 remain fixed.

For migration, we require the diffusion hypotheses

$$\lim_{\lambda\to0} \frac{\epsilon^2}{\lambda} \sum_{j:|j|<\theta/\epsilon} j^2\omega_j = \sigma_0^2, \tag{134a}$$

$$\lim_{\lambda\to0} \frac{1}{\lambda} \sum_{j:|j|\geq\theta/\epsilon} \omega_j = 0 \tag{134b}$$

for all fixed $\theta > 0$. (Recall that ω_j is even, and therefore has mean zero.) Clearly, σ_0^2 is the variance of the change in separation between individuals per new time unit, in the new length units; the corresponding variance in generations is $\sigma^2 = \lambda\sigma_0^2$. From (126) it is easy to prove that the variance of ω_j is twice that of m_j. Our scalings imply that selection ($s \propto \epsilon^2$), migration ($\sigma^2 \propto \epsilon^2$), and random drift ($\Gamma \propto \epsilon$) must be weak, and that the number of demes must be large ($n \propto 1/\epsilon$).

We can rewrite (129) as

$$\rho(-x, T) = \rho(x, T), \quad \rho(x + kL, T) = \rho(x, T) \tag{135}$$

for $k = 0, \pm1, \pm2, \ldots$ and every x and T.

Following the corresponding derivation for the MALÉCOT model (NAGYLAKI 1986), from (128), (130), (131), (134), and (135) we deduce the boundary-value problem

$$\rho_T = -2s_0\rho + \tfrac{1}{2}\sigma_0^2\rho_{xx}, \quad 0 < x < \tfrac{1}{2}L, \tag{136a}$$

$$\sigma_0^2\rho_x(0, T) = -\Gamma_0, \tag{136b}$$

$$\rho_x(\tfrac{1}{2}L, T) = 0, \tag{136c}$$

in which the subscripts T and x signify partial derivatives.

One can prove that if $\rho(x, 0) \geq 0$ for all x, then $\rho(x, T) \geq 0$ for all x and T (*cf.* NAGYLAKI 1986).

Equilibrium: We find easily that the stationary solution of (136) is

$$\hat{\rho}(x) = \frac{\beta \cosh\left[\alpha\left(1 - \frac{2x}{L}\right)\right]}{\sinh \alpha}, \quad 0 \leq x \leq \tfrac{1}{2}L, \tag{137a}$$

where

$$\alpha = \frac{L\sqrt{s_0}}{\sigma_0} = \frac{L\sqrt{s}}{\sigma}, \tag{137b}$$

$$\beta = \frac{\Gamma_0}{2\sigma_0\sqrt{s_0}} = \frac{\Gamma_1}{2\sigma\sqrt{s}} = \frac{V_g}{2d\sigma\sqrt{s}}. \tag{137c}$$

For the local variance of $\bar{Z}$, we have

$$\hat{\rho}(0) = \beta \coth \alpha; \tag{138}$$

the correlation at separation x reads

$$\hat{r}(x) = \frac{\hat{\rho}(x)}{\hat{\rho}(0)} = \frac{\cosh\left[\alpha\left(1 - \frac{2x}{L}\right)\right]}{\cosh \alpha}. \tag{139}$$

As expected, $\hat{\rho}(x)$ and $\hat{r}(x)$ are monotone decreasing in x. Therefore, setting $x = 0$ and $\tfrac{1}{2}L$ yields the bounds

$$\beta \operatorname{cosech} \alpha \leq \hat{\rho}(x) \leq \beta \coth \alpha, \tag{140a}$$

$$\operatorname{sech} \alpha \leq \hat{r}(x) \leq 1. \tag{140b}$$

From (138) we see that

$$\hat{\rho}(0) > \beta \max(1, 1/\alpha) \geq \beta/\alpha = \rho_r, \tag{140c}$$

where ρ_r denotes the panmictic value (51) in the diffusion limit. The correlation is independent of V_g and d.

It is interesting to note that, with suitable reinterpretation of α and β, the covariance $\hat{\rho}(x)$ differs from the probability of identity $\hat{f}(x)$ in the MALÉCOT model

(NAGYLAKI 1974a, 1986) only by a multiplicative factor, and hence $\hat{r}(x) = \hat{f}(x)/\hat{f}(0)$.

As a check, observe that (56) is exact in the diffusion limit. Furthermore, the homogeneous circular migration pattern is conservative (NAGYLAKI 1992a, p. 136), so $N_e = N_T$. Consequently, we obtain

$$\hat{\bar{\rho}} = \frac{V_g}{2sN_T} = \frac{V_g}{2sLd} = \frac{\beta}{\alpha}. \tag{141}$$

Invoking (135) and then (137a) to evaluate

$$\hat{\bar{\rho}} = \frac{1}{L^2}\int_{-\frac{1}{2}L}^{\frac{1}{2}L}\int_{-\frac{1}{2}L}^{\frac{1}{2}L} \hat{\rho}(x-y)\,dxdy \tag{142}$$

verifies (141)

Geographical differentiation is strong if

$$\hat{r}(½L) \ll 1 \Leftrightarrow \operatorname{sech}\alpha \ll 1 \Leftrightarrow \alpha \gg 1, \tag{143}$$

which corresponds to a large habitat, strong selection, or weak migration. If we fix δ in $[0, 1)$ and let $x = \delta(½L)$, then we have the approximations

$$\hat{\rho}(x) \approx \beta e^{-2\alpha x/L}, \tag{144a}$$

$$\hat{r}(x) \approx e^{-2\alpha x/L}. \tag{144b}$$

Differentiation is weak if

$$\hat{r}(½L) \approx 1 \Leftrightarrow \operatorname{sech}\alpha \approx 1 \Leftrightarrow \alpha \ll 1, \tag{145}$$

which corresponds to a small habitat, weak selection, or strong migration. In this case, (137a) reduces to the panmictic value

$$\hat{\rho}(x) \approx \beta/\alpha. \tag{146}$$

It is instructive to compare the amount of differentiation in a circular habitat with that in the island model. For the latter, if selection and migration are weak ($s \ll 1$ and $m \ll 1$), then (119b) yields

$$\hat{r}_i \approx \frac{1}{1+c}, \tag{147a}$$

where

$$c = \frac{2s}{b} \approx (n-1)\frac{s}{m}. \tag{147b}$$

To effect the comparison, for the circular habitat we posit symmetric nearest-neighbor migration at rate ½m in each direction. Then (137b) becomes

$$\alpha = \frac{n\epsilon\sqrt{s}}{\sqrt{m\epsilon}} = n\sqrt{\frac{s}{m}} = n\sqrt{\frac{c}{n-1}} > \sqrt{nc}. \tag{148}$$

From (139) we get

$$\hat{r}_c(½L) = \operatorname{sech}\alpha. \tag{149}$$

Since $n \geqslant 2$, we obtain from (148)

$$1 + c < 1 + \frac{\alpha^2}{n} < \cosh\alpha, \tag{150}$$

and (147a) and (149) then reveal that $\hat{r}_i > \hat{r}_c(½L)$, *i.e.*, as expected, differentiation is stronger in the circular habitat, where isolation is by distance, than in the island model, where the demes are equidistant with respect to migration.

