

APPLICATIONS OF SOME FINITE MARKOV CHAIN THEORIES TO SOME GENETIC PROBLEMS

Parent-Offspring Mating Type Model with Selection⁽¹⁾⁽²⁾

W. Y. TAN

*Department of Pure and Applied Mathematics, Washington State
University, Pullman, Washington, U. S. A.*

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1. Introduction

This is one of the two papers in which we utilize some finite Markov chain theories to study the effect of selection on the absorption probabilities and the change of frequencies in some inbreeding genetic systems. The present paper is basically concerned with the parent-offspring model as discussed in Horner (1956) and Karlin (1968). The second paper will be concerned with the two locus linkage selfing model as discussed in Nelder (1952) and Karlin (1968). Similar consideration of the application of some finite Markov chain theories to Sib-mating model has also been discussed in Bosso, Sorarrain and Favret (1969).

2. Some finite Markov chain results

Consider a finite Markov chain $X(t)$ with stationary transition probabilities and discrete time $t=0, 1, 2, \dots$. In this section we shall derive some simple formulas for the computations of various absorption probabilities, mean absorption times and variances of first absorption times, as well as absolute probability distributions. These results will then be utilized in our models to study the effect of selection on the changes of absorption probabilities and type frequencies.

Let C_1, C_2, \dots, C_k be the disjoint closed sets of persistent states and T the class of transient states. Then the transition probability matrix (one-step) P can be written in the following canonical form as

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- (1) A paper presented at the 9th Annual Symposium on Biomathematics and Computer Sciences, in the Life Sciences, held at University of Texas, Houston, Texas, March 22-24, 1971.
 - (2) This paper is dedicated to Dr. H. W. Li for his inspiring leadership during his tenure of office as Director of the Institute of Botany, Academia Sinica.

$$P = \begin{pmatrix} P_1 & & & & & \\ & P_2 & & & & \underline{0} \\ & & \cdot & & & \\ \underline{0} & & & \cdot & & \\ & & & & \cdot & \\ & & & & & P_k \\ R_1 & R_2 & \dots & R_k & & Q \end{pmatrix} \tag{2.1}$$

where P_j is the transition matrix corresponding to the closed set C_j and Q the matrix of transition probabilities from transient states to transient states.

From (2.1), we have then

$$P^n = \begin{pmatrix} P_1^n & & & & & \\ & P_2^n & & & & \underline{0} \\ & & \cdot & & & \\ \underline{0} & & & \cdot & & \\ & & & & \cdot & \\ & & & & & P_k^n \\ H_1^{(n)} & H_2^{(n)} & \dots & H_k^{(n)} & & Q^n \end{pmatrix} \tag{2.2}$$

where $H_j^{(n)} = R_j$ and

$H_j^{(n)} = \sum_{s=0}^{n-1} Q^s R_j P_j^{n-1-s}$ is the matrix of absorption probabilities of transient states into states of C_j at and before time n .

(i) The absorption probabilities and mean absorption times and variances of first absorption times.

Let m_j be the number of states in C_j and t the number of states in T . Furthermore, let $\underline{1}_m$ be the $m \times 1$ vector of 1's and put,

$\underline{h}_j^{(n)}$ = Vector of absorption probabilities of the transient states into C_j at and before time n ,

$\underline{\rho}_j$ = Vector of ultimate absorption probabilities of the transient states C_j ,

$\underline{\delta}_j^{(n)}$ = Vector of first absorption probabilities of the transient states into C_j at time n ,

$\underline{\delta}^{(n)} = \sum_{j=1}^k \underline{\delta}_j^{(n)}$ = Vector of first absorption probabilities of the transient states into persistent states at time n ,

\underline{U} = Vector of mean absorption times of the transient states into persistent states,

\underline{V} = Vector of variances of first absorption times of the transient states into persistent states,

$\underline{\theta}(s)$ = Vector of the probability generating functions of the first absorption times of the transient states into persistent states.

