Convergence of Covariance Structures in Additive Gaussian Polygenic Models

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SUMMARY

The purpose of this paper is to present convergence results for covariance structures of allelic effects over successive generations in Gaussian polygenic models for quantitative traits developed by Lande (1976, *Genetical Research* **26**, 221–235; 1977, *Genetics* **86**, 485–498) and Chevalet (1988, in *Proceedings of the Second International Conference on Quantitative Genetics*, 379–394). The proofs rely on concavity properties of transformations of covariance matrices.

1. Introduction

In the approximate Gaussian polygenic models developed by Lande (1976, 1977) to study the maintenance of variability of quantitative traits expressed in infinite diploid populations, the dynamics are summarized by recurrence equations for the means and covariances of *allelic effects* at n loci over successive generations. In an individual chosen at random at conception of generation t, the allelic effects are represented by two n-dimensional vectors $\mathbf{X}(t) = (X_1(t), \ldots, X_n(t))$ and $\mathbf{Y}(t) = (Y_1(t), \ldots, Y_n(t))$, whose components $X_i(t)$ and $Y_i(t)$ for $i = 1, \ldots, n$ correspond to the allelic effects carried by the maternal and paternal gametes, respectively, at locus i for $i = 1, \ldots, n$. It is assumed that $(\mathbf{X}(t), \mathbf{Y}(t))$ has a multinormal distribution with covariance matrix

$$\Sigma(t) = \begin{pmatrix} C(t) & B(t) \\ B(t)^T & C(t) \end{pmatrix}, \tag{1}$$

where $C(t) = ||C_{ij}(t)||_{i,j=1}^n$ and $B(t) = ||B_{ij}(t)||_{i,j=1}^n$ with $C_{ij}(t)$ and $B_{ij}(t)$ being the covariances of the allelic effects at loci i and j on a same gamete and on distinct united gametes, respectively, for $i, j = 1, \ldots, n$, that is,

$$C_{ij}(t) = \text{Cov}(X_i(t), X_j(t)) = \text{Cov}(Y_i(t), Y_j(t)), \tag{2}$$

$$B_{ij}(t) = \text{Cov}(X_i(t), Y_j(t)) = \text{Cov}(Y_i(t), X_j(t)), \tag{3}$$

for $i, j = 1, \ldots, n$. The quantitative trait takes the additive form

$$Z(t) = G(t) + E(t), \tag{4}$$

where

$$G(t) = X_1(t) + \cdots + X_n(t) + Y_1(t) + \cdots + Y_n(t) \tag{5}$$

and $E(t)$ is a random variable independent of $G(t)$ whose distribution is normal with constant mean 0 and constant variance σ_E^2. The variables $Z(t)$, $G(t)$, and $E(t)$ represent, respectively, the *phenotypic value*, the *genotypic value*, and the *environmental deviation*.

Factors of evolution come into play as follows. An individual whose phenotypic value is z has a probability of survival from conception to maturity that is proportional to

$$f(z) = \exp\left\{-\frac{1}{2}\frac{(z-\theta)^2}{\omega^2}\right\}, \tag{6}$$

Key words: Concavity properties; Covariance matrix; Genetic variability; Polygenic models.

where $-\infty < \theta < +\infty$ and $\omega^2 > 0$. The Gaussian function f is called a *selection function*. Among the gametes produced by a mature individual, there are on average as many gametes carrying the maternal allelic effect at any specific locus as gametes carrying the paternal allelic effect at the same locus. We say that we have *Mendelian segregation*. Moreover, there is an expected proportion r_{ij} of gametes with recombination of the maternal and paternal allelic effects at loci i and j for $i, j = 1, \ldots, n$. The recombination rates satisfy $0 \leq r_{ij} \leq 1/2$ for $i, j = 1, \ldots, n, j \neq i$, and $r_{ii} = 0$ for $i = 1, \ldots, n$. We define the *recombination matrix*

$$R = ||r_{ij}||_{i,j=1}^{n}. \tag{7}$$

Mutation occurs at locus i of any gamete with probability $\mu_i > 0$ and, in such a case, the change in the allelic effect has a normal distribution with constant mean 0 and constant variance $m_i^2 > 0$, for $i = 1, \ldots, n$. All mutations are mutually independent and independent of the allelic effects. The *mutation matrix* is defined as the diagonal matrix

$$D = ||\delta_{ij}\mu_i m_i^2||_{i,j=1}^{n}, \tag{8}$$

where $\delta_{ij} = 1$ if $j = i$ and 0 otherwise for $i, j = 1, \ldots, n$.

Mating is either random, consanguineous, or assortative (see Section 2). In each case, recurrence equations for the covariances of the allelic effects over two successive generations can be found. The equations admit a unique covariance matrix as an equilibrium, and numerical iterations show global stability of the equilibrium (Lande, 1976, 1977).

In this paper, we give analytical proofs of these convergence results. We also study the case of a finite population, developed by Chevalet (1988) to study the response to artificial selection. In this case, there is inbreeding created by genetic drift. In every case, we show that the transformation of the covariance matrix is concave as in purely phenotypic models studied by Karlin (1979). If there exists a unique equilibrium, this is sufficient to ensure global convergence to the equilibrium and, in particular, to preclude the existence of periodic orbits or chaos. However, the models are only approximate in that Gaussian distributions are actually not preserved under recombination and mutation (see, e.g., Felsenstein, 1977), not to mention limitation in population size. Nevertheless, this is almost the case if selection and mutation are weak enough (i.e., if $\omega^2 \gg 1$ and $\mu_i m_i^2 \ll 1$ for $i = 1, \ldots, n$; see, e.g., Fleming, 1979) and if the population size is large enough.

2. Lande's Models for Infinite Populations

In this section, we first recall the recurrence equations for the covariances of the allelic effects obtained by Lande (1976, 1977) in the cases of random mating, constant inbreeding, and constant assortative mating, and the corresponding covariance equilibrium structures.