Convergence: In view of (40), (130), and (131), we set

$$\rho(x, T) = \hat{\rho}(x) - e^{-2s_0T}\varphi(x, T). \tag{151}$$

Substituting (151) into (136) and using the fact that $\hat{\rho}(x)$ satisfies (136) at equilibrium, we find

$$\varphi_T = ½\sigma_0^2\varphi_{xx}, \quad 0 < x < ½L, \tag{152a}$$

$$\varphi_x(0, T) = 0, \tag{152b}$$

$$\varphi_x(½L, T) = 0, \tag{152c}$$

$$\varphi(x, 0) = \hat{\rho}(x) - \rho(x, 0). \tag{152d}$$

We simplify (152) by scaling space and time:

$$x = ½L\xi, \quad T = T_0\tau, \tag{153a}$$

$$T_0 = \frac{L^2}{4\sigma_0^2}, \quad \Phi(\xi, \tau) = \varphi(x, T). \tag{153b}$$

Then (152) becomes

$$\Phi_\tau = ½\Phi_{\xi\xi}, \quad 0 < \xi < 1, \tag{154a}$$

$$\Phi_\xi(0, \tau) = 0, \tag{154b}$$

$$\Phi_\xi(1, \tau) = 0, \tag{154c}$$

$$\Phi(\xi, 0) = \Phi_0(\xi) = \varphi(x, 0). \tag{154d}$$

It is easy to solve the boundary-value problem (154) *ab initio* with Laplace transforms. However, (154) is formally equivalent to the mathematical description of the temperature distribution in an insulated rod of unit length with initial temperature $\Phi_0(\xi)$, and it has the unique solution (CHURCHILL 1941, p. 109)

$$\Phi(\xi, \tau) = \sum_{j=0}^{\infty} a_j e^{-(1/2)j^2\pi^2\tau}\psi_j(\xi), \tag{155a}$$

$$a_j = \int_0^1 \Phi_0(\eta)\psi_j(\eta)\,d\eta, \tag{155b}$$

$$\psi_0(\xi) = 1; \quad \psi_j(\xi) = \sqrt{2}\cos(j\pi\xi), \quad j \geqslant 1. \tag{155c}$$

In this Fourier cosine series, note that (153) and (130) give

$$\tau = \left(\frac{4\sigma^2}{L^2}\right)t. \tag{156}$$

From (155) we see that as $\tau \to \infty$,

$$\Phi(\xi, \tau) \to a_0 = \int_0^1 \Phi_0(\eta)\,d\eta, \tag{157}$$

and (151), (153b), and (155) yield

$$\rho(x, T) = \hat{\rho}(x) - e^{-2s_0T}[a_0 + O(e^{-(1/2)\pi^2\tau})]. \tag{158}$$

The asymptotic rate of convergence and uniformity both agree with our general theory.

If the initial local average phenotypes are fixed, then $\rho(x, 0) = 0$ for all x, and therefore $\Phi_0(\xi) = \hat{\rho}(x)$. Inserting (137a) into (155b) leads to

$$a_0 = \frac{\beta}{\alpha}; \quad a_j = \frac{\sqrt{2}\alpha\beta}{\alpha^2 + j^2\pi^2}, \quad j \geqslant 1. \tag{159}$$

THE UNBOUNDED LINEAR STEPPING-STONE MODEL IN THE DIFFUSION LIMIT

We suppose that colonies of individuals are located at 0, ±1, ±2, ... Such a long linear habitat might represent organisms along or in a river, close to a seashore, or along a mountain range.

Equilibrium: We can obtain the equilibrium covariance most easily by letting the circumference tend to infinity in the result for the circular habitat: as $L \longrightarrow \infty$ with x fixed, (137) converges to

$$\hat{\rho}(x) = \beta e^{-2\sqrt{s}x/\sigma}, \quad x \geqslant 0. \tag{160}$$

Therefore, the variance and correlation are

$$\hat{\rho}(0) = \beta, \quad \hat{r}(x) = e^{-2\sqrt{s}x/\sigma}. \tag{161}$$

Thus, the characteristic length of the exponential decay is $\sigma/(2\sqrt{s})$.

As for the circular habitat, with suitable reinterpretation of the parameters, $\hat{\rho}(x)$ differs from the probability of identity $\hat{f}(x)$ in the diffusion approximation of the MALÉCOT model (NAGYLAKI 1974a, 1978a, 1986) only by a multiplicative factor, and hence $\hat{r}(x) = \hat{f}(x)/\hat{f}(0)$.

With the correct conversion of the parameters, (160) agrees with approximation (12b) of LANDE (1991).

Convergence: It is easiest to let $L \longrightarrow \infty$ in (152). We obtain

$$\varphi_T = \tfrac{1}{2}\sigma_0^2\varphi_{xx}, \quad x > 0, \tag{162a}$$

$$\varphi_x(0, T) = 0, \tag{162b}$$

$$\varphi(x, T) \longrightarrow 0 \quad \text{as } x \longrightarrow \infty \text{ with } T \text{ fixed}, \tag{162c}$$

$$\varphi(x, 0) = \varphi_0(x). \tag{162d}$$

The boundary-value problem (162) can be solved *ab initio* with either Fourier cosine or Laplace transforms. However, (162) is formally equivalent to the mathematical description of the temperature distribution in a semi-infinite rod insulated at the origin and with initial temperature $\varphi_0(x)$; it has the unique solution (ZAUDERER 1983, p. 222)

$$\varphi(x, T) = \int_0^\infty g(x, y, T)\varphi_0(y)\, dy, \tag{163a}$$

where

$$g(x, y, T) = \frac{1}{\sigma\sqrt{2\pi t}}\left\{\exp\left[-\frac{(x-y)^2}{2\sigma^2 t}\right] + \exp\left[-\frac{(x+y)^2}{2\sigma^2 t}\right]\right\}. \tag{163b}$$

Observe that $\sigma^2 t = \sigma_0^2 T$.

If

$$\int_0^\infty \varphi_0(y)\, dy < \infty, \tag{164}$$

then (163a) converges uniformly in T, which permits us to take the limit as $T \longrightarrow \infty$ with x fixed through the integral sign. Then (163) yields

$$\varphi(x, T) \sim \frac{1}{\sigma}\sqrt{\frac{2}{\pi t}} \int_0^\infty \varphi_0(y)\, dy \tag{165}$$

as $T \longrightarrow \infty$ with x fixed. The corresponding time dependence is $t^{-3/2}$ for the diffusion approximation of the MALÉCOT model, which has a linear rather than uniform spatial dependence (NAGYLAKI 1978a, 1986).

If $\rho(x, 0) = 0$ for all x, then

$$\varphi_0(x) = \hat{\rho}(x) = \beta e^{-2\sqrt{s}x/\sigma}. \tag{166}$$

Clearly, (164) holds, and (165) simplifies to

$$\varphi(x, T) \sim \frac{\beta}{\sqrt{2\pi s t}} \tag{167}$$

as $T \longrightarrow \infty$ with x fixed, in which $st = s_0 T$. Substituting (166) into (163a) leads to the exact solution

$$\varphi(x, T) = \tfrac{1}{2}\beta e^{2st}\left[e^{-2\sqrt{s}x/\sigma} \operatorname{erfc}\left(\sqrt{2st} - \frac{x}{\sigma\sqrt{2t}}\right) + e^{2\sqrt{s}x/\sigma} \operatorname{erfc}\left(\sqrt{2st} + \frac{x}{\sigma\sqrt{2t}}\right)\right], \tag{168a}$$

where the complementary error function is given by

$$\operatorname{erfc} u = \frac{2}{\sqrt{\pi}} \int_u^\infty e^{-v^2}\, dv. \tag{168b}$$

This enables us to verify (167) directly.

