Finally, we note that the Svirezhev–Shahshahani metric is equivalent to the following metric in the interior of S_k:

$$d(\boldsymbol{p},\boldsymbol{q}) = 2\arccos\Bigl(\sum_i \sqrt{p_i q_i}\Bigr) . \tag{A.23}$$

This is shown by recognizing that the change of coordinates $p_i = y_i^2/4$ transforms S_k with the Svirezhev–Shahshahani metric into the part of the $(k-1)$-dimensional sphere of radius 2 lying in the positive orthant, equipped with the Euclidean metric. On this sphere, the distance between two points $\boldsymbol{y}, \boldsymbol{z}$ is the geodesic distance $\arccos(\sum_i y_i z_i/4)$, i.e., the length of the great circle through these points. Interestingly, (A.23) has been proposed as a measure of genetic distance by Cavalli-Sforza and Edwards (1967) (see also Jacquard 1974, Antonelli and Strobeck 1977, and Akin 1979).

Various criteria for and applications of generalized gradients, as well as proofs of the above results may be found in Hofbauer and Sigmund (1998).

B PERRON–FROBENIUS THEORY OF NONNEGATIVE MATRICES

In this appendix we summarize some important results from the spectral theory of nonnegative matrices. These were discovered by Perron and Frobenius around 1910 and are useful tools in proving existence, uniqueness, positivity, and stability of equilibrium solutions in mutation-selection models. For a more complete account of the spectral theory of nonnegative matrices, including proofs, the reader is referred to Gantmacher (1959), Schaefer (1974, Chapter I), or Seneta (1981). The latter reference contains, in particular, a detailed treatment of countably infinite matrices.

1. FINITE MATRICES

A $k \times k$ matrix $\mathsf{A} = (a_{ij})$ is called *nonnegative*, $\mathsf{A} \geq 0$, if $a_{ij} \geq 0$ for every i,j. It is called *positive*, $\mathsf{A} > 0$, if $a_{ij} > 0$ for every i,j. Similarly, a vector $\boldsymbol{x} = (x_1,\dots,x_k)^\mathsf{T}$ is said to be nonnegative (positive) if $x_i \geq 0$ ($x_i > 0$) for every i.

The *spectral radius* $r = r(\mathsf{A})$ of an arbitrary matrix A is the radius of the smallest circle in the complex plain that contains all eigenvalues of A, i.e., $|\lambda| \leq r$ for all eigenvalues λ of A. It can be shown that $r = \lim_n \|\mathsf{A}^n\|^{1/n}$, where $\|\mathsf{A}\|$ is an arbitrary norm of the matrix A, e.g., $\|\mathsf{A}\| = \max_i \sum_{j=1}^k |a_{ij}|$. (Throughout this appendix, $\lim_n$ denotes the limit for $n \to \infty$.) Since the sequence $\|\mathsf{A}^n\|^{1/n}$ is monotone decreasing, $r \leq \|\mathsf{A}^n\|^{1/n}$ holds for every $n \geq 1$. Nonnegative matrices have the following important property:

Theorem B.1 *Let $\mathsf{A} \geq 0$. Then the spectral radius r of A is an eigenvalue and there is at least one nonnegative eigenvector $\boldsymbol{x} \geq 0$ ($\boldsymbol{x} \neq \boldsymbol{0}$), i.e., $\mathsf{A}\boldsymbol{x} = r\boldsymbol{x}$. In addition, if A has an eigenvalue λ with an associated positive eigenvector, then $\lambda = r$.*

We use the notation $\mathsf{A}^n = (a_{ij}^{(n)})$ for nth powers. A nonnegative matrix A is called *irreducible* if for every pair of indices (i,j) an integer $n = n(i,j) \geq 1$ exists such that $a_{ij}^{(n)} > 0$. Now we state the *Theorem of Perron–Frobenius.*

Theorem B.2 *If A is irreducible, then the following hold:*
1. *The spectral radius r is positive and a simple root of the characteristic equation.*
2. *To r there corresponds a positive right eigenvector $\boldsymbol{x} > 0$ such that $\mathsf{A}\boldsymbol{x} = r\boldsymbol{x}$, and $\boldsymbol{x}$ is unique except for multiplication by a positive constant.*
3. *No other eigenvalue of A is associated with a nonnegative eigenvector.*

This theorem is sufficient to prove our existence, uniqueness, and stability results for the haploid mutation-selection model in continuous time. As noted below III(1.6), in discrete time a stronger condition than irreducibility is needed.

A nonnegative matrix A is called *primitive* if an integer $n \geq 1$ exists such that $\mathsf{A}^n > 0$. Obviously, every positive matrix is primitive, and every primitive matrix is irreducible.

Theorem B.3 *For an irreducible matrix A with spectral radius r, the following assertions are equivalent:*
1. *A is primitive.*
2. *$|\lambda| < r$ for all eigenvalues $\lambda \neq r$ of A.*
3. *$\lim_n \left(r^{-1}\mathsf{A}\right)^n$ exists.*

Concerning property 3, it is readily shown that for an arbitrary matrix A, $\lim_n \mathsf{A}^n = 0$ is equivalent to $r(\mathsf{A}) < 1$, and that $r(\mathsf{A}) > 1$ always implies that $\lim_n \mathsf{A}^n$ does not exist. If $r(\mathsf{A}) = 1$, then $\lim_n \mathsf{A}^n$ exists if and only if $r(\mathsf{A}) = 1$ is a simple root of the minimal polynomial and all other eigenvalues satisfy $|\lambda| < 1$.

A stronger and more precise statement of Theorem B.3.3. is the following:

Theorem B.4 *Let A be primitive with spectral radius r and corresponding eigenvector $\boldsymbol{x} > 0$. Then there exists a decomposition $\mathsf{A} = r\mathsf{P} + \mathsf{B}$, where P is a projection on the eigenspace spanned by $\boldsymbol{x}$ (i.e., for every $\boldsymbol{y} \in \mathbf{R}^k$ there is a constant c such that $\mathsf{P}\boldsymbol{y} = c\boldsymbol{x}$, and $\mathsf{P}\boldsymbol{x} = \boldsymbol{x}$), $\mathsf{PB} = \mathsf{BP} = 0$, and $r(\mathsf{B}) < 1$. Consequently,*

$$\lim_n \left(r^{-1}\mathsf{A}\right)^n \boldsymbol{y} = c\boldsymbol{x} + \lim_n \left(r^{-1}\mathsf{B}\right)^n \boldsymbol{y} = c\boldsymbol{x} \tag{B.1}$$

holds for all $\boldsymbol{y} \in \mathbf{R}^k$.

Finally, the exponential

$$e^{\mathsf{A}} = \sum_{n=0}^{\infty} \frac{1}{n!}\mathsf{A}^n \tag{B.2}$$

of an irreducible matrix A is always positive and, hence, primitive. It follows that

$$\lim_{t\to\infty} e^{-rt}e^{\mathsf{A}t}\boldsymbol{y} = c\boldsymbol{x} \tag{B.3}$$

for some constant c depending on $\boldsymbol{y}$.

2. COUNTABLE STOCHASTIC MATRICES

Most of the above results for finite matrices can be extended to infinite matrices with a countable index set, and even further (see Appendix C). However, some complications occur. For instance, the notion of primitivity has to be defined in a different way, and, in part, additional assumptions are necessary.