Then, since $P_j^m \underline{l}_{m,j} = \underline{l}_{m,j}$ for all integer $m > 0$ and since the absolute value of the eigenvalues of Q is less than 1 (see Karlin (1966), for example), we have

$$\underline{h}_j^{(n)} = H_j^{(n)} \underline{l}_{m,j} = (I_t + Q + \dots + Q^{n-1}) R_j \underline{l}_{m,j} = (I_t - Q)^{-1} (I_t - Q^n) R_j \underline{l}_{m,j}, \quad (2.3)$$

$$\underline{\rho}_j = \lim_{n \rightarrow \infty} \underline{h}_j^{(n)} = (I_t - Q)^{-1} R_j \underline{l}_{m,j}, \quad (2.4)$$

$$\underline{\delta}_j^{(n)} = Q^{n-1} R_j \underline{l}_{m,j}, \quad (2.5)$$

$$\underline{\delta}^{(n)} = Q^{n-1} \sum_{j=1}^k R_j \underline{l}_{m,j} = Q^{n-1} (I_t - Q) \underline{l}_t \quad (2.6)$$

$$\underline{U} = \sum_{n=1}^{\infty} n \underline{\delta}^{(n)} = \sum_{n=1}^{\infty} n Q^{n-1} (I_t - Q) \underline{l}_t = (I_t - Q)^{-2} (I_t - Q) \underline{l}_t = (I_t - Q)^{-1} \underline{l}_t, \quad (2.7)$$

$$\begin{aligned} \underline{V} &= \sum_{n=1}^{\infty} n^2 Q^{n-1} (I_t - Q) \underline{l}_t - \underline{U}_{s,q} \\ &= \left\{ \sum_{n=1}^{\infty} n(n-1) Q^{n-1} + \sum_{n=1}^{\infty} n Q^{n-1} \right\} (I_t - Q) \underline{l}_t - \underline{U}_{s,q} \\ &= \{2Q(I_t - Q)^{-1} + I_t\} (I_t - Q)^{-1} \underline{l}_t - \underline{U}_{s,q} \\ &= \{2(I_t - Q)^{-1} - I_t\} \underline{U} - \underline{U}_{s,q} \end{aligned} \quad (2.8)$$

where $\underline{U}_{s,q} = (U_1^2, U_2^2, \dots, U_t^2)$ with $\underline{U}' = (U_1, U_2, \dots, U_t)$, and

$$\underline{\theta}(s) = \sum_{n=1}^{\infty} s^n Q^{n-1} (I_t - Q) \underline{l}_t = s(I_t - sQ)^{-1} (I_t - Q) \underline{l}_t \quad (2.9)$$

(ii) Computations using spectral expansion of Q .

Suppose now Q is diagonal so that, using lemma 1 as given in the appendix,

$$Q^n = \sum_{i=1}^l \lambda_i^n A_i \quad \text{and} \quad (I_t - Q)^{-1} = \sum_{i=1}^l \frac{1}{1 - \lambda_i} A_i,$$

where $\lambda_1, \lambda_2, \dots, \lambda_l$ are the distinct eigenvalues of Q and

$$A_i = \prod_{\substack{j=1 \\ j \neq i}}^l \frac{1}{(\lambda_i - \lambda_j)} (Q - \lambda_j I_t), \quad i=1, 2, \dots, l.$$

Then, (2.3)–(2.9) reduce respectively to

$$\underline{h}_j^{(n)} = \sum_{i=1}^l \frac{1 - \lambda_i^n}{1 - \lambda_i} A_i R_j \underline{l}_{m,j} \quad (2.10)$$

$$\underline{\rho}_j = \sum_{i=1}^l \frac{1}{1 - \lambda_i} A_i R_j \underline{l}_{m,j} \quad (2.11)$$

$$\underline{\delta}_j^{(n)} = \sum_{i=1}^l \lambda_i^{n-1} A_i R_j \underline{l}_{m,j} \quad (2.12)$$

3. The parent-offspring mating type model with selection

(a) The model.

We consider a single locus with two alleles A:a and the mating is such that the child mates always with the younger parent. Then there are 9 states in the state space and the states are the frequencies of the mating types

Parent \times Offspring

AA \times AA

aa \times aa

AA \times Aa

aa \times Aa

Aa \times AA

Aa \times aa

Aa \times Aa

aa \times AA

AA \times aa

To allow for the consideration of the effect of selection, it is assumed in this preliminary report that there is no difference in effects of selection regarding sex; and furthermore, the homozygous genotypes have the same selective values. Then, with no loss of generality, the selective values of the three genotypes can be written as

Selective values

AA	x
Aa	1
aa	x ,

where $x \geq 0$.

Notice that $x=1$ corresponds to no selection; $x < 1$ heterozygote superior and $x > 1$, heterozygote inferior. For $x=1$, the above model has been discussed in detail in Horner (1956) and Karlin (1968).