THE UNBOUNDED STEPPING-STONE MODEL

As discussed in the introduction, we do not have a satisfactory formulation of a continuous model in which individuals reproduce and migrate independently of each other. Furthermore, the diffusion approximation of the stepping-stone model fails in more than one spatial dimension (FLEMING and SU 1974; NAGYLAKI 1974b). This failure occurs essentially because the required scalings of space, time, and subpopulation number N [*cf.* (130) to (134)] lead to $N \longrightarrow \infty$ only in one dimension, and the divergence of N is necessary for the derivation of a limiting partial differential equation from the recursion relation (NAGYLAKI 1978b). Therefore, it is important to investigate directly the n-dimensional stepping-stone model.

Recursion relations: Suppose there are demes of N individuals each at the points of the infinite integer lattice in n dimensions. We denote position by n-dimensional vectors $\mathbf{x}$, $\mathbf{y}$, . . . with integer components. We assume that migration is homogeneous, *i.e.*, the migration rates depend only on displacement, rather than on the initial and final positions separately (MALÉCOT 1949, 1950, 1951; KIMURA 1953): $m_{\mathbf{x},\mathbf{y}} = m(\mathbf{x} - \mathbf{y})$. The probability that the separation between two individuals changes by $\mathbf{x}$ reads (NAGYLAKI 1974a, b, 1976, 1978a)

$$\omega(\mathbf{x}) = \sum_{\mathbf{y}} m(\mathbf{y})m(\mathbf{x} + \mathbf{y}). \tag{169}$$

Observe that $\omega(\mathbf{x})$ is even (NAGYLAKI 1974a, 1978a): $\omega(-\mathbf{x}) = \omega(\mathbf{x})$.

The recursion relations (29) now have the form

$$\rho'_{\mathbf{x},\mathbf{y}} = q \sum_{\mathbf{z},\mathbf{w}} m(\mathbf{x} - \mathbf{z})m(\mathbf{y} - \mathbf{w})\rho_{\mathbf{z},\mathbf{w}} + \Gamma\delta_{\mathbf{x},\mathbf{y}}, \tag{170}$$

where $\Gamma = V_g/N$, and $\delta_{\mathbf{x},\mathbf{y}} = 1$ if $\mathbf{x} = \mathbf{y}$ and $\delta_{\mathbf{x},\mathbf{y}} = 0$ if $\mathbf{x} \neq \mathbf{y}$. An easy proof shows that (170) preserves initial homogeneity of the covariances, which we posit. Writing $\rho_{\mathbf{x},\mathbf{y}} = \rho(\mathbf{x} - \mathbf{y}, t)$, we reduce (170) to

$$\rho(\mathbf{x}, t + 1) = q \sum_{\mathbf{y}} \omega(\mathbf{y})\rho(\mathbf{x} - \mathbf{y}, t) + \Gamma\delta_{\mathbf{x},0}. \tag{171}$$

We define $\rho(\mathbf{x}, 0)$ to be even. Then (171) implies

$$\rho(-\mathbf{x}, t) = \rho(\mathbf{x}, t) \tag{172}$$

for every $\mathbf{x}$ and t.

Since the equilibrium of (170) is unique, it will be obtained correctly from (171).

Equilibrium: We identify the probabilities $\omega(\mathbf{x})$ as the Fourier coefficients of the function

$$\Omega(\boldsymbol{\theta}) = \sum_{\mathbf{x}} \omega(\mathbf{x})e^{-i\boldsymbol{\theta}\cdot\mathbf{x}}, \tag{173}$$

in which $\boldsymbol{\theta}\cdot\mathbf{x}$ signifies the scalar product. Since $\omega(\mathbf{x})$ is even, (173) implies that $\Omega(\boldsymbol{\theta})$ is even and real:

$$\Omega(-\boldsymbol{\theta}) = \Omega^*(\boldsymbol{\theta}) = \Omega(\boldsymbol{\theta}), \tag{174}$$

where the asterisk denotes complex conjugation. Putting

$$M(\boldsymbol{\theta}) = \sum_{\mathbf{x}} m(\mathbf{x})e^{-i\boldsymbol{\theta}\cdot\mathbf{x}}, \tag{175}$$

from (173), (169), and (175) we establish easily that $\Omega(\boldsymbol{\theta}) = |M(\boldsymbol{\theta})|^2 \geq 0$. Since $0 \leq \omega(\mathbf{x}) \leq 1$, from (173) we infer that $\Omega(\boldsymbol{\theta}) \leq 1$.

At equilibrium, (171) becomes

$$\hat{\rho}(q, \mathbf{x}) = q \sum_{\mathbf{y}} \omega(\mathbf{y})\hat{\rho}(q, \mathbf{x} - \mathbf{y}) + \Gamma\delta_{\mathbf{x},0}, \tag{176}$$

in which we have displayed explicitly the dependence on q. From (176) we deduce that

$$\tilde{\rho}(q, \boldsymbol{\theta}) = \sum_{\mathbf{x}} \hat{\rho}(q, \mathbf{x})e^{-i\boldsymbol{\theta}\cdot\mathbf{x}} \tag{177}$$

satisfies

$$\tilde{\rho}(q, \boldsymbol{\theta}) = q\Omega(\boldsymbol{\theta})\tilde{\rho}(q, \boldsymbol{\theta}) + \Gamma. \tag{178}$$

Solving (178) for $\tilde{\rho}$ and evaluating the Fourier coefficients in (177) yields

$$\hat{\rho}(q, \mathbf{x}) = \Gamma \int_R \frac{e^{i\boldsymbol{\theta}\cdot\mathbf{x}}}{1 - q\Omega(\boldsymbol{\theta})} \frac{d^n\theta}{(2\pi)^n}, \tag{179}$$

where R designates the n-dimensional cube $|\theta_j| \leq \pi$ for $j = 1, 2, \ldots, n$.

We wish to approximate $\hat{\rho}(q, \mathbf{x})$ for weak selection, *i.e.*, as $s \to 0+$ and hence $q \to 1-$. We place two biologically trivial restrictions on the migration pattern m. First, we posit that the random walk generated by m is strongly aperiodic (SAWYER 1976, 1977; SPITZER 1976, p. 42). Then after a sufficiently long time any two genes have positive probability of being descended from the same gene. Second, we suppose that the covariance matrix of m is finite. Our two assumptions jointly imply that the eigenvalues of the covariance matrix of m are positive. From (169) it is easy to prove that the covariance matrix of ω is twice that of m.

Inserting the identity

$$\frac{1}{1 - q\Omega} = 1 + \frac{q\Omega}{1 - q\Omega}$$

into (179) gives

$$\hat{\rho}(q, \mathbf{x}) = \Gamma[\delta_{\mathbf{x},0} + H(q, \mathbf{x})], \tag{180a}$$

where the function

$$H(q, \mathbf{x}) = \int_R \frac{q\Omega(\boldsymbol{\theta})}{1 - q\Omega(\boldsymbol{\theta})} e^{i\boldsymbol{\theta}\cdot\mathbf{x}} \frac{d^n\theta}{(2\pi)^n} \tag{180b}$$

has been extensively analyzed in studies of the MALÉCOT model (NAGYLAKI 1976; SAWYER 1977).