2.1 *Random Mating*

Random mating is equivalent to random union of male and female gametes and therefore implies independence of $\mathbf{X}(t)$ and $\mathbf{Y}(t)$. In this case, the recurrence equations for the covariances established in Lande (1976) are

$$C_{ij}(t+1) = C_{ij}(t) - r_{ij}C_{ij}(t) - \frac{R_i(t)R_j(t)}{\omega^2 + \sigma_E^2 + \sigma_G^2(t)} + \delta_{ij}\mu_i m_i^2, \tag{9}$$

$$B_{ij}(t+1) = 0, \tag{10}$$

where $R_i(t) = \sum_j C_{ij}(t)$, $\sigma_G^2(t) = 2\sum_i R_i(t)$, and $\delta_{ij} = 1$ if $j = i$ and 0 otherwise for $i, j = 1, \ldots, n$. In matrix form, we have the following transformation:

$$T(C) = C - R \odot C - \frac{CUC}{\alpha^2 + 2\mathbf{1}^T C\mathbf{1}} + D, \tag{11}$$

where $\alpha^2 = \omega^2 + \sigma_E^2$, $\mathbf{1}$ is an n-dimensional vector with every component equal to 1, $U = \mathbf{1}\mathbf{1}^T$ (T for transpose), and $\odot$ denotes the Hadamard product, that is, $R \odot C = ||R_{ij}C_{ij}||_{i,j=1}^{n}$ for $R = ||R_{ij}||_{i,j=1}^{n}$ and $C = ||C_{ij}||_{i,j=1}^{n}$. The unique equilibrium is

$$\hat{C}_{ij} = -\frac{\hat{R}_i \hat{R}_j}{(\omega^2 + \sigma_E^2 + \hat{\sigma}_G^2)r_{ij}}, \qquad \text{for every } j \neq i, \tag{12}$$

$$\hat{C}_{ii} = \sqrt{\mu_i m_i^2}\left(\sqrt{\omega^2 + \sigma_E^2 + \hat{\sigma}_G^2} + \sum_{j \neq i}\frac{\sqrt{\mu_j m_j^2}}{r_{ij}}\right), \quad \text{for } i = 1, \ldots, n, \tag{13}$$

where

$$\hat{R}_i = \sqrt{\mu_i m_i{}^2(\omega^2 + \sigma_E^2 + \hat{\sigma}_G^2)}, \quad \text{for } i = 1, \ldots, n, \tag{14}$$

and

$$\hat{\sigma}_G^2 = 2 \left(\sum_i \sqrt{\mu_i m_i^2} \right)^2 + 2 \left(\sum_i \sqrt{\mu_i m_i^2} \right) \left(\omega^2 + \sigma_E^2 + \left(\sum_i \sqrt{\mu_i m_i^2} \right)^2 \right)^{1/2}. \tag{15}$$

2.2 Inbreeding

Lande (1977) introduced inbreeding by assuming a constant correlation coefficient between the allelic effects at the same locus in uniting gametes following Wright (1921); that is,

$$\frac{\text{Cov}(X_i(t+1), Y_i(t+1))}{\sqrt{\text{Var}(X_i(t+1))\text{Var}(Y_i(t+1))}} = f \tag{16}$$

for $i = 1, \ldots, n$, where f does not depend on i or t. The correlation coefficient f is called the *inbreeding coefficient*. The case $f = 0$ corresponds to random mating. The recurrence equations in the general case are

$$C_{ij}(t+1) = C_{ij}(t) - (1-f)\, r_{ij} C_{ij}(t) + \delta_{ij}\mu_i m_i^2 - (1+f)^2 \frac{R_i(t)R_j(t)}{\omega^2 + \sigma_E^2 + 2(1+f)\sum_{i,j} C_{ij}(t)}, \tag{17}$$

$$B_{ij}(t+1) = f C_{ij}(t+1), \tag{18}$$

for $i, j = 1, \ldots, n$. It suffices to solve (17). Using the previous notation, the matrix transformation summarizing (17) is

$$T(C) = C - (1-f)R \odot C + D - (1+f)^2 \frac{CUC}{\alpha^2 + 2(1+f)\mathbf{1}^T C \mathbf{1}}. \tag{19}$$

A unique equilibrium exists and is given by

$$\hat{C}_{ii} = \sqrt{\mu_i m_i^2} \left(\sqrt{\frac{\hat{\sigma}_Z^2}{\hat{k}(1+f)^2}} + \frac{1}{(1-f)} \sum_{j \neq i} \frac{\sqrt{\mu_j m_j^2}}{r_{ij}} \right) \tag{20}$$

for $i = 1, \ldots, n$, and

$$\hat{C}_{ij} = -\frac{\sqrt{\mu_i m_i^2 \mu_j m_j^2}}{(1-f)r_{ij}}, \tag{21}$$

for every $j \neq i$, where

$$\hat{\sigma}_Z^2 = 2(1+f)\left(\sum_{i,j} \hat{C}_{ij} \right) + \sigma_E^2 \tag{22}$$

and

$$\hat{k} = \frac{\hat{\sigma}_Z^2}{\omega^2 + \hat{\sigma}_Z^2}. \tag{23}$$

2.3 Assortative Mating

Let us suppose a constant correlation coefficient between the traits of mates at any generation t; that is,

$$\frac{\text{Cov}(Z_f^*(t), Z_m^*(t))}{\sqrt{\text{Var}(Z_f^*(t))\text{Var}(Z_m^*(t))}} = \rho, \tag{24}$$

where $Z_m^*(t)$ and $Z_f^*(t)$ denote the traits of a male and a female, respectively, mature and mated together at generation t. The case $\rho = 0$ corresponds to random mating. The correlation coefficient ρ, which models assortative mating, is assumed not to depend on generation t.

For this case, the recurrence equations obtained by Lande (1977) are

$$C_{ij}(t+1) = C_{ij}(t) - r_{ij}\left(C_{ij}(t) - B_{ij}(t)\right) - \frac{\left(\sum_j S_{ij}(t)\right)\left(\sum_i S_{ij}(t)\right)}{\omega^2 + \sigma_E^2 + 2\sum_{i,j} S_{ij}(t)} + \delta_{ij}\mu_i m_i^2, \quad (25)$$

$$B_{ij}(t+1) = \frac{\rho\,\omega^2\left(\sum_j S_{ij}(t)\right)\left(\sum_i S_{ij}(t)\right)}{\left(\omega^2 + \sigma_E^2 + 2\sum_{i,j} S_{ij}(t)\right)\left(\sigma_E^2 + 2\sum_{i,j} S_{ij}(t)\right)}, \quad (26)$$

where $S_{ij}(t) = C_{ij}(t) + B_{ij}(t)$. Equations (25) and (26) are described by the following matrix transformation:

$$C(t+1) = C(t) - R \odot (C(t) - B(t)) - \frac{(C(t) + B(t))\,U\,(C(t) + B(t))}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T(C(t) + B(t))\,\mathbf{1}} + D, \quad (27)$$

$$B(t+1) = \rho\omega^2 \frac{(C(t) + B(t))\,U\,(C(t) + B(t))}{\left[\omega^2 + \sigma_E^2 + 2\mathbf{1}^T(C(t) + B(t))\,\mathbf{1}\right]\left[\sigma_E^2 + 2\mathbf{1}^T(C(t) + B(t))\,\mathbf{1}\right]}. \quad (28)$$