The transition matrix for the above model is given by

The eigenvalues of Q are readily obtained as $\lambda_1=0$, $\lambda_2=-\frac{\sqrt{x}}{1+x}$, $\lambda_3=\frac{\sqrt{x}}{1+x}$,
 $\lambda_4=\frac{1}{2(1+x)}(1-\sqrt{1+4x})=\frac{\delta_1}{1+x}$ and $\lambda_5=\frac{1}{2(1+x)}(1+\sqrt{1+4x})=\frac{\delta_2}{1+x}$.

Using lemma 2 as given in the appendix and noting that $\sum_{j=1}^5 A_j = I_7$, we have for the spectral matrices of Q :

$$A_1 = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{1}{2x} & \frac{1}{2x} & 0 & 0 & \frac{1}{x} & 0 & 0 \\ \frac{1}{2x} & \frac{1}{2x} & 0 & 0 & \frac{1}{x} & 0 & 0 \\ -\frac{1}{2} & -\frac{1}{2} & 0 & 0 & 1 & 0 & 0 \\ \frac{1}{2} \frac{1+x}{x} & \frac{1}{2} \frac{1+x}{x} & -(1+x) & 0 & \frac{1+x}{x} & 1 & 0 \\ \frac{1}{2} \frac{1+x}{x} & \frac{1}{2} \frac{1+x}{x} & 0 & -(1+x) & \frac{1+x}{x} & 0 & 1 \end{pmatrix}$$

$$A = \frac{1}{4\sqrt{x}} \begin{pmatrix} \sqrt{x} & -\sqrt{x} & -x & x & 0 & 0 & 0 \\ -\sqrt{x} & \sqrt{x} & x & -x & 0 & 0 & 0 \\ -1 & 1 & \sqrt{x} & -\sqrt{x} & 0 & 0 & 0 \\ 1 & -1 & -\sqrt{x} & \sqrt{x} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ -(1+x) & (1+x) & \sqrt{x}(1+x) & -\sqrt{x}(1+x) & 0 & 0 & 0 \\ (1+x) & -(1+x) & -\sqrt{x}(1+x) & \sqrt{x}(1+x) & 0 & 0 & 0 \end{pmatrix}$$

$$A_3 = \frac{1}{4\sqrt{x}} \begin{pmatrix} \sqrt{x} & -\sqrt{x} & x & -x & 0 & 0 & 0 \\ -\sqrt{x} & \sqrt{x} & -x & x & 0 & 0 & 0 \\ 1 & -1 & \sqrt{x} & -\sqrt{x} & 0 & 0 & 0 \\ -1 & 1 & -\sqrt{x} & \sqrt{x} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ (1+x) & -(1+x) & \sqrt{x}(1+x) & -\sqrt{x}(1+x) & 0 & 0 & 0 \\ -(1+x) & (1+x) & -\sqrt{x}(1+x) & \sqrt{x}(1+x) & 0 & 0 & 0 \end{pmatrix}$$

$$A_4 = \frac{1}{\delta_1(\delta_1 - \delta_2)} \begin{pmatrix} \frac{x}{2} \delta_1 & \frac{x}{2} \delta_1 & \frac{x}{2} \delta_1^2 & \frac{x}{2} \delta_1^2 & \delta_1^2 & 0 & 0 \\ \frac{x}{2} \delta_1 & \frac{x}{2} \delta_1 & \frac{x}{2} \delta_1^2 & \frac{x}{2} \delta_1^2 & \delta_1^2 & 0 & 0 \\ \frac{x}{2} & \frac{x}{2} & \frac{x}{2} \delta_1 & \frac{x}{2} \delta_1 & \delta_1 & 0 & 0 \\ \frac{x}{2} & \frac{x}{2} & \frac{x}{2} \delta_1 & \frac{x}{2} \delta_1 & \delta_1 & 0 & 0 \end{pmatrix}$$

$$\begin{pmatrix} \frac{x}{2}\delta_1 & \frac{x}{2}\delta_1 & \frac{x}{2}\delta_1^2 & \frac{x}{2}\delta_1^2 & \delta_1^2 & 0 & 0 \\ \frac{x}{2}(1+x) & \frac{x}{2}(1+x) & \frac{x}{2}\delta_1(1+x) & \frac{x\delta_1}{2}(1+x) & \delta_1(1+x) & 0 & 0 \\ \frac{x}{2}(1+x) & \frac{x}{2}(1+x) & \frac{x}{2}\delta_1(1+x) & \frac{x\delta_1}{2}(1+x) & \delta_1(1+x) & 0 & 0 \end{pmatrix}$$