To express the results in simple form, first rotate coordinates so as to diagonalize the covariance matrix of $\omega(\mathbf{x})$ (the same rotation diagonalizes that of m); denote the eigenvalues by $\sigma_j^2 > 0$ for $j = 1, 2, \ldots, n$ and set

$$\xi = 2\sqrt{s}\left[\sum_{j=1}^{n} \left(\frac{\tilde{x}_j}{\sigma_j}\right)^2\right]^{1/2} \tag{181}$$

in the rotated coordinates $\tilde{x}_j$. Thus, ξ represents a scaled separation between demes.

One dimension: We have (NAGYLAKI 1976)

$$H(q, x) = \frac{1}{2\sigma\sqrt{s}} [e^{-\xi} + \tilde{h}(q, x)], \qquad (182)$$

where

$$\tilde{h}(q, x) = o(1) \qquad (183a)$$

uniformly in x as $s \longrightarrow 0$. If $\omega(x)$ satisfies

$$\mathscr{E}(|X|^{3+\eta}) < \infty \qquad (183b)$$

for some η such that $0 < \eta \leq 1$, then (183a) can be strengthened to

$$\tilde{h}(q, x) = O(\sqrt{s}) \qquad (183c)$$

uniformly in x as $s \longrightarrow 0$. The condition (183b) is biologically plausible and holds whenever the fourth moment $\mathscr{E}(X^4)$ exists. See SAWYER (1977) for similar results.

Substituting (182) into (180a), we get

$$\hat{\rho}(q, x) = \frac{\Gamma}{2\sigma\sqrt{s}} [e^{-\xi} + h(q, x)], \qquad (184a)$$

where

$$h(q, x) = 2\sigma\sqrt{s}\delta_{x,0} + \tilde{h}(q, x) \qquad (184b)$$

also satisfies (183). Thus, if ξ is bounded above, we may approximate $\hat{\rho}$ by neglecting h in (184a). More precisely,

$$\hat{\rho}(q, x) \sim \left(\frac{\Gamma}{2\sigma\sqrt{s}}\right) e^{-\xi} \qquad (185)$$

as $s \longrightarrow 0$ and $x \longrightarrow \infty$ with ξ fixed, in agreement with (160) and approximation (12b) of Lande (1991).

From (184a) we obtain the correlation

$$\hat{r}(q, x) = e^{-\xi} + \hat{h}(q, x), \qquad (186)$$

where $\hat{h}(q, x)$ also satisfies (183). Consequently,

$$\hat{r}(q, x) \longrightarrow e^{-\xi} \qquad (187)$$

as $s \longrightarrow 0$ and $x \longrightarrow \infty$ with ξ fixed, in agreement with $\hat{f}(x)/\hat{f}(0)$ for the MALÉCOT model (MALÉCOT 1950, 1965; WEISS and KIMURA 1965; NAGYLAKI 1976, 1986; SAWYER 1977).

Two dimensions: Now we have (NAGYLAKI 1976)

$$H(q, \mathbf{0}) = -\frac{\ln 2s}{2\pi\sigma_1\sigma_2} [1 + \tilde{h}(q, \mathbf{0})], \qquad (188)$$

where

$$\tilde{h}(q, \mathbf{0}) = o(1) \qquad (189a)$$

as $s \longrightarrow 0$. If

$$\mathscr{E}(X^{2+\eta}) < \infty \qquad (189b)$$

for some η such that $0 < \eta \leq 2$, where $X = \|\mathbf{X}\|$ denotes the length of the random vector $\mathbf{X}$, then (189a) can be strengthened to

$$\tilde{h}(q, \mathbf{0}) = O(-1/\ln 2s) \qquad (189c)$$

as $s \longrightarrow 0$. The condition (189b) is biologically trivial; again, the existence of the fourth moment suffices. See SAWYER (1977) for similar results.

Substituting (188) into (180a) produces the local variance

$$\hat{\rho}(q, \mathbf{0}) = -\frac{\Gamma \ln 2s}{2\pi\sigma_1\sigma_2} [1 + h(q, \mathbf{0})], \qquad (190a)$$

where

$$h(q, \mathbf{0}) = -\left(\frac{2\pi\sigma_1\sigma_2}{\ln 2s}\right) \delta_{\mathbf{x},0} + \tilde{h}(q, \mathbf{0}) \qquad (190b)$$

also satisfies (189). Therefore, we may neglect the error term h in (190a). If migration is isotropic ($\sigma_1 = \sigma_2 = \sigma$), the leading term in (190a) reduces to approximation (13a) of LANDE (1991).

For the decay in space, SAWYER (1977, Appendix II) assumed (189b) and proved that

$$H(q, \mathbf{x}) = \frac{K_0(\xi)}{\pi\sigma_1\sigma_2} [1 + O(s)] + \tilde{h}(q, \mathbf{x}) \qquad (191a)$$

for $x \neq 0$, in which K_0 designates the modified Bessel function of the second kind of order zero, $O(s)$ is uniform in $\mathbf{x}$ as $s \longrightarrow 0$, and

$$\tilde{h}(q, \mathbf{x}) = h_1(q, \mathbf{x}) + h_2(q, \mathbf{x}), \qquad (191b)$$

where

$$h_1(q, \mathbf{x}) = O(s^{\eta/2}) \qquad (191c)$$

uniformly in $\mathbf{x}$ as $s \longrightarrow 0$ and ($x = \|\mathbf{x}\|$)

$$h_2(q, \mathbf{x}) = \begin{cases} O(x^{-\eta/2}), & \eta < 2, \\ O(x^{-1} \ln x), & \eta = 2 \end{cases} \qquad (191d)$$

uniformly in s as $x \longrightarrow \infty$.

Inserting (191a) into (180a) produces

$$\hat{\rho}(q, \mathbf{x}) = \frac{\Gamma K_0(\xi)}{\pi\sigma_1\sigma_2} [1 + O(s)] + h(q, \mathbf{x}), \qquad (192a)$$

where

$$h(q, \mathbf{x}) = \Gamma[\delta_{\mathbf{x},0} + \tilde{h}(q, \mathbf{x})] \qquad (192b)$$

also satisfies (191b–d). Thus, if ξ is bounded away from 0 and ∞, we may approximate $\hat{\rho}$ by neglecting $O(s)$ and h in (192a). From (191) and (192) we infer

$$\hat{\rho}(q, \mathbf{x}) \longrightarrow \frac{\Gamma K_0(\xi)}{\pi\sigma_1\sigma_2} \qquad (193)$$

as $s \longrightarrow 0$ and $x \longrightarrow \infty$ with ξ fixed, which reduces to LANDE's (1991) approximation (13c) in the isotropic case. If $\xi \gg 1$, we may approximate (193) as (Olver 1964, p. 378)

$$\hat{\rho}(q, \mathbf{x}) \approx \left(\frac{\Gamma}{\sigma_1\sigma_2}\right)\frac{e^{-\xi}}{\sqrt{2\pi\xi}}. \tag{194}$$

From (190) and (193) we see that

$$\hat{r}(q, \mathbf{x}) \sim -\frac{2K_0(\xi)}{\ln 2s} \tag{195}$$

as $s \to 0$ and $x \to \infty$ with ξ fixed, in agreement with $\hat{f}(\mathbf{x})/\hat{f}(\mathbf{0})$ for the Malécot model (Sawyer 1977). If $\xi \gg 1$, (195) simplifies to

$$\hat{r}(q, \mathbf{x}) \approx -\sqrt{\frac{2\pi}{\xi}}\,\frac{e^{-\xi}}{\ln 2s}. \tag{196}$$

Convergence: In accordance with (40), we let

$$\rho(\mathbf{x}, t) = \hat{\rho}(q, \mathbf{x}) - q^t\varphi(\mathbf{x}, t). \tag{197}$$

We present here the asymptotic form of $\varphi(\mathbf{x}, t)$ as $t \to \infty$ with $\mathbf{x}$ fixed; the proofs are in the APPENDIX.

