A Mendelian Markov Process.. with Multinomial

Transition Probabilities[1] I.   The Binomial Case.

by

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1. Introduction

In any finite genetic population, the effect of chance involved in the

sampling by which one generation replaces another causes gene frequency

change as long as fixation or extinction is not achieved.   In genetic ter-

minology this fluctuation in gene frequency due to the finiteness of a popu-

lation is called ''random genetic drift''.

Fisher (1922), using an equation of the diffusion type, was the first

to make an effort to quantitatively describe the phenomenn of random genetic

drift.   In the corrected version of this work (1930 b), he found the general

result that the rate of decrease of the genetic variance in the population

due to drift was $1/2N$ per generation, where N = number of individuals

of mating potential.   This result was confirmed by various authors using

different methods (e.g., Wright (1931), Malecot (1944), Feller (1950)).

The particular form of the diffusion model which has had the widest use

was introduced into genetical literature by Wright (1945).   This equation

which plays a fundamental role in the theory of gene frequencies is the Kol-

mogorov forward equation or ---- as is commonly known among physicists ---

the Fokker-Planck equation.   Earlier Kolmogorov (1935) had introduced the

steady state form of the forward equation in genetics.   The complete solu-

tions to the problem however, were obtained much later and are due to

Kimura (1955).

The problem of random genetic drift as a problem in finite Markov chains was first considered by Malécot (1944). Based on the largest non-unit characteristic root of the transition probability matrix Malécot obtained the asymptotic rate of decrease of heterozygosity. This is essentially the same as the previously known results due to Fisher and Wright for steady decay. Feller (1951) succeeded in finding a general expression for all the characteristic roots of the transition probability matrix.

In using diffusion approximations to explain what happens in a finite population the authors started with a somewhat inconsistent premise of an infinite population. Their treatment has a serious drawback in that though in actuality the state space is made up of discrete values it is treated as though it were continuous. The tacit assumption in such an approach is that for large population size the approximation of the discrete time, discrete space process by the continuous diffusion process does not result in serious error. It was only recently that a rigorous justification of the diffusion approach was given by Watterson (1962) with respect to the processes considered by Wright (1945) and Kimura (1954, 1955).

The validity of the diffusion approximation as providing adequate numerical solution to the problem concerning the probability that a particular gene is lost or fixed by a certain time was considered by Ewens (1963). Since exact expressions were not available his method of getting exact results consisted in simply powering the transition matrix using a high speed computer and collecting the appropriate terms.

In spite of the exhaustive literature on the subject it must be pointed out that work to date has failed to provide exact answers to problems under random genetic drift from the true perspective of the finiteness of the

population size. It is the objective of this paper to fill this void.

2. Population Structure

Let us consider a random mating population of N diploid monoecious individuals which is kept constant in size by maintaining N individuals in every generation. Such a population could also be regarded as composed of 2N haploids. In order to simplify the discussion, we assume an idealized situation where selection, migration and mutation are absent and generations do not overlap. The discussion in this paper will be restricted to the case where there is only one segregating locus with two allelomorphs A and a.

As far as the mating system is concerned we are demanding a somewhat stronger version of random mating in that a) each individual is capable of at least N offspring per generation b) the fact that a parent is used once in no way affects the probability of his being used again. Thus the 2N gametes which are picked to form the next generation are obtained in 2N independent and identical Bernoulli trials.

Let us suppose that the frequencies of A and a in some generation are respectively i and 2N-i. Our basic chance quantities are Bernoulli random variables X_α, $(\alpha = 1,2,\ldots,2N)$ where,

$$X_\alpha = \begin{cases} 1 & \text{if } \alpha\text{th gene in the next generation is } A \\ \\ 0 & \text{if } \alpha\text{th gene in the next generation is } a. \end{cases}$$

and

(1) $$P(X_\alpha = 1) = i/2N.$$

Denoting by $\underline{\bar{X}}$ the total frequency of the A gene in the next generation, we have the relation $\underline{\bar{X}} = \sum_{\alpha=1}^{2N} x_\alpha$, where clearly,

(2) $$P(\underline{\bar{X}} = j) = \binom{2N}{j} (i/2N)^j (1 - i/2N)^{2N-j} .$$

Now letting $\underline{\bar{X}}_n$ represent the frequency of A in generation n, it is clear that the sequence $\underline{\bar{X}}_0, \underline{\bar{X}}_1, \underline{\bar{X}}_2, \ldots$ represents a Markov Chain with $2N+1$ states (the possible frequencies for A), and the transition probabilities $p_{ij} = P(\underline{\bar{X}}_n = j | \underline{\bar{X}}_{n-1} = i)$ are given by (2) above. (In the sequel we will denote $2N$ by M and transition matrix $||p_{ij}||$ by P).

In defining the transition probabilities in the above manner we adopt the mathematical convention that $0^0 = 1$. This makes sense from the genetic point of view since with this convention $p_{00} = 1$ and $p_{MM} = 1$ which merely says that once the population becomes homozygous for any gene it remains in that condition forever.

We now define $p_{ij}^n = P(\underline{\bar{X}}_{n+k} = j | \underline{\bar{X}}_k = i)$. p_{ij}^n is thus the probability that, starting in the kth generation with i A-alleles, the population will consist of j A-alleles and $2N-j$ a-alleles n generations later.

3. Exact Expressions for the n-stage Transition Probabilities.

In this section we will express the n-stage transition probabilities in terms of the moments of $\underline{\bar{X}}_{n-1}$. Let $i \neq 0$ or M; then, by the Chapman-Kolmogorov equation we have

$$p_{ij}^{n} = \sum_{k=0}^{M} p_{ik}^{n-1} \, p_{kj}$$

$$= \sum_{k=0}^{M} p_{ik}^{n-1} \binom{M}{j} \left(\frac{k}{M}\right)^{j} \left(1-\frac{k}{M}\right)^{M-j}$$

$$= \sum_{k=0}^{M} p_{ik}^{n-1} \binom{M}{j} \left(\frac{k}{M}\right)^{j} \sum_{t=0}^{M-j} \binom{M-j}{t}(-1)^{t} \left(\frac{k}{M}\right)^{t}$$

$$= \sum_{t=0}^{M-j} (-1)^{t} \binom{M}{j}\binom{M-j}{t} M^{-t-j} \sum_{k=0}^{M} p_{ik}^{n-1} k^{j+t},$$

whence

$$(3) \qquad p_{ij}^{n} = \sum_{t=0}^{M-j} (-1)^{t} \binom{M}{j}\binom{M-j}{t} M^{-t-j} \, E(\overline{X}_{n-1}^{j+t}|\overline{X}_{0} = i) \ .$$

The above relation suggests a procedure for calculating p_{ij}^{n} alternative to the calculation of the nth power of the transition matrix $P=||p_{ij}||$. Thus, if the moments of order $1,2\ldots M$ of the random variable $\overline{X}_{n-1}$ are known for each i, the above relation could be used. The procedure for obtaining these moments is outlined in the appendix.