The unique equilibrium is given by

$$\hat{C}_{ii} = \sqrt{\mu_i m_i^2}\left[\sqrt{\frac{\hat{\sigma}_Z^2}{\hat{k}}}\left(1 - \frac{(1-\hat{k})\rho\hat{h}^2}{2}\right) + \sum_{j \neq i}\sqrt{\mu_j m_j^2}\left[\frac{1}{r_{ij}} - \frac{\rho(1-\hat{k})}{\hat{k}}\right]\right] \quad (29)$$

for $i = 1,\ldots,n$, where

$$\hat{\sigma}_Z^2 = 2\sum_{i,j}\hat{C}_{ij} + \sigma_E^2, \quad (30)$$

$$\hat{k} = \frac{\hat{\sigma}_Z^2}{\hat{\sigma}_Z^2 + \omega^2}, \quad (31)$$

$$\hat{h}^2 = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_Z^2}, \quad (32)$$

and

$$\hat{C}_{ij} = -\sqrt{\mu_i m_i^2 \mu_j m_j^2}\left[\frac{1}{r_{ij}} - \frac{\rho(1-\hat{k})}{\hat{k}}\right], \quad (33)$$

for every $j \neq i$. It is worth noting that in Lande (1977) the equilibrium genetic and phenotypic variances are independent of f and ρ; that is, they are the same as under random mating.

3. Chevalet's Model for Finite Populations

In the additive model developed by Chevalet (1988) for finite diploid populations, a single trait determined by n nonmutable loci numbered $1,\ldots,n$ with corresponding weights $\beta_1,\ldots,\beta_n$ is considered. These weights allow variable contributions of the different loci to the quantitative trait. The selection scheme is truncation adjusted by a function proportional to a Gaussian function with variance ω^2, as used in Slatkin (1970) and Lande (1976). At each generation, the population is made up of N reproducing individuals randomly chosen in a large population based on the Wright–Fisher sampling scheme. An environmental effect with mean 0 and variance σ_E^2 is added to the global expression of the observable trait.

The recurrence equations for the covariances within population between gene effects from generation t to generation $t + 1$ are given by

$$C_{ij}(t+1) = \left(1 - \frac{1}{2N}\right)C_{ij}(t) - r_{ij}C_{ij}(t) - \left(1 - \frac{1}{N}\right)\frac{1}{\omega^2 + \sigma_E^2 + \sigma_G^2(t)}K_i(t)K_j(t) \quad (34)$$

for $i, j = 1, \ldots, n$, where

$$K_i(t) = \sum_j C_{ij}(t)\beta_j$$

for $i = 1, \ldots, n$, and

$$\sigma_G^2(t) = 2\sum_i \beta_i \dot{K}_i(t).$$

The matrix transformation corresponding to (34) is given by

$$\mathcal{T}(C) = \left(1 - \frac{1}{2N}\right)C - R \odot C - \left(1 - \frac{1}{N}\right)\frac{C\beta\beta^T C}{\alpha^2 + 2\beta^T C\beta}, \tag{35}$$

where

$$\alpha^2 = \omega^2 + \sigma_E^2 \quad \text{and} \quad \beta = (\beta_1, \ldots, \beta_n)^T.$$

At equilibrium, equation (34) gives

$$\hat{C}_{ii} = -2(N-1)\frac{\hat{K}_i^2}{\omega^2 + \sigma_E^2 + \hat{\sigma}_G^2} \leq 0 \tag{36}$$

for $i = 1, \ldots, n$. The only admissible solution to equation (36) is $\hat{C}_{ii} = 0$ for $i = 1, \ldots, n$. From the well-known inequality $|\hat{C}_{ij}| \leq \{\hat{C}_{ii}\hat{C}_{jj}\}^{1/2}$, we deduce that $\hat{C}_{ij} = 0$ for every $j \neq i$ and therefore $\hat{C} = ||\hat{C}_{ij}||_{i,j=1}^n = 0$.

4. Basic Convergence Theorems

Let us recall the following classical definitions before presenting convergence theorems for transformations of covariance matrices.

DEFINITION 4.1. *A symmetric matrix A is positive definite, respectively, positive semidefinite, if for any nonzero vector $\mathbf{X}$ we have $\mathbf{X}^T A \mathbf{X} > 0$, respectively, ≥ 0.*

DEFINITION 4.2. *Let A and B be two positive semidefinite symmetric matrices. We say that A is greater than B, and we write $A \geq B$, respectively, A is strictly greater than B, and we write $A > B$, if $A - B$ is positive semidefinite, respectively, positive definite.*

We are now ready to state the following theorem on the iterates of transformations of covariance matrices, which are necessarily positive semidefinite symmetric matrices.

THEOREM 4.1. *Let T be a continuous transformation for positive semidefinite symmetric matrices that is concave; that is, for any positive semidefinite symmetric matrices C_1 and C_2, we have*

$$T\left(\frac{C_1 + C_2}{2}\right) \geq \frac{T(C_1) + T(C_2)}{2}.$$

If T possesses a unique fixed point $\hat{C}$, which is a positive definite symmetric matrix, that is, $T(\hat{C}) = \hat{C} > 0$, then, for any positive definite symmetric matrix C, we have

$$\lim_{n \to \infty} T^{(n)}(C) = \hat{C}.$$

A similar result with reference to Krasnosel'skii (1964) was used by Karlin (1979) for phenotypic models, but with the assumption that T is strictly concave ($>$ instead of $\geq$ earlier) and strictly increasing ($T(C_2) > T(C_1)$ if $C_2 > C_1$). However, the increasing property is actually redundant with the other hypotheses. A direct proof of Theorem 4.1 is given in Lessard and Mahdi (1995).

In the case of an equilibrium $\hat{C} = 0$, we have the following theorem.

THEOREM 4.2. *Let T be a continuous concave transformation for positive semidefinite symmetric matrices that admits the unique fixed point $\hat{C} = 0$. If T satisfies the property*

$$T(kI) \leq kI, \quad \text{for any real } k > 0, \tag{37}$$

where I is the identity matrix, then, for any positive semidefinite symmetric matrix C, we have

$$\lim_{n\to\infty} T^{(n)}(C) = 0.$$

The proof of theorem 4.2 is given in the Appendix. Theorems 4.1 and 4.2 give conditions for an equilibrium covariance matrix to be globally stable.

5. Convergence in Lande's Models

Because a unique positive definite equilibrium for the covariance matrix exists in each of Lande's models, it suffices in each case, according to Theorem 4.1, to prove the concavity property for the transformation of the covariance matrix to establish global stability of the equilibrium.