We suppose that the initial covariance decays fairly fast in space: there exists $\eta > 0$ such that

$$\rho(\mathbf{x}, 0) = O(x^{-2-\eta}) \tag{198}$$

as $x \to \infty$. The mild assumption (198) obviously holds in the important special case $\rho(\mathbf{x}, 0) = 0$.

We posit also that $\{\varphi(\mathbf{x}, t)\}$ and $\{t\varphi(\mathbf{x}, t)\}$ are monotone for sufficiently large t and fixed $\mathbf{x}$ in one and two dimensions, respectively. This ultimate monotonicity is plausible, but ought to be proved. Similar hypotheses are required to derive the asymptotic behavior of the Malécot model (Nagylaki 1976; Sawyer 1976).

As $t \to \infty$ with $\mathbf{x}$ fixed, we have

$$\varphi(\mathbf{x}, t) \sim \begin{cases} \dfrac{A}{\sigma\sqrt{2\pi t}}, & n = 1, \qquad \text{(199a)} \\ \dfrac{A}{2\pi\sigma_1\sigma_2 t}, & n = 2, \qquad \text{(199b)} \end{cases}$$

where the constant A depends on the initial covariance:

$$A = \sum_{\mathbf{y}} \varphi(\mathbf{y}, 0) \tag{200a}$$

$$= \frac{\Gamma}{1-q} - \sum_{\mathbf{y}} \rho(\mathbf{y}, 0). \tag{200b}$$

Observe that the convergence pattern (199) is uniform, in contrast to the complex spatial dependence in the Malécot model (Nagylaki 1976; Sawyer 1976). Here, convergence is slower in one dimension than in two; for the Malécot model, the opposite holds because the corresponding rates are proportional to $t^{-3/2}$ and $t^{-1}(\ln t)^{-2}$, respectively (Nagylaki 1976; Sawyer 1976).

Rewriting (200a) in one dimension as

$$A = \varphi(0, 0) + 2\sum_{y=1}^{\infty} \varphi(y, 0) \tag{201}$$

and passing to the continuum, we see that (199a) agrees with the diffusion result (165).

If $\rho(\mathbf{x}, 0) = 0$ for all $\mathbf{x}$, the sum is absent from (200b); by recalling (137c) and the fact that $1 - q \sim 2s$ as $s \to 0$, we see that (199a) agrees with (167).

DISCUSSION

Here, we reference and summarize our main results and discuss open problems.

As discussed in the introduction, the discrete-space model constructed and investigated in this paper is a more natural, rigorous, and general reformulation of Lande's (1991) continuous-space model. Our asymptotic results for the one- and two-dimensional stepping-stone model at equilibrium confirm Lande's approximations for isolation by distance. The same agreement occurs in the Malécot model (Nagylaki 1989b and references therein).

We established a number of general properties of our model for the evolution of the local averages of a quantitative character under migration, selection, and random genetic drift in a subdivided population. The general solution for the random vector $\bar{Z}(t)$ of local averages in generation t is (13). If the number of demes is finite and the backward migration matrix, M, is irreducible, then (18) gives the weighted grand mean $\bar{\bar{Z}}(t)$ of the local averages. The solution (13) corresponds to the characteristic function (22), which has the stationary limit (23).

As $t \to \infty$, the vector of means $\mu(t) = \mathscr{E}[\bar{Z}(t)]$ converges to the optimum ($\mathbf{0}$) at least as fast as $p^t = (1 - s)^t$, where s denotes the selection intensity, and the equilibrium $\mu = \mathbf{0}$ is unique. For finitely many demes, $\mu(t)$ is given by (26). If M is irreducible, we have the simple solution (28) for the weighted grand mean $\bar{\mu} = \mathscr{E}(\bar{\bar{Z}})$. If M is ergodic (*i.e.*, irreducible and aperiodic), then $\mu(t) \to \mathbf{0}$ at the generic asymptotic rate p^t, and the asymptotic pattern of the means is uniform.

The rest of our general and specific results concern the covariances (11). As $t \to \infty$, the matrix of covariances $\rho(t)$ converges at least as fast as $q^t = (1 - s)^{2t}$ to the unique equilibrium $\hat{\rho}$. For finitely many demes, (44) is the transient solution; if M is irreducible, the grand mean (45) is constant. If M is ergodic, the asymptotic rate of convergence is generically q^t, and the asymptotic transient pattern of the covariances is uniform.

For finitely many demes, (48) provides the matrix solution for the equilibrium $\hat{p}$. If M is irreducible, the variance (33) of the grand mean $\bar{\bar{Z}}$ is given at equilibrium in terms of the migration effective population number (35) by the simple formula (50). If M is ergodic and if selection and random drift are both much weaker than migration, then the approximation (61) holds for the covariances. This strong-migration limit is equivalent to panmixia if and only if the migration effective population number N_e equals N_T, the total population number, and this occurs if and only if migration is conservative, *i.e.*, does not change the subpopulation numbers.

Random outbreeding and site homing is a model of population subdivision without isolation by distance; it has the Levene and island models as important special cases. Equation 71 specifies the covariances and correlations at equilibrium; this yields the conditions (76) and (80) for strong and weak interdeme differentiation, which lead to the simplifications (77) and (79), and (81), respectively. Further reduction occurs for weak selection [see (82) to (88)] and weak migration [see (89) to (92)]. The exact transient solution is (95); it exemplifies our general result on the asymptotic rate and pattern of convergence with ergodic M.

For the Levene model, (97) gives the covariances and correlations at equilibrium; differentiation is strong or weak according as (98) or (100) holds. For weak selection, (97) simplifies to (101).

For the island model, (110) is the exact equilibrium. For strong differentiation [(113) or (115)], we have (114) or (116); under the condition (117) for weak differentiation, (118) holds. If selection is weak, we have the approximate results (120) to (122). The exact transient solution is (125).

Our remaining models involve isolation by distance. For a finite population, the simplest of them is the circular habitat, which we investigated in the diffusion approximation. The covariance, local variance, and correlation are given by (137), (138), and (139), respectively. Differentiation is strong if (143) applies, in which case we have the approximation (144); differentiation is weak if (145) applies, in which case the panmictic approximation (146) holds. We proved that, for properly identified parameters, differentiation at equilibrium is stronger in the circular habitat than in the island model. The exact transient solution is (155), with the important special case (159) for fixed initial local averages (*i.e.*, initial covariance zero). The asymptotic rate and pattern of convergence (158) again exemplify our general theory.

From the diffusion solution for the circular habitat, we deduced that for the unbounded linear stepping-stone model. At equilibrium, we have (160) and (161). The exact transient solution is (163), with the asymptotic form (165). If the initial covariance is zero, these reduce to (168) and (167), respectively.