Let $_{i}E_{n} = (_{i}\mu_{n}^{1}, \ _{i}\mu_{n}^{2}, \ldots, \ _{i}\mu_{n}^{r}, \ldots, \ _{i}\mu_{n}^{M})'$, where the prime indicates the transpose, and $_{i}\mu_{n}^{r} = E(\overline{X}_{n}^{r}|\overline{X}_{0}= i)$. It is shown as a result of Theorem 1 of the appendix that the following recursive relation exists among the vectors of conditional moments:

$$_{i}E_{n+1} = C_{i}E_{n},$$

where

$$C = \begin{bmatrix} a_{11}M^{(1)}/M & 0 & 0 \ldots \ldots 0 \ldots \ldots 0 \\ a_{21}M^{(1)}/M & a_{22}M^{(2)}/M^2 & 0 \ldots \ldots 0 \ldots \ldots 0 \\ a_{r1}M^{(1)}/M & a_{r2}M^{(2)}/M^2 \ldots \ldots a_{rr}M^{(r)}/M^r \ldots \ldots 0 \\ a_{M1}M^{(1)}/M & a_{M2}M^{(2)}/M^2 & a_{Mr}M^{(r)}/M^r \ldots a_{MM}M^{(M)}/M^M \end{bmatrix}$$

with

$$a_{rs} = \sum_{i=0}^{s-1} \frac{(-1)^i (s-i)^{r-1}}{(s-i-1)! \, i!} \qquad \text{for } s \in \{1,2,\ldots r\}$$

and

$$M^{(s)} = M(M-1) \ldots \ldots (M-s+1).$$

By successive iteration we get

(4) $$_iE_{n-1} = C^{n-1} \, _iE_0$$

where, since the initial number of A-alleles is i, $_iE_0 = (i, i^2, \ldots, i^r, \ldots, i^M)'$. In order to obtain the conditional moments of $\overline{X}_n$ given $\overline{X}_0 = i$ we are thus led to find the $(n-1)$th power of C. This is accomplished by means of a similarity transformation which diagonalizes C. C has M distinct eigenvalues, $\lambda_s = M^{(s)}/M^s$, $s = 1,2\ldots M$ and hence C^{n-1} can be written as

$$c^{n-1} = \sum_{s=1}^{M} \lambda_s^{n-1} \, \bar{U}_s \bar{V}_s' \; ,$$

where $\bar{U}_s$, $\bar{V}_s'$ are respectively the post-and pre-eigenvectors of C corresponding to the eigenvalue λ_s. (See appendix section A.2.1 and A.2.) Hence

$$_i E_{n-1} = \sum_{s=1}^{M} \lambda_s^{n-1} \, \bar{U}_s \bar{V}_s' \; _i E_0.$$

Since $\lambda_1 = M^{(1)}/M = 1$, we may also write

(5)
$$_i E_{n-1} = \bar{U}_1 \bar{V}_1' \; _i E_0 + \sum_{s=2}^{M} \lambda_s^{n-1} \, \bar{U}_s \bar{V}_s' \; _i E_0.$$

Expression (5) gives us the vector of the conditional moments of order
r, $r = 1,2....M$, in the (n-1)th generation. We have the following two cases
to consider for finding the n-stage transition probabilities by (3).

1) $j=t=0$. In such a case $E(\bar{X}_{n-1}^{j+t}|\bar{X}_0 = i) = 1$.

2) $j+t>0$. If $j+t>0$, $E(\bar{X}_{n-1}^{j+t}|\bar{X}_0 = i)$ is the (j+t)th component of the
column vector $_i E_{n-1}$. That is,

(6)
$$E(\bar{X}_{n-1}^{j+t}|\bar{X}_0 = i) = \sum_{\beta=1}^{M} u_{j+t,1} v_{1\beta} i^\beta + \sum_{s=2}^{M} (M^{(s)}/M^s)^{n-1} u_{j+t,s} \sum_{\beta=1}^{M} v_{s\beta} i^\beta$$

where u_{kr} is the rth element of the post-eigenvector corresponding to λ_k,
and v_{kr} is the rth element of the pre-eigenvector corresponding to λ_k.
Now it is indicated in appendix section A.2.2 that $v_{s\beta} = \begin{cases} 0 & \text{if } \beta > s \\ 1 & \text{if } \beta = s \end{cases}$

Therefore, $v_{1\beta} = \begin{cases} 0 & \text{if } \beta > 1 \\ 1 & \text{if } \beta = 1 \end{cases}$ Also it can be shown (see appendix A.2.1)

that $u_{j+t,1} = M^{j+t-1}$, $j+t = 1,2,\ldots.M$. Hence from (6)

$$(7) \qquad E(\overline{X}_{n-1}^{j+t}|X_0 = i) = i\,M^{t+j-1} + \sum_{s=2}^{M} \sum_{\beta=1}^{s} (M^{(s)}/M^s)^{n-1}\,u_{j+t,s}\,v_{s\beta}\,i^\beta .$$

Let us now consider (3) in which we have expressed p_{ij}^n in terms of the moments of $\overline{X}_{n-1}$. There are two distinct cases that need to be considered:

Case 1: $j > 0.$ Consequently $j+t > 0$, $E(\overline{X}_{n-1}^{j+t}|\overline{X}_0 = i)$ is given by (7). Hence

$$p_{ij}^n = \sum_{t=0}^{M-j} (-1)^t \binom{M}{j}\binom{M-j}{t} M^{-t-j} \left\{ iM^{t+j-1} + \sum_{s=2}^{M} \sum_{\beta=1}^{s} (M^{(s)}/M^s)^{n-1} u_{j+t,s} v_{s,\beta}\, i^\beta \right\} .$$

In the above consider only the term

$$\sum_{t=0}^{M-j} (-1)^t \binom{M}{j}\binom{M-j}{t} M^{-t-j}_i\, M^{t+j-1}$$

$$= (i/M)\binom{M}{j} \sum_{t=0}^{M-j} (-1)^t \binom{M-j}{t},$$

which on account of the relation

$$\sum_{t=0}^{M-j} (-1)^t \binom{M-j}{t} = \begin{cases} 0 & \text{if } j \neq M \\ 1 & \text{if } j = M \end{cases} ,$$

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yields

$$\sum_{t=0}^{M-j} (-1)^t \binom{M}{j}\binom{M-j}{t} M^{-t-j} i\, M^{t+j-1} = \begin{cases} 0 & \text{if } j \neq M \\[2mm] \dfrac{i}{M} & \text{if } j = M. \end{cases}$$