5.1 *Convergence in the Case of Random Mating or Inbreeding*

THEOREM 5.1. *The equilibrium covariance matrix in Lande's model in the case of random mating or inbreeding is globally stable.*

The proof of Theorem 5.1 is a direct consequence of Theorem 4.1 and of the following lemma.

LEMMA 5.1. *The covariance matrix transformation in Lande's model in the case of random mating or inbreeding is concave.*

Proof of Lemma 5.1. For any positive semidefinite symmetric matrices C_1 and C_2, we have for matrix transformation (19) in the case of inbreeding

$$T\left(\frac{C_1+C_2}{2}\right) - \frac{T(C_1)+T(C_2)}{2} = \frac{1}{4}(1+f)^2$$
$$\times \left\{ \frac{\left(\alpha^2 + 2(1+f)\mathbf{1}^T C_2 \mathbf{1}\right) C_1 U C_1}{\left(\alpha^2 + (1+f)\mathbf{1}^T (C_1+C_2)\mathbf{1}\right)\left(\alpha^2 + 2(1+f)\mathbf{1}^T C_1 \mathbf{1}\right)} \right.$$
$$+ \frac{\left(\alpha^2 + 2(1+f)\mathbf{1}^T C_1 \mathbf{1}\right) C_2 U C_2}{\left(\alpha^2 + (1+f)\mathbf{1}^T (C_1+C_2)\mathbf{1}\right)\left(\alpha^2 + 2(1+f)\mathbf{1}^T C_2 \mathbf{1}\right)}$$
$$\left. - \frac{C_1 U C_2 + C_2 U C_1}{\left(\alpha^2 + (1+f)\mathbf{1}^T (C_1+C_2)\mathbf{1}\right)} \right\}. \tag{38}$$

Introducing a nonzero vector $\mathbf{X}$ and the following quantities:

$$z_1 = \mathbf{X}^T C_1 \mathbf{1}, \qquad z_2 = \mathbf{X}^T C_2 \mathbf{1}, \qquad a = \mathbf{1}^T C_1 \mathbf{1}, \qquad b = \mathbf{1}^T C_2 \mathbf{1},$$

we get after some simplifications

$$\mathbf{X}^T \left\{ T\left(\frac{C_1+C_2}{2}\right) - \frac{T(C_1)+T(C_2)}{2} \right\} \mathbf{X} = \frac{1}{4}(1+f)^2$$
$$\times \left[\sqrt{\frac{\alpha^2 + 2(1+f)b}{\left(\alpha^2 + (1+f)(a+b)\right)\left(\alpha^2 + 2(1+f)a\right)}} z_1 \right.$$
$$\left. - \sqrt{\frac{\alpha^2 + 2(1+f)a}{\left(\alpha^2 + (1+f)(a+b)\right)\left(\alpha^2 + 2(1+f)b\right)}} z_2 \right]^2$$
$$\geq 0. \tag{39}$$

This establishes the concavity property in the case of inbreeding. In particular, if we put $f = 0$ in (39), we get the concavity property in the case of random mating.

5.2 *Convergence in the Case of Assortative Mating*

To study Lande's model in the case of assortative mating, we will consider separately the cases $\rho < 0$ and $\rho > 0$, but let us first prove the following.

LEMMA 5.2. *The symmetric matrices $S(t) = C(t) + B(t)$ and $\Delta(t) = C(t) - B(t)$ are both positive semidefinite.*

Proof of Lemma 5.2. For any nonzero $2n$-dimensional vector $\begin{pmatrix} \mathbf{X} \\ \mathbf{Y} \end{pmatrix}$, we have

$$\begin{pmatrix} \mathbf{X} \\ \mathbf{Y} \end{pmatrix}^T \Sigma(t) \begin{pmatrix} \mathbf{X} \\ \mathbf{Y} \end{pmatrix} \geq 0. \tag{40}$$

If we put $\mathbf{Y} = \mathbf{X}$ in (40), we get $2\mathbf{X}^T S(t)\mathbf{X} \geq 0$. Similarly, if we put $\mathbf{Y} = -\mathbf{X}$ in (40), we get $\mathbf{X}^T \Delta(t)\mathbf{X} \geq 0$. This establishes that the symmetric matrices $S(t)$ and $\Delta(t)$ are positive semidefinite.

Case 1. For the case $\rho < 0$, we consider the transformation T_1 defined as

$$T_1 \begin{bmatrix} C & 0 \\ 0 & S \end{bmatrix} = \begin{bmatrix} C' & 0 \\ 0 & S' \end{bmatrix}, \tag{41}$$

where

$$C' = \frac{1}{2}(U - 2R) \odot (2C - S) + \frac{S}{2} - \frac{SUS}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S\mathbf{1}} + D, \tag{42}$$

$$S' = C - R \odot (2C - S) + D - \left(1 - \frac{\rho\omega^2}{\sigma_E^2 + 2\mathbf{1}^T S\mathbf{1}}\right) \frac{SUS}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S\mathbf{1}}. \tag{43}$$

Case 2. For the case $\rho > 0$, we consider the transformation T_2 defined as

$$T_2 \begin{bmatrix} C & 0 \\ 0 & \Delta \end{bmatrix} = \begin{bmatrix} C' & 0 \\ 0 & \Delta' \end{bmatrix}, \tag{44}$$

where

$$C' = (U - R) \odot \Delta + (C - \Delta) - \frac{(2C - \Delta)U(2C - \Delta)}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T (2C - \Delta)\mathbf{1}} + D, \tag{45}$$

$$\Delta' = (U - R) \odot \Delta + (C - \Delta) + D$$
$$- \left(1 + \frac{\rho\omega^2}{\sigma_E^2 + 2\mathbf{1}^T(2C - \Delta)\mathbf{1}}\right) \frac{(2C - \Delta)U(2C - \Delta)}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T(2C - \Delta)\mathbf{1}}. \tag{46}$$

To prove convergence of the sequences $C(t)$ and $B(t)$ in the assortative mating case, it suffices to prove that the transformations T_1 and T_2 are concave.