Finally, we analyzed the unbounded stepping-stone model in one and two dimensions. As explained at the beginning of the previous section, because of the unavailability of a satisfactory continuous model and the failure of the diffusion approximation in more than one spatial dimension, this is the only known rigorous approach to the important bidimensional case. For weak selection, the unidimensional equilibrium covariance has the approximations (184) and (185), and the correlation satisfies (186) and (187). In two dimensions, we have the approximations (190) for the local variance, (192) to (194) for the spatial decay of the covariance, and (195) and (196) for the correlation. Equations 199 and 200 give the asymptotic rate and pattern of convergence.

The models treated in this paper involve no environmental inhomogeneities. The influence of boundaries and geographical barriers will be studied in future work. More difficult would be the incorporation of spatial variation in the selection pattern, which would enable us to investigate clines.

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APPENDIX

Here, we prove the results (199) and (200) for the rate of convergence of the unbounded stepping-stone model in one and two dimensions.

Inserting (197) into (171) and appealing to (176), we obtain

$$\varphi(\mathbf{x}, t + 1) = \sum_{\mathbf{y}} \omega(\mathbf{y})\varphi(\mathbf{x} - \mathbf{y}, t). \tag{A1}$$

Recalling (173), we see that

$$\tilde{\varphi}(\boldsymbol{\theta}, t) = \sum_{\mathbf{x}} \varphi(\mathbf{x}, t)e^{-i\boldsymbol{\theta}\cdot\mathbf{x}} \tag{A2}$$

satisfies

$$\tilde{\varphi}(\boldsymbol{\theta}, t + 1) = \Omega(\boldsymbol{\theta})\tilde{\varphi}(\boldsymbol{\theta}, t), \tag{A3}$$

whence

$$\tilde{\varphi}(\boldsymbol{\theta}, t) = \tilde{\varphi}(\boldsymbol{\theta}, 0)[\Omega(\boldsymbol{\theta})]^t. \tag{A4}$$

Consequently, the Fourier coefficients in (A2) are

$$\varphi(\mathbf{x}, t) = \int_R \tilde{\varphi}(\boldsymbol{\theta}, t)e^{i\boldsymbol{\theta}\cdot\mathbf{x}} \frac{d^n\theta}{(2\pi)^n} \tag{A5}$$

$$= \sum_{\mathbf{y}} \varphi(\mathbf{y}, 0)G(\mathbf{x} - \mathbf{y}, t), \tag{A6}$$

where R is the same as in (179) and

$$G(\mathbf{x}, t) = \int_R [\Omega(\boldsymbol{\theta})]^t e^{i\boldsymbol{\theta}\cdot\mathbf{x}} \frac{d^n\theta}{(2\pi)^n}. \tag{A7}$$

We use probability-generating functions and a Tauberian theorem to investigate the behavior of (A6) as $t \to \infty$ with $\mathbf{x}$ fixed. Since $0 \leqslant \Omega(\boldsymbol{\theta}) \leqslant 1$, expanding the fraction in (180b) in a Maclaurin series and employing (A7) yields

$$H(z, \mathbf{x}) = \sum_{t=1}^{\infty} G(\mathbf{x}, t)z^t \tag{A8}$$

for $|z| < 1$. From (A6) and (A8) we deduce

$$F(z, \mathbf{x}) = \sum_{t=1}^{\infty} \varphi(\mathbf{x}, t)z^t \tag{A9}$$

$$= \sum_{\mathbf{y}} \varphi(\mathbf{y}, 0)H(z, \mathbf{x} - \mathbf{y}). \tag{A10}$$

In principle, we know $\varphi(\mathbf{x}, 0)$ and $G(\mathbf{x}, t)$. We wish to determine from (A8) the behavior of $H(z, \mathbf{x})$ as $z \to 1-$ with $\mathbf{x}$ fixed, and hence that of $F(z, \mathbf{x})$ from (A10); then (A9) and the Tauberian theorem will give the behavior of $\varphi(\mathbf{x}, t)$ as $t \to \infty$ with $\mathbf{x}$ fixed.

Instead of treating the general case immediately, we shall begin with the important special case $\rho(\mathbf{x}, 0) = 0$, for which the derivation is much easier.

An important special case: If $\rho(\mathbf{x}, 0) = 0$ for all $\mathbf{x}$, then setting $t = 0$ in (197) shows that (A10) becomes

$$F(z, \mathbf{x}) = F_0(z, \mathbf{x}) = \sum_{\mathbf{y}} \hat{\rho}(q, \mathbf{y})H(z, \mathbf{x} - \mathbf{y}). \tag{A11}$$

We define the functions

$$\tilde{F}_0(z, \boldsymbol{\theta}) = \sum_{\mathbf{x}} F_0(z, \mathbf{x})e^{-i\boldsymbol{\theta}\cdot\mathbf{x}}, \tag{A12}$$

$$\tilde{H}(z, \boldsymbol{\theta}) = \sum_{\mathbf{x}} H(z, \mathbf{x})e^{-i\boldsymbol{\theta}\cdot\mathbf{x}}, \tag{A13}$$

recall (177), and transform the convolution (A11) into

$$\tilde{F}_0(z, \boldsymbol{\theta}) = \tilde{\rho}(q, \boldsymbol{\theta})\tilde{H}(z, \boldsymbol{\theta}). \tag{A14}$$

We substitute for $\tilde{\rho}$ and $\tilde{H}$ from (179) and (180b), respectively, and rearrange to deduce

$$\tilde{F}_0(z, \boldsymbol{\theta}) = \frac{z}{z - q} [\tilde{\rho}(z, \boldsymbol{\theta}) - \tilde{\rho}(q, \boldsymbol{\theta})], \tag{A15}$$

which yields the Fourier coefficients

$$F_0(z, \mathbf{x}) = \frac{z}{z - q} [\hat{\rho}(z, \mathbf{x}) - \hat{\rho}(q, \mathbf{x})]. \tag{A16}$$

Finally, we insert (180a) into (A16) to derive

$$F_0(z, \mathbf{x}) = \frac{\Gamma z}{z - q}[H(z, \mathbf{x}) - H(q, \mathbf{x})] \tag{A17}$$

$$= \frac{\Gamma z}{z - q}[H(z, \mathbf{0}) - \bar{H}(z, \mathbf{x}) - H(q, \mathbf{x})], \tag{A18}$$

where

$$\bar{H}(z, \mathbf{x}) = H(z, \mathbf{0}) - H(z, \mathbf{x}). \tag{A19}$$

Note that (NAGYLAKI 1976; SPITZER 1976, pp. 124, 345)

$$\bar{H}(z, \mathbf{x}) \to \bar{H}(1, \mathbf{x}) < \infty \tag{A20}$$

as $z \to 1-$ with $\mathbf{x}$ fixed.

We must treat one and two dimensions separately.

One dimension: From (A18), (182), and (A20) we find

$$F_0(z, x) \sim \left(\frac{\Gamma}{1 - q}\right) H(z, 0)$$

$$\sim \left(\frac{\Gamma}{1 - q}\right) \frac{1}{\sigma\sqrt{2(1 - z)}} \tag{A21}$$

as $z \to 1-$ with x fixed. If $\{\varphi(x, t)\}$ is ultimately monotone in t with x fixed, then (A9), (A21), and a standard Tauberian theorem (Feller 1971, p. 447) give

$$\varphi(x, t) \sim \frac{\Gamma}{\sigma(1-q)} \frac{1}{\sqrt{2\pi t}} \tag{A22}$$

as $t \longrightarrow \infty$ with x fixed. This proves the special case of (199a).