We thus get, for $j \neq M$,

$$(8) \quad P_{ij}^n = \binom{M}{j}\sum_{t=0}^{M-j}(-1)^t\binom{M-j}{t}M^{-t-j}\sum_{s=2}^{M}\sum_{\beta=1}^{s}(M^{(s)}/M^s)^{n-1}\, u_{j+t,s}\, v_{s,\beta}\, i^\beta ,$$

and for $j = M$

$$(9) \quad p_{iM}^n = \frac{i}{M} + M^{-M}\sum_{s=2}^{M}\sum_{\beta=1}^{s}(M^{(s)}/M^s)^{n-1}\, u_{Ms}\, v_{s\beta}\, i^\beta .$$

Case 2: $j = 0$. If $j = 0$, $E(\overline{X}_{n-1}^{j+t}|\overline{X}_0 = i) = 1$ when $t = 0$. Therefore, from (3) we get

$$p_{i0}^n = 1 + \sum_{t=1}^{M}(-1)^t\binom{M}{t}M^{-t}\, E(\overline{X}_{n-1}^{t}|\overline{X}_0 = i).$$

Since $t > 0$ in the summation, $E(\overline{X}_{n-1}^{t}|\overline{X}_0 = i)$ can be obtained from (7) with $j = 0$. Consequently,

$$p_{i0}^n = 1 + \sum_{t=1}^{M}(-1)^t\binom{M}{t}M^{-t}\, iM^{t-1}$$

$$+ \sum_{t=1}^{M}(-1)^t\binom{M}{t}M^{-t}\sum_{s=2}^{M}\sum_{\beta=1}^{s}(M^{(s)}/M^s)^{n-1}\, u_{ts}\, v_{s\beta}\, i^\beta .$$

Since $\displaystyle\sum_{t=1}^{M} (-1)^t \binom{M}{t} = -1$, the term $\displaystyle\sum_{t=1}^{M} (-1)^t \binom{M}{t} M^{-t} i\, M^{t-1}$ in the above ex-

pression reduces to $-\dfrac{i}{M}$. Whence

$$(10) \qquad p_{i0}^{n} = 1 - \frac{i}{M} + \sum_{t=1}^{M} (-1)^t \binom{M}{t} M^{-t} \sum_{s=2}^{M} \sum_{\beta=1}^{s} (M^{(s)}/M^s)^{n-1} u_{ts}\, v_{s\beta}\, i^{\beta}.$$

The three expressions (8), (9) and (10) together give us the n-stage transition probabilities of the system. It may be seen that in order to obtain these probabilities the quantities that need to be found are u_{ts} and $v_{s\beta}$. These quantities which depend only on M (not on n) are easily obtainable since they are the elements of the post and pre-eigenvectors of the triangular matrix C.

Let us next consider the limiting behavior of these transition probabilities as the number of generations becomes indefinitely large. For $s = 2,3,\ldots,M$ we note that

$$M^{(s)}/M^s = (1 - \frac{1}{M})(1 - \frac{2}{M})\cdots(1 - \frac{s-1}{M}) < 1.$$

Therefore $\displaystyle\lim_{n \to \infty} (M^{(s)}/M^s)^{n-1} = 0$ for $s = 2,3,\ldots,M$.

Consequently, since $u_{ts}, v_{s\beta}$ do not depend on n, we get

1) $\displaystyle\lim_{n \to \infty} p_{i0}^{n} = 1 - \frac{i}{M}$

2) $\displaystyle\lim_{n \to \infty} p_{iM}^{n} = \frac{i}{M}$.

and 3) if $j \neq 0$ or M, $\displaystyle\lim_{n \to \infty} p_{ij}^{n} = 0.$

The extinction or fixation of A is thus bound to occur if the population is allowed to mate at random for a large number of generations. These observations are in accord with the findings of earlier investigators.

Because of symmetry it can be easily seen that $p_{i0}^n = p_{M-i,M}^n$. The set of probabilities of fixation of a gene, $\left\{ p_{iM}^n : i = 1,2...M-1 \right\}$, is thus sufficient to specify the probabilities of its loss. A formal proof of the symmetry argument is found in Khazanie (1965), but is not included here.

It is clear that for each n and i, the set of ordered pairs $\left\{ j, p_{ij}^n \right\}$ is a conditional probability function. (See Khazanie (1965)).

Lemma: $\sum_{j=0}^{M} p_{ij}^n = 1$, where the p_{ij}^n are given by (8), (9), and (10).

4. Distribution of Time to Homozygosity

It was pointed out near the end of the previous section that extinction or fixation of the A gene is bound to occur. This conclusion suggests the interesting problem of determining the time required for the population to reach one of the homozygous conditions. We may define the problem formally as follows:

Let τ_i denote the time taken to reach either 0 or M for the first time given that initially there were i $(0 < i < M)$ A-alleles. ($\tau_0 = \tau_M = 0$ identically, and therefore these cases are excluded). Clearly,

$$P(\tau_i = n) = P(\underline{X}_n = 0 \text{ or } M | \underline{X}_{n-1} \neq 0 \text{ or } M, \underline{X}_0 = i) .$$

The population will become homozygous in the very first generation if it becomes aa (i.e. A is lost) or AA (i.e. A is fixed) in just one transition from i. Thus in order that A be lost in one generation a one-step transition $i \longrightarrow 0$ has to take place and the probability of such a

transition is p_{i0}. In a similar manner the probability that the gene is fixed in one generation is p_{iM}. Consequently

$$(11) \qquad P(\tau_i = 1) = p_{i0} + p_{iM}.$$

If $n > 1$, the gene A will be lost exactly in the nth generation if it exists in the population in the (n-1)th generation but is lost in the nth. The probability of such an event is $p_{i0}^n - p_{i0}^{n-1}$. A similar argument applies to the fixation of that gene and the probability is $p_{iM}^n - p_{iM}^{n-1}$. Clearly, then,

$$(12) \qquad P(\tau_i = n) = p_{iM}^n - p_{iM}^{n-1} + p_{i0}^n - p_{i0}^{n-1}.$$

Now by symmetry $p_{i0}^n = p_{M-i,M}^n$ and as a result,

$$(13) \qquad P(\tau_i = n) = p_{iM}^n - p_{iM}^{n-1} + p_{M-i,M}^n - p_{M-i,M}^{n-1}.$$

Substituting in (13) the values of p_{iM}^n and $p_{M-i,M}^n$ as given by (9) we get after simplification, for $n \geq 2$,

$$(14) \qquad P(\tau_i = n) = M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} (M^{(s)}/M^s)^{n-2} (M^{(s)}/M^s - 1)[i^\beta + (M-i)^\beta] u_{Ms} v_{s\beta}.$$

Letting $C(i,s,\beta) = (M^{(s)}/M^s - 1)[i^\beta + (M-i)^\beta] u_{Ms} v_{s\beta}$ it follows that

$$P(\tau_i = n) = M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta) (M^{(s)}/M^s)^{n-2}$$

(We note above that $C(i,s,\beta)$ does not depend on n). (11) and (14) together give us the probability function of τ_i.