Proof That T_1 is Concave in Case 1. We have to consider two positive semidefinite symmetric matrices, $\widetilde{C}_1$ and $\widetilde{C}_2$, such that $\widetilde{C}_1 = \begin{bmatrix} C_1 & 0 \\ 0 & S_1 \end{bmatrix}$ with $C_1, S_1 \geq 0$, and $\widetilde{C}_2 = \begin{bmatrix} C_2 & 0 \\ 0 & S_2 \end{bmatrix}$ with $C_2, S_2 \geq 0$, and to show that

$$T_1 \left(\frac{\widetilde{C}_1 + \widetilde{C}_2}{2}\right) - \frac{T_1\left(\widetilde{C}_1\right) + T_1\left(\widetilde{C}_2\right)}{2} \geq 0.$$

We find

$$T_1 \left(\frac{\widetilde{C}_1 + \widetilde{C}_2}{2}\right) - \frac{T_1\left(\widetilde{C}_1\right) + T_1\left(\widetilde{C}_2\right)}{2} = \begin{bmatrix} F_{11} & 0 \\ 0 & F_{22} \end{bmatrix}, \tag{47}$$

where

$$F_{11} = -\frac{(S_1 + S_2)U(S_1 + S_2)}{\omega^2 + \sigma_E^2 + \mathbf{1}^T(S_1 + S_2)\mathbf{1}} + 2\left(\frac{S_1 U S_1}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_1\mathbf{1}}\right) + 2\left(\frac{S_2 U S_2}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_2\mathbf{1}}\right) \tag{48}$$

and

$$F_{22} = -\left(1 - \frac{\rho\omega^2}{\sigma_E^2 + \mathbf{1}^T(S_1 + S_2)\mathbf{1}}\right)\left(\frac{(S_1 + S_2)U(S_1 + S_2)}{\omega^2 + \sigma_E^2 + \mathbf{1}^T(S_1 + S_2)\mathbf{1}}\right)$$
$$+ 2\left(1 - \frac{\rho\omega^2}{\sigma_E^2 + 2\mathbf{1}^T S_1\mathbf{1}}\right)\left(\frac{S_1 U S_1}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_1\mathbf{1}}\right)$$
$$+ 2\left(1 - \frac{\rho\omega^2}{\sigma_E^2 + 2\mathbf{1}^T S_2\mathbf{1}}\right)\left(\frac{S_2 U S_2}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_2\mathbf{1}}\right). \tag{49}$$

If we multiply the matrix $\begin{pmatrix} F_{11} & 0 \\ 0 & F_{22} \end{pmatrix}$ on the right by a nonzero $2n$-dimensional vector $\begin{pmatrix} \mathbf{X} \\ \mathbf{Y} \end{pmatrix}$ and on the left by its transpose $\begin{pmatrix} \mathbf{X} \\ \mathbf{Y} \end{pmatrix}^T$, we get

$$\mathbf{X}^T F_{11} \mathbf{X} + \mathbf{Y}^T F_{22} \mathbf{Y},$$

where

$$\mathbf{X}^T F_{11} \mathbf{X} = \left[\frac{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_2 \mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_1 \mathbf{1} \right) \left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)} \right] \mathbf{X}^T (S_1 U S_1) \mathbf{X}$$
$$+ \left[\frac{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_1 \mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_2 \mathbf{1} \right) \left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)} \right] \mathbf{X}^T (S_2 U S_2) \mathbf{X}$$
$$- \left[\frac{2}{\left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)} \right] \mathbf{X}^T (S_1 U S_2) \mathbf{X} \tag{50}$$

and

$$\mathbf{Y}^T F_{22} \mathbf{Y} = \left[\frac{\left(\rho\omega^2 - \sigma_E^2 - \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right) \left(\sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)} \right.$$
$$\left. - 2 \frac{\left(\rho\omega^2 - \sigma_E^2 - 2\mathbf{1}^T S_1 \mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_1 \mathbf{1} \right) \left(\sigma_E^2 + 2\mathbf{1}^T S_1 \mathbf{1} \right)} \right] \mathbf{Y}^T (S_1 U S_1) \mathbf{Y}$$
$$+ \left[\frac{\left(\rho\omega^2 - \sigma_E^2 - \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right) \left(\sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)} \right.$$
$$\left. - 2 \frac{\left(\rho\omega^2 - \sigma_E^2 - 2\mathbf{1}^T S_2 \mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_2 \mathbf{1} \right) \left(\sigma_E^2 + 2\mathbf{1}^T S_2 \mathbf{1} \right)} \right] \mathbf{Y}^T (S_2 U S_2) \mathbf{Y}$$
$$+ \left[\frac{2 \left(\rho\omega^2 - \sigma_E^2 - \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right) \left(\sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)} \right] \mathbf{Y}^T (S_1 U S_2) \mathbf{Y}. \tag{51}$$

Introducing the quantities $z_1 = \mathbf{X}^T S_1 \mathbf{1}$, $z_2 = \mathbf{X}^T S_2 \mathbf{1}$,

$$k_1 = \frac{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_2 \mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_1 \mathbf{1} \right) \left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)}, \tag{52}$$

and

$$k_2 = \frac{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_1 \mathbf{1} \right)}{\left(\omega^2 + \sigma_E^2 + 2\mathbf{1}^T S_2 \mathbf{1} \right) \left(\omega^2 + \sigma_E^2 + \mathbf{1}^T (S_1 + S_2)\mathbf{1} \right)}, \tag{53}$$

we get

$$\mathbf{X}^T F_{11} \mathbf{X} = \left(z_1 \sqrt{k_1} - z_2 \sqrt{k_2} \right)^2 \geq 0. \tag{54}$$

On the other hand, if we introduce the quantities $u = \mathbf{Y}^T S_1 \mathbf{1}$, $v = \mathbf{Y}^T S_2 \mathbf{1}$, and if we denote the coefficients of $\mathbf{Y}^T (S_1 U S_1) \mathbf{Y}$, $\mathbf{Y}^T (S_2 U S_2) \mathbf{Y}$, and $\mathbf{Y}^T (S_1 U S_2) \mathbf{Y}$ in (51) by A, B, and $2C$, respectively, we get

$$\mathbf{Y}^T F_{22} \mathbf{Y} = Au^2 + Bv^2 + 2Cuv. \tag{55}$$

Introducing the additional quantities $s_1 = \mathbf{1}^T S_1 \mathbf{1} \geq 0$, $s_2 = \mathbf{1}^T S_2 \mathbf{1} \geq 0$, the coefficients A, B, and C can be expressed as follows after some algebraic manipulations:

$$A = \left[\omega^2 \sigma_E^4 (1 - \rho) + 2\omega^2 s_1^2 (1 + \rho) - \rho \left(\sigma_E^2 \omega^4 + 4\sigma_E^2 \omega^2 s_2 + 2\omega^4 s_2 + 4\omega^2 s_1 s_2 + 2\omega^2 s_2^2 \right) \right.$$
$$+ \sigma_E^6 + 3\sigma_E^4 s_1 + 3\sigma_E^2 \omega^2 s_1 + 2\sigma_E^2 s_1^2 + 3\sigma_E^4 s_2 + \sigma_E^2 \omega^2 s_2 + 8\sigma_E^2 s_1 s_2 + 2\omega^2 s_1 s_2$$
$$\left. + 4 s_1^2 s_2 + 2\sigma_E^2 s_2^2 + 4 s_2^2 s_1 \right] \Big/ \left[(\sigma_E^2 + 2s_1)(\sigma_E^2 + \omega^2 + 2s_1)(\sigma_E^2 + s_1 + s_2) \right.$$
$$\left. (\sigma_E^2 + \omega^2 + s_1 + s_2) \right], \tag{56}$$