Two dimensions: To apply the Tauberian theorem, we must study the partial derivative of F_0 with respect to z. From (A9) we get

$$F_{0,z}(z, \mathbf{x}) = z^{-1} \sum_{t=1}^{\infty} t\varphi(\mathbf{x}, t) z^t. \tag{A23}$$

Formal differentiation of (188) suggests that

$$H_z(z, \mathbf{0}) \sim \frac{1}{2\pi\sigma_1\sigma_2}\left(\frac{1}{1-z}\right) \tag{A24}$$

as $z \longrightarrow 1-$. Although asymptotic results cannot always be differentiated, it follows from Sawyer (1976, pp. 712–714, 721) that (A24) is, in fact, correct. One can also prove (A24) *ab initio* by direct asymptotic analysis of (188b). We have also (Nagylaki 1976)

$$\bar{H}_z(z, \mathbf{x}) \sim -\frac{\hat{x}^2 \ln(1-z)}{4\pi\sigma_1\sigma_2} \tag{A25}$$

as $z \longrightarrow 1-$ with $\mathbf{x}$ fixed, where $\hat{x}_j = \tilde{x}_j/\sigma_j$ is the scaled, rotated jth coordinate and $\hat{x} = \|\hat{\mathbf{x}}\|$.

Differentiating (A18), letting $z \longrightarrow 1-$ with $\mathbf{x}$ fixed, and inserting (188), (A20), (A24), and (A25), we find

$$F_{0,z}(z, \mathbf{x}) \sim \frac{\Gamma}{1-q}\left(\frac{1}{2\pi\sigma_1\sigma_2}\right)\left(\frac{1}{1-z}\right). \tag{A26}$$

If $\{t\varphi(\mathbf{x}, t)\}$ is ultimately monotone in t with $\mathbf{x}$ fixed, then (A23), (A26), and the Tauberian theorem (Feller 1971, p. 447) imply

$$\varphi(\mathbf{x}, t) \sim \frac{\Gamma}{2\pi\sigma_1\sigma_2(1-q)t} \tag{A27}$$

as $t \longrightarrow \infty$ with $\mathbf{x}$ fixed. This proves the special case of (199b).

The general case: Substituting (A19) into (A10) yields

$$F(z, \mathbf{x}) = AH(z, \mathbf{0}) - F_1(z, \mathbf{x}), \tag{A28}$$

where A is given by (200a) and

$$F_1(z, \mathbf{x}) = \sum_{\mathbf{y}} \varphi(\mathbf{y}, 0)\bar{H}(z, \mathbf{x}-\mathbf{y}). \tag{A29}$$

According to (182), (188), and (A20), the function $H(z, \mathbf{0})$ diverges as $z \longrightarrow 1-$, whereas $\bar{H}(z, \mathbf{x})$ does not. Therefore, we expect the first term in (A28) to dominate as $z \longrightarrow 1-$, as it does in (A18). This suggests that the general result can be obtained by replacing $\Gamma/(1-q)$ in (A22) and (A27) by A. Demonstrating this will establish (199).

First, we prove (200b). From (197) at $t = 0$, (177) with $\boldsymbol{\theta} = \mathbf{0}$, (179), and the fact that $\Omega(\mathbf{0}) = 1$ [see (173)], we derive

$$\begin{aligned} A &= \sum_{\mathbf{y}} [\hat{\rho}(q, \mathbf{y}) - \rho(\mathbf{y}, 0)] \\ &= \tilde{\rho}(q, \mathbf{0}) - \sum_{\mathbf{y}} \rho(\mathbf{y}, 0) \\ &= \frac{\Gamma}{1-q} - \sum_{\mathbf{y}} \rho(\mathbf{y}, 0), \end{aligned} \tag{A30}$$

as required. On account of (198), we have $A < \infty$.

Next, use (197) to decompose F_1:

$$F_1(z, \mathbf{x}) = F_{11}(z, \mathbf{x}) - F_{12}(z, \mathbf{x}), \tag{A31a}$$

where

$$F_{11}(z, \mathbf{x}) = \sum_{\mathbf{y}} \hat{\rho}(q, \mathbf{y})\bar{H}(z, \mathbf{x}-\mathbf{y}), \tag{A31b}$$

$$F_{12}(z, \mathbf{x}) = \sum_{\mathbf{y}} \rho(\mathbf{y}, 0)\bar{H}(z, \mathbf{x}-\mathbf{y}). \tag{A31c}$$

For F_{11}, we invoke (A19), the calculation that leads to (A30), (A11), and (A18):

$$\begin{aligned} F_{11}(z, \mathbf{x}) &= \sum_{\mathbf{y}} \hat{\rho}(q, \mathbf{y})[H(z, \mathbf{0}) - H(z, \mathbf{x}-\mathbf{y})] \\ &= \left(\frac{\Gamma}{1-q}\right) H(z, \mathbf{0}) - F_0(z, \mathbf{x}) \\ &= -\frac{\Gamma q(1-z)}{(1-q)(z-q)} H(z, \mathbf{0}) \\ &\quad + \frac{\Gamma z}{z-q}[\bar{H}(z, \mathbf{x}) + H(q, \mathbf{x})]. \end{aligned} \tag{A32}$$

From (182), (188), and (A20) we get

$$F_{11}(z, \mathbf{x}) \longrightarrow \frac{\Gamma}{1-q}[\bar{H}(1, \mathbf{x}) + H(q, \mathbf{x})] \tag{A33}$$

as $z \longrightarrow 1-$ with $\mathbf{x}$ fixed.

The investigation of F_{12} requires some estimates. From (A19), (180b), and (174) we obtain

$$\bar{H}(z, \mathbf{x}) = \int_R \frac{z\Omega(\boldsymbol{\theta})(1 - \cos \boldsymbol{\theta}\cdot\mathbf{x})}{1 - z\Omega(\boldsymbol{\theta})} \frac{d^n\theta}{(2\pi)^n}. \tag{A34}$$

Since, as observed below (175), we have $0 \leqslant \Omega(\boldsymbol{\theta}) \leqslant 1$, therefore $\bar{H}(z, \mathbf{x}) \geqslant 0$ and $\bar{H}_z(z, \mathbf{x}) \geqslant 0$ if $0 \leqslant z \leqslant 1$. Furthermore (Nagylaki 1976; Sawyer 1976; Spitzer 1976, pp. 124, 345),

$$\bar{H}(1, \mathbf{x}) \sim \begin{cases} \hat{x}/\sigma, & n = 1, \\ \dfrac{\ln \hat{x}}{\pi\sigma_1\sigma_2}, & n = 2 \end{cases} \tag{A35}$$

as $x \longrightarrow \infty$. Recalling (198) and (A20), we conclude from (A31c) that

$$|F_{12}(z, \mathbf{x})| \leqslant \sum_{\mathbf{y}} |\rho(\mathbf{y}, 0)|\bar{H}(1, \mathbf{x}-\mathbf{y}) < \infty, \tag{A36}$$

which demonstrates that (A31c) converges uniformly in z for $0 \leqslant z \leqslant 1$. Hence, we may take the limit as $z \longrightarrow 1-$ with $\mathbf{x}$ fixed through the summation sign:

$$F_{12}(z, \mathbf{x}) \longrightarrow \sum_{\mathbf{y}} \rho(\mathbf{y}, 0)\bar{H}(1, \mathbf{x} - \mathbf{y}). \qquad \text{(A37)}$$

Then (A28), (A31a), (A33), and (A37) inform us that

$$F(z, \mathbf{x}) = AH(z, \mathbf{0}) + O(1) \qquad \text{(A38)}$$

as $z \longrightarrow 1-$ with $\mathbf{x}$ fixed.