Moments of τ_i: In order to find the moments of τ_i we will first derive the probability generating function of τ_i. Then

$$G_i(z) = E(z^{\tau_i})$$

$$= \left[(1-\tfrac{i}{M})^M + (\tfrac{i}{M})^M\right] z + M^{-M} \sum_{n=2}^{\infty} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta)(M^{(s)}/M^s)^{n-2} z^n$$

$$= \left[(1-\tfrac{i}{M})^M + (\tfrac{i}{M})^M\right] z + M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta)z^2 \sum_{n=2}^{\infty} (zM^{(s)}/M^s)^{n-2}.$$

It is seen from the above that $G_i(z)$ is defined at least for values of z such that $|z| < \frac{M}{M-1}$. Therefore $\sum_{n=2}^{\infty} (zM^{(s)}/M^s)^{n-2} = 1/(1-zM^{(s)}/M^s)$ and consequently,

$$(15) \qquad G_i(z) = \left[(1-\tfrac{i}{M})^M + (\tfrac{i}{M})^M\right] z + M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta) \frac{z^2}{(1-zM^{(s)}/M^s)}$$

Differentiating $G_i(z)$ once with respect to z and setting $z=1$ we get $E(\tau_i)$. Thus

$$E(\tau_i) = \frac{\partial}{\partial z} \left. G_i(z) \right|_{z=1}$$

$$= (1 - \tfrac{i}{M})^M + (\tfrac{i}{M})^M + M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta) \left. \frac{2z - z^2 M^{(s)}/M^s}{(1 - zM^{(s)}/M^s)^2} \right|_{z=1}$$

which yields

$$(16) \qquad E(\tau_i) = (1 - \tfrac{i}{M})^M + (\tfrac{i}{M})^M + M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta) \frac{2 - M^{(s)}/M^s}{(1 - M^{(s)}/M^s)^2} \ .$$

Differentiating $G_i(z)$ twice with respect to z and setting $z=1$ we get $E(\tau_i(\tau_i - 1))$ from which we can obtain the variance of τ_i by means of the relation $V(\tau_i) = E(\tau_i(\tau_i - 1)) + E(\tau_i) - [E(\tau_i)]^2$. We have

$$E(\tau_i(\tau_i-1)) = M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta) \left. \frac{2(1 - \frac{zM^{(s)}}{M^s})^2 + 2(2z - \frac{z^2 M^{(s)}}{M^s}) \frac{M^{(s)}}{M^s}}{(1 - \frac{zM^{(s)}}{M^s})^3} \right|_{z=1}$$

which gives

$$(17) \qquad E(\tau_i(\tau_i - 1)) = M^{-M} \sum_{s=2}^{M} \sum_{\beta=1}^{s} C(i,s,\beta) \frac{2}{(1 - M^{(s)}/M^s)^3} \ .$$

By the above-mentioned relation the variance of τ_i can now be obtained.

5. Discussion

Tables* 1 to 6 give the distribution of time to reach homozygosity for various population sizes and for all possible corresponding initial gene frequencies of A. On account of distribution symmetry the values corresponding to i and M-i are identical. It will be seen that for small populations fixation or extinction usually occurs early-in the first few generations. For M=4 it is almost certain that the population will be homozygous much before the 40th generation is reached. On an average, the number of generations is less than five whatever the initial gene frequency. Even for a population of size eight, by the 40th generation there is less than one per cent chance that the population will remain heterozygous, irrespective of the initial gene frequency. As the population size increases the expected number of generations to homozygosity also increases, and as would be anticipated, the closer i is to M/2 the larger is the expected number of generations to homozygosity. It may be observed further that larger variance tends to be associated with larger expected number of generations.

Ewens (1963) investigated the accuracy of the diffusion approximations by comparing them with the exact results that he obtained by numerical methods with the aid of a high speed computer. By the method of inversion Ewens obtained the exact values for the mean times for a population of size 12. His results are in agreement with ours given at the bottom of Table 5. Ewens alos found numerically the probability of fixation of the A-gene by the nth generation by powering the transition matrix P. It was pointed out by Ewens that the diffusion approximation underestimates the true absorption probability for all initial gene frequencies and all the generations that he considered (8, 16, 32 and 64). From Table 7 it appears that the values in

*Other tables may be found in Khazanie (1965).

our rows 7, 15 and 31 come closer to the values from the diffusion approximation for generations 8, 16, and 32, although the reason for this is not apparent to the authors.

6. Summary

For the case of a finite random mating population with one segregating locus and two alleles, whose gene frequency is subjected only to the force of genetic sampling, exact expressions are obtained for the n-stage transition probabilities and for the time to homozygosity with regard to any initial gene frequency. Tables of the cumulative distribution function of time-to-homozygosity are provided for several small populations, as well as table of the probability of fixation for one population size [M=12].

In a subsequent paper the above approach has been extended to the general case of several independently segregating loci each with an arbitrary number of alleles.

Table 1. Cumulative Distribution of τ_i, Time to Homozygosity (M=4)

Initial Frequency Generation	$i = 1$ ($i = 3$)	$i = 2$
1	0.32031	0.12500
6	0.84109	0.78812
11	0.96229	0.94972
16	0.99105	0.98807
21	0.99788	0.99717
26	0.99950	0.99933
31	0.99988	0.99984
36	0.99997	0.99996
41	0.99999	0.99999
46	1.00000	1.00000
Expected Value of τ_i	3.68966	4.55172
Variance of τ_i	11.52913	12.36147

Table 2. Cumulative Distribution of τ_i, Time to Homozygosity (M=6)

Initial Frequency Generation	i = 1 (i = 5)	i = 2 (i = 4)	i = 3
1	0.33492	0.08916	0.03125
6	0.76458	0.62358	0.57662
11	0.90544	0.84871	0.82980
16	0.96200	0.93920	0.93160
21	0.98473	0.97557	0.97251
26	0.99386	0.99018	0.98895
31	0.99753	0.99605	0.99556
36	0.99901	0.99841	0.99822
41	0.99960	0.99936	0.99928
46	0.99984	0.99974	0.99971
51	0.99994	0.99990	0.99988
56	0.99997	0.99996	0.99995
61	0.99999	0.99998	0.99998
66	1.00000	0.99999	0.99999
71	1.00000	1.00000	1.00000
Expected Value of τ_i	4.62300	6.58484	7.20503
Variance of τ_i	25.70988	30.57276	30.84244