$$B = \left[\sigma_E^6 + \omega^2\sigma_E^4 - \rho\sigma_E^4\omega^2 - \rho\sigma_E^2\omega^4 + 3\sigma_E^4 s_1 + \sigma_E^2\omega^2 s_1(1-4\rho) - 2\rho\omega^4 s_1\right.$$
$$+ 2\sigma_E^2 s_1^2 - 2\rho\omega^2 s_1^2 + 3\sigma_E^4 s_2 + 3\sigma_E^2\omega^2 s_2 + 8\sigma_E^2 s_1 s_2 + 2\omega^2 s_1 s_2(1-2\rho) + 4s_1^2 s_2$$
$$\left. + 2\sigma_E^2 s_2{}^2 + 2\omega^2 s_2{}^2(1+\rho) + 4s_1 s_2^2\right] / \left[(\sigma_E^2 + 2s_2)(\sigma_E^2 + \omega^2 + 2s_2)\right.$$
$$\left. (\sigma_E^2 + s_1 + s_2)(\sigma_E^2 + \omega^2 + s_1 + s_2)\right], \quad (57)$$

and

$$C = \frac{\rho\omega^2 - \sigma_E^2 - s_1 - s_2}{(\sigma_E^2 + s_1 + s_2)(\omega^2 + \sigma_E^2 + s_1 + s_2)}. \quad (58)$$

Moreover, we have

$$AB - C^2 = \left[-4\rho(1+\rho)\omega^4(s_2 - s_1)^2\right] / \left[(\sigma_E^2 + \omega^2 + 2s_1)(\sigma_E^2 + 2s_1)\right.$$
$$(\sigma_E^2 + \omega^2 + 2s_2)(\sigma_E^2 + 2s_2)(\sigma_E^2 + \omega^2 + s_1 + s_2)$$
$$\left. (\sigma_E^2 + s_1 + s_2)\right]. \quad (59)$$

Because $-1 \le \rho < 0$, we have that $A \ge 0$ and $AB - C^2 \ge 0$. We conclude that the quadratic form (55) is positive semidefinite because the matrix $\begin{pmatrix} A & C \\ C & B \end{pmatrix}$ is positive semidefinite if and only if all its principal submatrices have nonnegative determinants (see, e.g., Strang, 1980). Therefore, the concavity of T_1 is proved.

Proof That T_2 is Concave in Case 2. The concavity of T_2 is proved in a similar way. Following the steps in case 1, we have only to prove the concavity of the transformation

$$\Psi(\Sigma) = -\left(1 + \frac{\rho\omega^2}{\sigma_E^2 + 2\mathbf{1}^T\Sigma\mathbf{1}}\right)\frac{\Sigma U\Sigma}{\omega^2 + \sigma_E^2 + 2\mathbf{1}^T\Sigma\mathbf{1}}, \quad (60)$$

where

$$\Sigma = (2C - \Delta) \ge 0.$$

For any nonzero vector $\mathbf{Z}$, we evaluate

$$\mathbf{Z}^T\left\{\Psi\left(\frac{\Sigma_1 + \Sigma_2}{2}\right) - \frac{\Psi(\Sigma_1)}{2} - \frac{\Psi(\Sigma_2)}{2}\right\}\mathbf{Z},$$

and we find, after some simplifications, the expression

$$Q(z_1, z_2) = \left[\frac{-\sigma_E^2 - \rho\omega^2 - d_1 - d_2}{(\sigma_E^2 + d_1 + d_2)(\sigma_E^2 + d_1 + d_2 + \omega^2)} - 2\frac{-\sigma_E^2 - \rho\omega^2 - 2d_1}{(\sigma_E^2 + 2d_1)(\sigma_E^2 + \omega^2 + 2d_1)}\right]z_1^2$$
$$+ \left[\frac{-\sigma_E^2 - \rho\omega^2 - d_1 - d_2}{(\sigma_E^2 + d_1 + d_2)(\sigma_E^2 + d_1 + d_2 + \omega^2)} - 2\frac{-\sigma_E^2 - \rho\omega^2 - 2d_2}{(\sigma_E^2 + 2d_2)(\sigma_E^2 + \omega^2 + 2d_2)}\right]z_2^2$$
$$+ 2\left[\frac{-\sigma_E^2 - \rho\omega^2 - d_1 - d_2}{(\sigma_E^2 + d_1 + d_2)(\sigma_E^2 + d_1 + d_2 + \omega^2)}\right]z_1 z_2, \quad (61)$$

where $d_1 = \mathbf{1}^T\Sigma_1\mathbf{1}, d_2 = \mathbf{1}^T\Sigma_2\mathbf{1}, z_1 = \mathbf{Z}^T\Sigma_1\mathbf{1}, z_2 = \mathbf{Z}^T\Sigma_2\mathbf{1}$. Writing (61) in the form

$$Q(z_1, z_2) = A'z_1^2 + B'z_2^2 + 2C'z_1 z_2, \quad (62)$$

we get after further simplifications

$$A' = \left[(1+\rho)\sigma_E^4\omega^2 + 2(1-\rho)\omega^2 d_1^2 + \rho\left(\sigma_E^2\omega^4 + 4\sigma_E^2\omega^2 d_2 + 2\omega^4 d_2 + 4\omega^2 d_1 d_2 + 2\omega^2 d_2^2\right)\right.$$
$$+ \sigma_E^6 + 3\sigma_E^4 d_1 + 3\sigma_E^2\omega^2 d_1 + 2\sigma_E^2 d_1^2 + 3\sigma_E^4 d_2 + \sigma_E^2\omega^2 d_2 + 8\sigma_E^2 d_1 d_2$$
$$\left. + 2\omega^2 d_1 d_2 + 4d_1^2 d_2 + 2\sigma_E^2 d_2^2 + 4d_2^2 d_1\right] / \left[(\sigma_E^2 + 2d_1)(\sigma_E^2 + \omega^2 + 2d_1)\right.$$
$$\left. (\sigma_E^2 + d_1 + d_2)(\sigma_E^2 + \omega^2 + d_1 + d_2)\right], \quad (63)$$