In *one dimension*, (A21) shows that (A38) proves (199a).

In *two dimensions*, we must again employ partial derivatives. From (A28) and (A31a) we get

$$F_z(z, \mathbf{x}) = AH_z(z, \mathbf{0}) - F_{1,z}(z, \mathbf{x}), \qquad \text{(A39a)}$$

where

$$F_{1,z}(z, \mathbf{x}) = F_{11,z}(z, \mathbf{x}) - F_{12,z}(z, \mathbf{x}). \qquad \text{(A39b)}$$

Appealing to (A32), (188), (A24), (A20), and (A25), we find

$$\begin{aligned} &F_{11,z}(z, \mathbf{x}) \\ &\quad = \frac{\Gamma q}{(1-q)^2} H(z, \mathbf{0}) + \left(\frac{\Gamma}{1-q}\right) \bar{H}_z(z, \mathbf{x}) + O(1) \\ &\quad \sim -\frac{\Gamma \ln(1-z)}{2\pi\sigma_1\sigma_2(1-q)} \left(\frac{q}{1-q} + \frac{\hat{x}^2}{2}\right) \end{aligned} \qquad \text{(A40)}$$

as $z \longrightarrow 1-$ with $\mathbf{x}$ fixed. Therefore, by (A24), to demonstrate that the first term dominates in (A39a), it will suffice to establish that

$$F_{12,z}(z, \mathbf{x}) = o[1/(1 - z)] \qquad \text{(A41)}$$

as $z \longrightarrow 1-$ with $\mathbf{x}$ fixed. This will prove (199b).

By (A31c),

$$F_{12,z}(z, \mathbf{x}) = \sum_{\mathbf{y}} \rho(\mathbf{y}, 0)\bar{H}_z(z, \mathbf{x} - \mathbf{y}), \qquad \text{(A42)}$$

so we need a suitable estimate on $\bar{H}_z$.

From (A34) we obtain

$$\bar{H}_z(z, \mathbf{x}) = \int_R \frac{\Omega(\boldsymbol{\theta})\sin^2(\tfrac{1}{2}\boldsymbol{\theta}\cdot\mathbf{x})}{[1 - z\Omega(\boldsymbol{\theta})]^2} \frac{d^2\theta}{2\pi^2} \geqslant 0, \qquad \text{(A43)}$$

whence

$$\bar{H}_z(z, \mathbf{x}) \leqslant J(z, \mathbf{x}) + B, \qquad \text{(A44a)}$$

in which

$$J(z, \mathbf{x}) = \int_{\theta \leqslant \pi} \frac{\sin^2(\tfrac{1}{2}\boldsymbol{\theta}\cdot\mathbf{x})}{[1 - z\Omega(\boldsymbol{\theta})]^2} \frac{d^2\theta}{2\pi^2}, \qquad \text{(A44b)}$$

$$B = \int_{R_0} \frac{1}{[1 - \Omega(\boldsymbol{\theta})]^2} \frac{d^2\theta}{2\pi^2} < \infty, \qquad \text{(A44c)}$$

where $\theta = \|\boldsymbol{\theta}\|$ and R_0 denotes the part of R with $\theta \leqslant \pi$ excluded.

To estimate J, observe first that

$$\begin{aligned} |\sin(\tfrac{1}{2}\boldsymbol{\theta}\cdot\mathbf{x})| &\leqslant \begin{cases} \tfrac{1}{2}|\boldsymbol{\theta}\cdot\mathbf{x}| \leqslant \tfrac{1}{2}\theta x, & \tfrac{1}{2}\theta x \leqslant 1, \\ 1, & \tfrac{1}{2}\theta x \geqslant 1 \end{cases} \\ &\leqslant (\tfrac{1}{2}\theta x)^a \end{aligned} \qquad \text{(A45)}$$

for all a in $[0, 1]$. Second, note that for every aperiodic random walk, there exists $\lambda > 0$ such that

$$\operatorname{Re}\,\Omega(\boldsymbol{\theta}) \leqslant 1 - \lambda\theta^2 \qquad \text{(A46)}$$

for all $\boldsymbol{\theta}$ in R (SPITZER 1976, p. 70). Here, $\Omega(\boldsymbol{\theta})$ is real.

Inserting (A45) and (A46) into (A44b) and then performing the angular integration leads to

$$J(z, \mathbf{x}) \leqslant \frac{x^{2a}}{2^{2a}\pi} \int_0^{\pi} \frac{\theta^{2a+1}d\theta}{(1 - z + \lambda z\theta^2)^2}. \qquad \text{(A47)}$$

The substitutions

$$\zeta = \frac{1 - z}{\lambda z}, \quad \theta = \sqrt{\zeta}u \qquad \text{(A48)}$$

reduce (A47) to

$$J(z, \mathbf{x}) \leqslant \frac{x^{2a}\zeta^{a-1}}{2^{2a}\pi\lambda^2 z^2} \int_0^{\pi\sqrt{\zeta}} \frac{u^{2a+1}du}{(1 + u^2)^2}. \qquad \text{(A49)}$$

Taking $a < 1$, we may replace the upper limit in (A49) by infinity. For $0 < z_0 \leqslant z < 1$, we conclude that

$$J(z, \mathbf{x}) \leqslant Cx^{2a}(1 - z)^{a-1}, \qquad \text{(A50a)}$$

where

$$C = \frac{1}{2^{2a}\pi(\lambda z_0)^{a+1}} \int_0^{\infty} \frac{u^{2a+1}du}{(1 + u^2)^2}, \qquad \text{(A50b)}$$

and therefore (A44a) becomes

$$\bar{H}_z(z, \mathbf{x}) \leqslant B + Cx^{2a}(1 - z)^{a-1}. \qquad \text{(A51)}$$

Inserting (A51) into (A42) yields

$$\begin{aligned} &|F_{12,z}(z, \mathbf{x})| \\ &\quad \leqslant \sum_{\mathbf{y}} |\rho(\mathbf{y}, 0)|[B + C\|\mathbf{x} - \mathbf{y}\|^{2a}(1 - z)^{a-1}]; \end{aligned} \qquad \text{(A52)}$$

(198) reveals that (A52) has the form

$$|F_{12,z}(z, \mathbf{x})| \leqslant D + \psi(\mathbf{x})(1 - z)^{a-1}, \qquad \text{(A53a)}$$

where

$$D = B \sum_{\mathbf{y}} |\rho(\mathbf{y}, 0)|, \qquad \text{(A53b)}$$

$$\psi(\mathbf{x}) = C \sum_{\mathbf{y}} |\rho(\mathbf{y}, 0)| \cdot \|\mathbf{x} - \mathbf{y}\|^{2a}, \qquad \text{(A53c)}$$

provided $2a < \eta$. Thus, (A41) holds if we choose $a = \tfrac{1}{4}\eta$ and $0 < \eta < 4$. This completes the proof.