Table 3. Cumulative Distribution of τ_i, Time to Homozygosity (M=8)

Initial Frequency	i = 1 (i = 7)	i = 2 (i = 6)	i = 3 (i = 5)	i = 4
Generation				
1	0.34361	0.10013	0.02367	0.00781
6	0.74159	0.55946	0.45115	0.41521
11	0.86834	0.77433	0.71793	0.69914
16	0.93248	0.88425	0.85532	0.84567
21	0.96537	0.94063	0.92579	0.92084
26	0.98224	0.96955	0.96194	0.95940
31	0.99089	0.98438	0.98048	0.97918
36	0.99533	0.99199	0.98999	0.98932
41	0.99760	0.99589	0.99486	0.99452
46	0.99877	0.99789	0.99737	0.99719
51	0.99937	0.99892	0.99865	0.99856
56	0.99968	0.99945	0.99931	0.99926
61	0.99983	0.99972	0.99964	0.99962
66	0.99991	0.99985	0.99982	0.99981
71	0.99996	0.99993	0.99991	0.99990
76	0.99998	0.99996	0.99995	0.99995
81	0.99999	0.99998	0.99998	0.99997
86	0.99999	0.99999	0.99999	0.99999
91	1.00000	0.99999	0.99999	0.99999
96	1.00000	1.00000	1.00000	1.00000
Expected Value of τ_i	5.26484	7.93824	9.41533	9.88868
Variance of τ_i	42.47679	54.98743	57.46264	57.60497

Table 4. Cumulative Distribution of τ_i, Time to Homozygosity (M=10)

Initial Frequency	$i = 1$ ($i = 9$)	$i = 2$ ($i = 8$)	$i = 3$ ($i = 7$)	$i = 4$ ($i = 6$)	$i = 5$
Generation					
1	0.34868	0.10737	0.02825	0.00615	0.00195
6	0.73797	0.54131	0.40467	0.32421	0.29764
11	0.84894	0.73168	0.64805	0.59792	0.58122
16	0.91092	0.84164	0.79217	0.76248	0.75258
21	0.94740	0.90650	0.87728	0.85974	0.85390
26	0.96894	0.94479	0.92753	0.91718	0.91373
31	0.98166	0.96740	0.95721	0.95110	0.94906
36	0.98917	0.98075	0.97473	0.97112	0.96992
41	0.99361	0.98863	0.98508	0.98295	0.98224
46	0.99622	0.99329	0.99119	0.98993	0.98951
51	0.99777	0.99604	0.99480	0.99405	0.99381
56	0.99868	0.99766	0.99693	0.99649	0.99634
61	0.99922	0.99862	0.99819	0.99793	0.99784
66	0.99954	0.99918	0.99893	0.99878	0.99872
71	0.99973	0.99952	0.99937	0.99928	0.99925
76	0.99984	0.99972	0.99963	0.99957	0.99956
81	0.99991	0.99983	0.99978	0.99975	0.99974
86	0.99994	0.99990	0.99987	0.99985	0.99984
91	0.99997	0.99994	0.99992	0.99991	0.99991
96	0.99998	0.99997	0.99995	0.99995	0.99995
Expected Value of τ_i	5.75328	8.95376	11.03112	12.20835	12.59052
Variance of τ_i	60.86641	83.69559	91.00894	92.55735	92.65473

Table 5. Cumulative Distribution of τ_i, Time to Homozygosity (M=12)

Initial Frequency	i = 1 (i = 11)	i = 2 (i = 10)	i = 3 (i = 9)	i = 4 (i = 8)	i = 5 (i = 7)	i = 6
Generation						
1	0.35200	0.11216	0.03168	0.00771	0.00158	0.00049
6	0.73984	0.53990	0.39238	0.29128	0.23232	0.21295
11	0.84007	0.71002	0.60935	0.53772	0.49484	0.48057
16	0.89701	0.81280	0.74733	0.70058	0.67254	0.66319
21	0.93337	0.87887	0.83647	0.80619	0.78802	0.78197
26	0.95688	0.92160	0.89416	0.87456	0.86280	0.85888
31	0.97209	0.94926	0.93150	0.91881	0.91120	0.90866
36	0.98194	0.96716	0.95566	0.94745	0.94253	0.94088
41	0.98831	0.97874	0.97130	0.96599	0.96280	0.96174
46	0.99243	0.98624	0.98143	0.97799	0.97592	0.97524
51	0.99510	0.99110	0.98798	0.98575	0.98442	0.98397
56	0.99683	0.99424	0.99222	0.99078	0.98991	0.98963
61	0.99795	0.99627	0.99496	0.99403	0.99347	0.99329
66	0.99867	0.99759	0.99674	0.99614	0.99578	0.99565
71	0.99914	0.99844	0.99789	0.99750	0.99727	0.99719
76	0.99944	0.99899	0.99863	0.99838	0.99823	0.99818
81	0.99964	0.99935	0.99912	0.99895	0.99885	0.99882
86	0.99977	0.99958	0.99943	0.99932	0.99926	0.99924
91	0.99985	0.99973	0.99963	0.99956	0.99952	0.99951
96	0.99990	0.99982	0.99976	0.99972	0.99969	0.99968
Expected Value of τ_i	6.14721	9.76618	12.30623	14.00436	14.98402	15.30467
Variance of τ_i	80.37432	115.50017	129.92218	134.83344	135.91264	135.98308

Table 6. Cumulative Distribution of τ_i, Time to Homozygosity (M = 16)