$$B' = [\sigma_E^6 + \omega^2\sigma_E^4 + \rho\sigma_E^4\omega^2 + \rho\sigma_E^2\omega^4 + 3\sigma_E^4 d_1 + \sigma_E^2\omega^2 d_1(1 + 4\rho)$$
$$+ 2\rho\omega^4 d_1 + 2\sigma_E^2 d_1^2 + 2\rho\omega^2 d_1^2 + 3\sigma_E^4 d_2 + 3\sigma_E^2\omega^2 d_2 + 8\sigma_E^2 d_1 d_2$$
$$+ 2\omega^2 d_1 d_2(1 + 2\rho) + 4d_1^2 d_2 + 2\sigma_E^2 d_2{}^2 + 2\omega^2 d_2{}^2(1 - \rho)$$

$$+ 4d_1d_2{}^2]/[(\sigma_E^2 + 2d_2)(\sigma_E^2 + \omega^2 + 2d_2)(\sigma_E^2 + d_1 + d_2)$$
$$(\sigma_E^2 + \omega^2 + d_1 + d_2)], \tag{64}$$

and

$$C' = -\frac{\rho\omega^2 + \sigma_E^2 + d_1 + d_2}{(\sigma_E^2 + d_1 + d_2)(\omega^2 + \sigma_E^2 + d_1 + d_2)}. \tag{65}$$

Evaluating the determinant of the matrix $\begin{pmatrix} A' & C' \\ C' & B' \end{pmatrix}$, we get

$$A'B' - C'^2 = [4\rho(1-\rho)\omega^4(d_2 - d_1)^2] / [(\sigma_E^2 + \omega^2 + 2d_1)(\sigma_E^2 + 2d_1)$$
$$(\sigma_E^2 + \omega^2 + 2d_2)(\sigma_E^2 + 2d_2)(\sigma_E^2 + \omega^2 + d_1 + d_2)$$
$$(\sigma_E^2 + d_1 + d_2)]. \tag{66}$$

Because $0 < \rho \leq 1$ and $d_1, d_2 \geq 0$, it comes that $A' \geq 0$ and $A'B' - C'^2 \geq 0$. This establishes the concavity of T_2.

Hence, we conclude the following.

THEOREM 5.2. *The equilibrium covariance matrix in Lande's model in the case of assortative mating is globally stable.*

6. Convergence in Chevalet's Model

For Chevalet's model, we have the following result.

THEOREM 6.1. *The equilibrium covariance matrix $\hat{C} = 0$ of transformation* (35) *is globally stable.*

Proof of Theorem 6.1. For any positive semidefinite matrices C_1 and C_2, we have

$$\mathcal{T}\left(\frac{C_1 + C_2}{2}\right) - \frac{\mathcal{T}(C_1) + \mathcal{T}(C_2)}{2}$$
$$= \frac{1}{4}\left(1 - \frac{1}{N}\right)\left\{(\alpha^2 + 2\beta^T C_2\beta)\left((\alpha^2 + \beta^T(C_1 + C_2)\beta)(\alpha^2 + 2\beta^T C_1\beta)\right)^{-1} C_1\beta\beta^T C_1\right.$$
$$+ (\alpha^2 + 2\beta^T C_1\beta)\left((\alpha^2 + \beta^T(C_1 + C_2)\beta)(\alpha^2 + 2\beta^T C_2\beta)\right)^{-1} C_2\beta\beta^T C_2$$
$$\left. - (\alpha^2 + \beta^T(C_1 + C_2)\beta)^{-1}\left(C_1\beta\beta^T C_2 + C_2\beta\beta^T C_1\right)\right\}. \tag{67}$$

Multiplying on the right by a nonzero vector $\mathbf{X}$ and on the left by its transpose $\mathbf{X}^T$, and using the notation $\mathbf{X}^T C_1\beta = y_1$, $\beta^T C_1\beta = \lambda_1$, $\mathbf{X}^T C_2\beta = y_2$, and $\beta^T C_2\beta = \lambda_2$, we get after some simplifications

$$\mathbf{X}^T\left\{\mathcal{T}\left(\frac{C_1 + C_2}{2}\right) - \frac{\mathcal{T}(C_1) + \mathcal{T}(C_2)}{2}\right\}\mathbf{X}$$
$$= \frac{1}{4}\left(1 - \frac{1}{N}\right)\left[y_1\sqrt{\frac{\alpha^2 + 2\lambda_2}{(\alpha^2 + 2\lambda_1)(\alpha^2 + \lambda_1 + \lambda_2)}} - y_2\sqrt{\frac{\alpha^2 + 2\lambda_1}{(\alpha^2 + 2\lambda_2)(\alpha^2 + \lambda_1 + \lambda_2)}}\right]^2$$
$$\geq 0, \tag{68}$$

which proves the concavity of $\mathcal{T}$.

Moreover, for any real $k > 0$ and any symmetric matrix $C \geq 0$, we have

$$\mathcal{T}(kI) - kI = -\frac{1}{2N}kI - \left(1 - \frac{1}{N}\right)\frac{k^2\beta\beta^T}{\alpha^2 + 2k\beta^T\beta} \leq 0. \tag{69}$$

This establishes property (37) and therefore completes the proof of Theorem 6.1 owing to Theorem 4.2.

Remark 6.1. If we take mutation into account in Chevalet's model, the system of equation (34) becomes

$$C_{ij}(t+1) = (1 - \frac{1}{2N})C_{ij}(t) - r_{ij}C_{ij}(t) - (1 - \frac{1}{N})\frac{1}{\omega^2 + \sigma_E^2 + \sigma_G^2(t)}K_i(t)K_j(t) + \delta_{ij}\mu_i m_i^2 \quad (70)$$

for $i, j = 1, \ldots, n$. In the case where this system admits a unique positive definite matrix as equilibrium, it is globally stable by virtue of Theorem 4.1. Such an equilibrium, however, seems difficult to find in general. In the particular case of free recombination, unitary weights and homogeneous mutation, that is, $r_{ij} = (1/2)(1 - \delta_{ij})$, $\beta_i = 1$, and $\mu_i m_i^2 = \mu m^2$ for $i, j = 1, \ldots, n$, we find as globally stable equilibrium

$$\hat{C}_{ii} = -2(N-1)\frac{\hat{K}_i^2}{\alpha^2 + \hat{\sigma}_G^2} + 2N\mu m^2 \quad \text{for } i = 1, \ldots, n, \quad (71)$$

$$\hat{C}_{ij} = -2\frac{(N-1)}{(N+1)}\frac{\hat{K}_i\hat{K}_j}{\alpha^2 + \hat{\sigma}_G^2} \quad \text{for every } j \neq i, \quad (72)$$

where $\hat{K}_i = \sum_j \hat{C}_{ij}$ for $i = 1, \ldots, n$ and $\hat{\sigma}_G^2 = 2\sum_i \hat{K}_i$ are given by