Initial Frequency Generation	i = 1 (i = 15)	i = 2 (i = 14)	i = 3 (i = 13)	i = 4 (i = 12)	i = 5 (i = 11)	i = 6 (i = 10)	i = 7 (i = 9)	i = 8
1	0.35607	0.11807	0.03607	0.01002	0.00249	0.00054	0.00010	0.00003
6	0.74535	0.54778	0.39701	0.28463	0.20394	0.14987	0.11083	0.10872
11	0.83613	0.69708	0.58157	0.48853	0.41707	0.36652	0.33638	0.32637
16	0.88400	0.78385	0.69940	0.63049	0.57702	0.53889	0.51603	0.50842
21	0.91634	0.84389	0.78263	0.73252	0.69357	0.66576	0.64907	0.64351
26	0.93946	0.88700	0.84262	0.80631	0.77807	0.75790	0.74580	0.74177
31	0.95617	0.91818	0.88603	0.85973	0.83928	0.82467	0.81590	0.81298
36	0.96826	0.94074	0.91747	0.89842	0.88361	0.87302	0.86667	0.86456
41	0.97701	0.95709	0.94023	0.92644	0.91571	0.90804	0.90345	0.90191
46	0.98335	0.96892	0.95671	0.94672	0.93896	0.93341	0.93008	0.92897
51	0.98794	0.97749	0.96865	0.96142	0.95579	0.95177	0.94936	0.94856
56	0.99127	0.98370	0.97730	0.97206	0.96798	0.96507	0.96333	0.96275
61	0.99368	0.98820	0.98356	0.97977	0.97681	0.97471	0.97344	0.97302
66	0.99542	0.99145	0.98809	0.98535	0.98321	0.98168	0.98077	0.98046
71	0.99668	0.99381	0.99138	0.98939	0.98784	0.98673	0.98607	0.98585
76	0.99760	0.99552	0.99376	0.99231	0.99119	0.99039	0.98991	0.98975
81	0.99826	0.99675	0.99548	0.99443	0.99362	0.99304	0.99270	0.99258
86	0.99874	0.99765	0.99673	0.99597	0.99538	0.99496	0.99471	0.99463
91	0.99909	0.99830	0.99763	0.99708	0.99666	0.99635	0.99617	0.99611
96	0.99934	0.99877	0.99828	0.99789	0.99758	0.99736	0.99723	0.99718
Expected Value of τ_i	6.76085	11.02290	14.25681	16.71208	18.52639	19.77862	20.51420	20.75691
Variance of τ_i	121.66284	185.60579	219.47065	236.50133	244.10575	246.81785	247.42791	247.46803

Table 7. Exact Values of p_{1M}^n, Probability of Fixation by Generation n (M=12)

Initial Frequency	i = 1	i = 2	i = 3	i = 4	i = 5
Generation					
1	0.00000	0.00000	0.00000	0.00003	0.00024
2	0.00000	0.00001	0.00007	0.00040	0.00175
3	0.00001	0.00017	0.00089	0.00320	0.00919
4	0.00015	0.00100	0.00365	0.01001	0.02309
5	0.00063	0.00304	0.00893	0.02071	0.04171
6	0.00168	0.00655	0.01660	0.03438	0.06306
7	0.00341	0.01145	0.02617	0.04995	0.08559
8	0.00580	0.01753	0.03707	0.06654	0.10829
9	0.00876	0.02448	0.04879	0.08348	0.13049
10	0.01216	0.03200	0.06090	0.10031	0.15181
11	0.01586	0.03984	0.07306	0.11672	0.17203
12	0.01972	0.04777	0.08505	0.13249	0.19105
13	0.02366	0.05564	0.09668	0.14749	0.20884
14	0.02757	0.06332	0.10783	0.16166	0.22540
15	0.03139	0.07072	0.11843	0.17497	0.24077
16	0.03509	0.07779	0.12845	0.18740	0.25500
17	0.03862	0.08448	0.13785	0.19898	0.26815
18	0.04197	0.09078	0.14664	0.20973	0.28028
19	0.04513	0.09669	0.15483	0.21970	0.29146
20	0.04810	0.10220	0.16243	0.22891	0.30175
21	0.05087	0.10733	0.16948	0.23741	0.31122
22	0.05344	0.11209	0.17600	0.24526	0.31992
23	0.05584	0.11649	0.18202	0.25248	0.32792
24	0.05805	0.12056	0.18758	0.25913	0.33527
25	0.06010	0.12432	0.19269	0.26525	0.34201
26	0.06199	0.12779	0.19740	0.27087	0.34821
27	0.06374	0.13098	0.20174	0.27604	0.35389
28	0.06535	0.13391	0.20572	0.28078	0.35911
29	0.06682	0.13662	0.20938	0.28514	0.36389
30	0.06819	0.13910	0.21275	0.28914	0.36828
31	0.06944	0.14138	0.21583	0.29281	0.37230
32	0.07059	0.14347	0.21867	0.29617	0.37600
33	0.07164	0.14540	0.22127	0.29926	0.37938
34	0.07261	0.14716	0.22366	0.30210	0.38248
35	0.07350	0.14878	0.22585	0.30469	0.38533
36	0.07432	0.15027	0.22785	0.30708	0.38794
37	0.07507	0.15163	0.22970	0.30926	0.39033
38	0.07575	0.15288	0.23139	0.31127	0.39253
39	0.07638	0.15403	0.23293	0.31310	0.39454
40	0.07696	0.15508	0.23436	0.31479	0.39638
41	0.07749	0.15604	0.23566	0.31633	0.39807
46	0.07955	0.15979	0.24072	0.32233	0.40463
51	0.08088	0.16221	0.24399	0.32621	0.40888
56	0.08175	0.16379	0.24611	0.32872	0.41162
61	0.08231	0.16480	0.24748	0.33035	0.41340
66	0.08267	0.16546	0.24837	0.33140	0.41455
71	0.08290	0.16589	0.24895	0.33208	0.41530
76	0.08306	0.16616	0.24932	0.33252	0.41578
81	0.08315	0.16634	0.24956	0.33281	0.41609
86	0.08322	0.16645	0.24971	0.33299	0.41630
91	0.08326	0.16653	0.24981	0.33311	0.41643
96	0.08328	0.16658	0.24988	0.33319	0.41651

Table 7. (Continued)

Initial Frequency Generation	i = 6	i = 7	i = 8	i = 9	i = 10	i = 11
1	0.00024	0.00155	0.00771	0.03168	0.11216	0.35200
2	0.00608	0.01799	0.04712	0.11217	0.24710	0.51063
3	0.02268	0.05015	0.10195	0.19397	0.34965	0.60264
4	0.04741	0.08942	0.15804	0.26526	0.42683	0.66313
5	0.07628	0.13007	0.21016	0.32533	0.48632	0.70606
6	0.10648	0.16927	0.25690	0.37578	0.53335	0.73816
7	0.13633	0.20584	0.29829	0.41838	0.57136	0.76308
8	0.16495	0.23940	0.33481	0.45465	0.60268	0.78299
9	0.19190	0.26996	0.36707	0.48580	0.62889	0.79926
10	0.21702	0.29769	0.39563	0.51276	0.65111	0.81279
11	0.24028	0.32281	0.42100	0.53629	0.67018	0.82421
12	0.26175	0.34558	0.44363	0.55696	0.68669	0.83398
13	0.28150	0.36624	0.46387	0.57522	0.70111	0.84242
14	0.29964	0.38499	0.48204	0.59144	0.71380	0.84977
15	0.31631	0.40203	0.49841	0.60591	0.72502	0.85622
16	0.33159	0.41753	0.51318	0.61888	0.73501	0.86192
17	0.34562	0.43166	0.52654	0.63054	0.74393	0.86699
18	0.35848	0.44453	0.53866	0.64106	0.75194	0.87152
19	0.37027	0.45628	0.54966	0.65056	0.75915	0.87557
20	0.38108	0.46701	0.55967	0.65917	0.76565	0.87922
21	0.39098	0.47681	0.56878	0.66699	0.77154	0.88251
22	0.40007	0.48577	0.57709	0.67410	0.77688	0.88549
23	0.40840	0.49396	0.58467	0.68057	0.78172	0.88818
24	0.41603	0.50146	0.59159	0.68647	0.78613	0.89063
25	0.42303	0.50831	0.59791	0.69185	0.79015	0.89286
26	0.42944	0.51459	0.60369	0.69676	0.79381	0.89489
27	0.43532	0.52034	0.60898	0.70124	0.79716	0.89674
28	0.44071	0.52561	0.61382	0.70534	0.80021	0.89842
29	0.44565	0.53043	0.61824	0.70909	0.80300	0.89996
30	0.45018	0.53485	0.62230	0.71253	0.80555	0.90137
31	0.45433	0.53890	0.62601	0.71566	0.80788	0.90266
32	0.45814	0.54261	0.62940	0.71854	0.81001	0.90383
33	0.46163	0.54600	0.63252	0.72117	0.81197	0.90491
34	0.46482	0.54912	0.63537	0.72358	0.81375	0.90589
35	0.46776	0.55197	0.63798	0.72579	0.81539	0.90679
36	0.47044	0.55459	0.64038	0.72781	0.81689	0.90762
37	0.47291	0.55698	0.64257	0.72966	0.81826	0.90838
38	0.47516	0.55918	0.64458	0.73136	0.81952	0.90907
39	0.47723	0.56119	0.64642	0.73292	0.82068	0.90970
40	0.47913	0.56304	0.64811	0.73434	0.82173	0.91028
41	0.48087	0.56473	0.64966	0.73565	0.82270	0.91082
46	0.48762	0.57129	0.65566	0.74071	0.82645	0.91288
51	0.49199	0.57554	0.65954	0.74399	0.82888	0.91422
56	0.49481	0.57829	0.66206	0.74611	0.83045	0.91508
61	0.49664	0.58007	0.66368	0.74748	0.83147	0.91564
66	0.49783	0.58122	0.66474	0.74837	0.83213	0.91600
71	0.49859	0.58197	0.66542	0.74895	0.83255	0.91624
76	0.49909	0.58245	0.66586	0.74932	0.83283	0.91639
81	0.49941	0.58276	0.66614	0.74956	0.83301	0.91649
86	0.49962	0.58296	0.66633	0.74971	0.83312	0.91655
91	0.49975	0.58309	0.66645	0.74981	0.83320	0.91659
96	0.49984	0.58318	0.66652	0.74988	0.83324	0.91662

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Appendix. The Moment Recurrence Relation

A.1. _A useful property of the binomial distribution._ The properties of the binomial distribution (the parameters being specified by the genetic situation) to be developed in this appendix form the cornerstone of the entire development of the work in this paper. The particular property in the binomial case was utilized by A. Robertson (1952) for obtaining expressions for the variances (within and between lines) as inbreeding progresses in a population of limited size.

We will state the following well-known result, without proof, in the form of a lemma.

Lemma 1: If $\{\bar{\underline{X}}_n, \ n \geq 1\}$ is a sequence of random variables with the Markov property, then

$$E(\bar{\underline{X}}_{n+1}^r | \bar{\underline{X}}_0 = i) = E\left[E(\bar{\underline{X}}_{n+1}^r | X_n) | \bar{\underline{X}}_0 = i\right].$$

Theorem 1. If the distribution of $\bar{\underline{X}}_{n+1}$ given $\bar{\underline{X}}_n$ is binomial with probability of success $\bar{\underline{X}}_n / M$, then

(A.1) $$E(\bar{\underline{X}}_{n+1}^r | \bar{\underline{X}}_0 = i) = \sum_{s=1}^{r} a_{rs} (M^{(s)} / M^s) \ E(\bar{\underline{X}}_n^s | \bar{\underline{X}}_0 = i)$$

where a_{rs}, $s=1,2....r$, are Stirling's numbers of the second kind defined by,

$$a_{rs} = \sum_{i=0}^{s-1} \frac{(-1)^i (s-i)^{r-1}}{(s-i-1)! \ i!} \ , \quad s \in \{1,2...r\}.$$

<u>Proof</u>: By definition

$$E(X_{n+1}^r | X_n) = \sum_{j=0}^{M} j^r \binom{M}{j} \left(\frac{\overline{X}_n}{M}\right)^j \left(1 - \frac{\overline{X}_n}{M}\right)^{M-j} .$$

Now for every non-negative integer r the term j^r can be expressed as a linear combination of the factorial powers of j not higher than the rth. That is, letting

$$j^{(s)} = \begin{cases} j(j-1)\cdots(j-s+1), & \text{if } s > 0 \\ 1 & , \text{if } s = 0 \end{cases}$$

there are numbers $a_{r1}, a_{r2}, \ldots, a_{rr}$ such that $j^r = \sum_{s=1}^{r} a_{rs} j^{(s)}$. Hence

$$E(X_{n+1}^r | X_n) = \sum_{j=0}^{M} \sum_{s=1}^{r} a_{rs} j^{(s)} \binom{M}{j} \left(\frac{X_n}{M}\right)^j \left(1 - \frac{X_n}{M}\right)^{M-j}$$

$$= \sum_{s=1}^{r} a_{rs} \sum_{j=s}^{M} j^{(s)} \frac{M!}{j!(M-j)!} \left(\frac{\overline{X}_n}{M}\right)^j \left(1 - \frac{\overline{X}_n}{M}\right)^{M-j}$$

$$= \sum_{s=1}^{r} a_{rs} M^{(s)} \left(\frac{\overline{X}_n}{M}\right)^s \sum_{j=s}^{M} \frac{(M-s)!}{(j-s)!(M-j)!} \left(\frac{X_n}{M}\right)^{j-s} \left(1 - \frac{X_n}{M}\right)^{M-j}$$

$$= \sum_{s=1}^{r} a_{rs} M^{(s)} \left(\frac{\overline{X}_n}{M}\right)^s .$$

Applying lemma 1, it now follows that

$$E(\underline{X}_{n+1}^r | \underline{X}_0 = i) = E\left[\sum_{s=1}^{r} a_{rs} \, M^{(s)} \left(\frac{\overline{X}_n}{M}\right)^s \Big| \underline{X}_0 = i \right],$$

thus giving

$$E(\underline{X}_{n+1}^r | X_0 = i) = \sum_{s=1}^{r} a_{rs} (M^{(s)}/M^s) \, E(\overline{X}_n^s | \underline{X}_0 = i).$$

We see that (A.1) establishes a relation between the rth order moment in the (n+1)th generation and all the moments up to order r in the nth generation. Let $E(\underline{X}_{n+1}^r | \underline{X}_0 = i) = {}_i\mu_{n+1}^r$. Then

$$_i\mu_{n+1} = {}_i\mu_n$$

$$_i\mu_{n+1}^2 = {}_i\mu_n + (1-\tfrac{1}{M}) \, {}_i\mu_n^2$$

$$_i\mu_{n+1}^3 = {}_i\mu_n + 3(1-\tfrac{1}{M}) \, {}_i\mu_n^2 + (1-\tfrac{1}{M})(1-\tfrac{2}{M}) \, {}_i\mu_n^3.$$

and so on.