$$\hat{K}_i = \{4N(N-1)\}^{-1}\left[\left((\alpha^2 + N(\alpha^2 + 2\hat{\sigma}_G^2))^2 + 16N^2(N^2-1)(\alpha^2 + \hat{\sigma}_G^2)\mu m^2\right)^{1/2}\right.$$
$$\left. - (\alpha^2 + N(\alpha^2 + 2\hat{\sigma}_G^2))\right] \quad \text{for } i = 1, \ldots, n \quad (73)$$

and

$$\hat{\sigma}_G^2 = \{2N(N+2n-1)\}^{-1}\left[-(N+1)n(\alpha^2 - 4Nn\mu m^2)\right.$$
$$+ \left\{(N+1)n^2\left((N+1)(\alpha^2 - 4Nn\mu m^2)^2\right.\right.$$
$$\left.\left. + 16N^2(N+2n-1)\alpha^2\mu m^2\right)\right\}^{1/2}\right]. \quad (74)$$

7. Discussion

In this paper, we have studied transformations of covariance matrices for allelic effects at several linked loci from one generation to the next proposed by Lande (1976, 1977) and Chevalet (1988) for additive polygenic models in the cases of random mating, constant inbreeding, assortative mating and random genetic drift. In each case, we have shown global convergence to an equilibrium covariance structure, which exists and is unique, by checking a concavity property first used by Karlin (1979) for purely phenotypic models. This is a strong mathematical result. Moreover, numerical studies have shown rapid convergence to equilibrium, usually in less than 100 iterations.

We must remind ourselves, however, that the transformations studied are only approximate for polygenic models, because they are obtained by assuming multinormal distributions for the allelic effects, while it is known that Mendelian segregation and recombination, not to mention mutation, do not preserve such distributions (see, e.g., Felsenstein, 1977). This assumption makes sense when selection and mutation are weak enough compared to the recombination rates (see, e.g., Kimura, 1965; Fleming, 1979) and leads to a closed system of recurrence equations for the variances and covariances of the allelic effects, at least in populations without sex differences (see, e.g., Chevalet, 1988). But in general, moments of higher order come into play (see, e.g., Turelli and Barton, 1990, and references therein). Therefore, our results might actually suggest local stability of the equilibrium covariance structures in the exact models rather than global stability.

Note that Lande (1976, 1977) assumed in his models, on the basis of numerical iterations, that the equilibrium covariance structures had been reached before studying the dynamics of the means. Our analytical results support this approach (for a rigorous treatment, see Mahdi, 1994).

Finally, the techniques used in this paper to study convergence of covariance structures can be applied to a wider range of Gaussian polygenic models for pleiotropic mutations affecting multiple characters (Lande, 1980) or nonnecessarily additive polygenic models with fertility selection as well as viability selection (Lessard and Mahdi, 1995).

Résumé

Cet article présente des résultats de convergence pour des structures de covariance d'effets alléliques, sur des générations successives, dans des modèles polygéniques gaussiens pour des traits quantitatifs, développés par Lande (1976, *Genetical Research* **26**, 221–235; 1977, *Genetics* **86**, 485–498) et Chevalet (1988, in *Proceedings of the Second International Conference on Quantitative Genetics*, 379–394). Les preuves reposent sur les propriétés de concavité des transformations des matrices de covariance.

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Appendix

Proof of Theorem 4.2

Because T is a continuous concave transformation for positive semidefinite symmetric matrices, it is increasing; that is, for any $C_2 \geq C_1 \geq 0$, we have $T(C_2) \geq T(C_1) \geq 0$ (see Lessard and Mahdi, 1995).

Using property (37), we get for any real $k > 0$ and for any integer $n \geq 1$

$$0 \leq T^{(n)}(kI) \leq T^{(n-1)}(kI) \leq kI. \tag{75}$$

The sequence $T^{(n)}(kI)$ being decreasing and bounded below is convergent. Let $L = \lim_{n \to \infty} T^{(n)}(kI)$. From the continuity of T, we have

$$L = \lim_{n \to \infty} T^{(n)}(kI) = \lim_{n \to \infty} T(T^{(n-1)}(kI)) = T\left(\lim_{n \to \infty} T^{(n-1)}(kI)\right) = T(L). \tag{76}$$

Because $\hat{C} = 0$ is the unique fixed point for T, we conclude that $L = 0$.

COROLLARY A.1. *For any positive semidefinite symmetric matrix C, we have*

$$\lim_{n \to \infty} T^{(n)}(C) = 0.$$

Proof of Corollary A.1. First let us prove that for any positive semidefinite symmetric matrix C there exists a real $k > 0$ such that $C \leq kI$; that is, for any nonzero vector $\mathbf{X}$, we have $\mathbf{X}^T C \mathbf{X} \leq k \mathbf{X}^T \mathbf{X}$.

For this purpose, let us define the compact set $E = \{\mathbf{X} \text{ such that } ||\mathbf{X}|| = 1\}$ and the following function

$$\Psi(\mathbf{X}) = \frac{\mathbf{X}^T C \mathbf{X}}{\mathbf{X}^T \mathbf{X}}. \tag{77}$$

Because Ψ is continuous on E, it follows that there exists a real $k > 0$ and a vector $\mathbf{Z}$ in E such that

$$\Psi(\mathbf{Z}) = \max_{\mathbf{X} \in E} \Psi(\mathbf{X}) = k. \tag{78}$$

Therefore, for any $\mathbf{X}$ in E, we have

$$\mathbf{X}^T C \mathbf{X} \leq k \mathbf{X}^T \mathbf{X}. \tag{79}$$

Moreover, for any n-dimensional nonzero vector $\mathbf{Y}$, there exists a real $\lambda_{\mathbf{Y}}$ and a vector $\mathbf{X}$ in E such that $\mathbf{Y} = \lambda_{\mathbf{Y}} \mathbf{X}$, and then

$$\mathbf{Y}^T C \mathbf{Y} = \lambda_{\mathbf{Y}}^2 \mathbf{X}^T C \mathbf{X} \leq k \lambda_{\mathbf{Y}}^2 \mathbf{X}^T \mathbf{X} = k \mathbf{Y}^T \mathbf{Y}. \tag{80}$$

Applying n times the transformation T to

$$0 \leq C \leq kI, \tag{81}$$

we get

$$0 \leq T^{(n)}(C) \leq T^{(n)}(kI). \tag{82}$$

Using the convergence of $T^{(n)}(kI)$ to 0 as n goes to ∞, we conclude that

$$\lim_{n \to \infty} T^{(n)}(C) = 0.$$