Putting these relations into matrix notation, noting that $a_{r1} = 1$ and $a_{rr} = 1$ for every r, we get

$$
\begin{bmatrix} {}_i\mu^1_{n+1} \\ \\ {}_i\mu^2_{n+1} \\ \cdot \\ \cdot \\ {}_i\mu^r_{n+1} \\ \cdot \\ \cdot \\ {}_i\mu^M_{n+1} \end{bmatrix}
=
\begin{bmatrix}
1 & 0 & 0 & 0 & & 0 \\
1 & \dfrac{M^{(2)}}{M^2} & 0\cdots\cdots & 0 & \cdots\cdots\cdots & 0 \\
\cdot & & & & & \\
1 & a_{r2}\dfrac{M^{(2)}}{M^2} & \cdots\cdots & \dfrac{M^{(r)}}{M^r} & 0\cdots\cdots & 0 \\
\cdot & & & & & \\
1 & a_{M2}\dfrac{M^{(2)}}{M^2} & \cdots\cdots a_{Mr}\dfrac{M^{(r)}}{M^r} & & \cdots\cdots\dfrac{M^{(M)}}{M^M} &
\end{bmatrix}
\begin{bmatrix} {}_i\mu^1_n \\ \\ {}_i\mu^2_n \\ \cdot \\ \cdot \\ {}_i\mu^r_n \\ \cdot \\ \cdot \\ {}_i\mu^M_n \end{bmatrix}
$$

That is, ${}_iE_{n+1} = C \; {}_iE_n$ where ${}_iE_{n+1}$ is the vector of moments in the (n+1)th generation and C is the matrix of coefficients. By successive iteration we then get ${}_iE_{n+1} = C^{n+1} \; {}_iE_0$, where since the initial number of A-alleles is i, ${}_iE_0 = (i,i^2,\ldots,i^r,\ldots,i^M)'$. As can be seen, in order to find the moments conditional on i in the nth generation we are led to find the nth power of C which, being triangular, is relatively easy to handle. The method will be outlined below.

A.2. <u>The eigenvectors of C</u>. Our objective in this section is to obtain the spectral resolution of C, $C = \displaystyle\sum_{s=1}^{M} \lambda_s U_s V'_s$, where U_s and V'_s are respectively the post- and pre-eigenvectors of C corresponding to the eigenvalue λ_s. Since C is a triangular matrix its eigenvalues are its diagonal elements. Hence the general eigenvalue is $M^{(s)}/M^s$. Since all the eigenvalues are distinct ($M^{(j)}/M^j \neq M^{(i)}/M^i$, $i \neq j$) we know that there exists a matrix π such that

$$
\pi^{-1} C \pi = \operatorname{diag}\left(1, M^{(2)}/M^2, \ldots, M^{(M)}/M^M\right) = \Lambda, \quad \text{say.}
$$

A.2.1. <u>The Post-eigenvectors of C.</u> Let $\lambda_s = M^{(s)}/M^s$ and let $U_s = (u_{1s}, u_{2s}, \ldots u_{Ms})'$ be the corresponding post-eigenvector. Then U_s satisfies $C\,U_s = \lambda_s\,U_s$. In order to obtain $u_{1s}, \ldots u_{Ms}$, the system of equations to be solved is

$$\sum_{i=1}^{j} a_{ji}\,\lambda_i\,u_{is} = \lambda_s u_{js}, \quad j = 1,2\ldots M.$$

It immediately follows then that for $i = 1,2\ldots s-1$, $u_{is} = 0$. The system then reduces to

$$\sum_{i=s}^{j} a_{ji}\,\lambda_i\,u_{is} = \lambda_s\,u_{js}, \quad j = s,\ldots,M.$$

From the above we see that u_{ss} may be chosen arbitrarily. Let us use $u_{ss} = 1$. After transposing and simplifying, we have to solve

(A.2)
$$\sum_{i=s+1}^{j} a_{ji}\,\lambda_i u_{is} + (\lambda_j - \lambda_s)u_{js} = -a_{js}\lambda_s, \quad j=s+1,\ldots,M.$$

Since $(\lambda_j - \lambda_s) \neq 0$ for $i > s+1$ we can successively find $u_{s+1,s}, u_{s+2,s}, \ldots, u_{Ms}$ in that order and thus obtain the vector $U_s = (0,0\ldots,1,u_{s+1,s},\ldots,u_{Ms})'$. In particular, $U_1 = (1,M,M^2,\ldots,M^{M-1})$, as can be shown explicitly (Khazanie, 1965).

A.2.2. <u>The Pre-eigenvectors of C.</u> If $V'_s = (v_{s1}, v_{s2}, \ldots, v_{sM})$ represents the pre-eigenvector corresponding to λ_s then V'_s satisfies $V'_s\,C = \lambda_s V'_s$. The system of equations to be solved is

$$\sum_{i=j}^{M} a_{ij} \lambda_j v_{si} = \lambda_s v_{sj}, \quad j = 1,2,\ldots,M .$$

From equations $j = s+1,\ldots,M$ immediately follows $v_{sj} = 0$ for $j > s$.
As a result the system reduces to

$$\sum_{i=j}^{s} a_{ij} \lambda_j v_{si} = \lambda_s v_{sj} \quad j = 1,2,\ldots,s.$$

Also, it can be seen from equation s that v_{ss} can be chosen arbitrarily.
Setting $v_{ss} = 1$ and transposing as in the earlier case we get

$$(A.3) \qquad (\lambda_j - \lambda_s) v_{sj} + \sum_{i=j+1}^{s-1} a_{ij} \lambda_j v_{si} = -a_{sj} \lambda_j, \quad j=1,2,\ldots,s-1 .$$

Now $(\lambda_j - \lambda_s) \neq 0$ if $j \neq s$. Therefore, we can first obtain $v_{s,s-1}$

by means of the relation $v_{s,s-1} = \dfrac{-a_{s,s-1} \lambda_{s-1}}{\lambda_{s-1} - \lambda_s}$ and then working backwards

successively get V'_s as $(v_{s1}, v_{s2}, \ldots, v_{s,s-1}, 1, 0 \ldots 0)$.

small s