and

$$A_5 = \frac{1}{\delta_2^2(\delta_2 - \delta_1)} \begin{pmatrix} \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2^2 & \frac{x}{2}\delta_2^2 & \delta_2^2 & 0 & 0 \\ \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2^2 & \frac{x}{2}\delta_2^2 & \delta_2^2 & 0 & 0 \\ \frac{x}{2} & \frac{x}{2} & \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2 & \delta_2 & 0 & 0 \\ \frac{x}{2} & \frac{x}{2} & \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2 & \delta_2 & 0 & 0 \\ \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2 & \frac{x}{2}\delta_2^2 & \frac{x}{2}\delta_2^2 & \delta_2^2 & 0 & 0 \\ \frac{1}{2}x(1+x) & \frac{1}{2}x(1+x) & \frac{x\delta_2}{2}(1+x) & \frac{x\delta_2}{2}(1+x) & \delta_2(1+x) & 0 & 0 \\ \frac{1}{2}x(1+x) & \frac{1}{2}x(1+x) & \frac{x\delta_2}{2}(1+x) & \frac{x\delta_2}{2}(1+x) & \delta_2(1+x) & 0 & 0 \end{pmatrix}$$

(b) The absorption probabilities

Using the above results and formulale (2.11), we obtain the respective vectors of ultimate absorption probabilities into $AA \times AA$ and $aa \times aa$ given the transient states as

$$\rho_{(1)} = \begin{pmatrix} \frac{1}{2} + \frac{1}{2} \frac{x^2}{1+x+x^2} \\ \frac{1}{2} - \frac{1}{2} \frac{x^2}{1+x+x^2} \\ \frac{1}{2} + \frac{1}{2} \frac{x+x^2}{1+x+x^2} \\ \frac{1}{2} - \frac{1}{2} \frac{x+x^2}{1+x+x^2} \\ \frac{1}{2} \\ \frac{1}{2} + \frac{1}{2} \frac{x^2}{1+x+x^2} \\ \frac{1}{2} - \frac{1}{2} \frac{x^2}{1+x+x^2} \end{pmatrix} \quad \text{and} \quad \rho_{(2)} = \begin{pmatrix} \frac{1}{2} - \frac{1}{2} \frac{x^2}{1+x+x^2} \\ \frac{1}{2} + \frac{1}{2} \frac{x^2}{1+x+x^2} \\ \frac{1}{2} - \frac{1}{2} \frac{x+x^2}{1+x+x^2} \\ \frac{1}{2} + \frac{1}{2} \frac{x+x^2}{1+x+x^2} \\ \frac{1}{2} \\ \frac{1}{2} - \frac{1}{2} \frac{x^2}{1+x+x^2} \\ \frac{1}{2} + \frac{1}{2} \frac{x^2}{1+x+x^2} \end{pmatrix}$$

It is easily seen that both $\frac{x^2}{1+x+x^2}$ and $\frac{x+x^2}{1+x+x^2}$ are monotonic increasing functions of x for $x \geq 0$, and both = 0 if $x=0$ (homozygotes lethal) and both $\uparrow 1$ as $x \rightarrow \infty$. Hence,

$$\rho'_{(1)} = \rho'_{(2)} = \left(\frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2}, \frac{1}{2} \right) \text{ if } x=0, \text{ and}$$

$$\rho'_{(1)} \rightarrow (1, 0, 1, 0, \frac{1}{2}, 1, 0) \text{ and}$$

$$\rho'_{(2)} \rightarrow (0, 1, 0, 1, \frac{1}{2}, 0, 1), \text{ as } x \rightarrow \infty.$$

Moreover, the following conclusions are trivial:

(a) The effect of selection on the ultimate absorption into AA×AA is opposite to the effect of selection on the ultimate absorption into aa×aa. This follows from the fact that the ultimate absorption probabilities into AA×AA and into aa×aa sum to 1.

(b) The ultimate absorption probabilities into AA×AA given initially AA×Aa, Aa×AA and aa×AA (or the ultimate absorption probabilities into aa×Aa, Aa×aa and AA×aa) increase with x and hence are greater than those of no selection case ($x=1$) if $x>1$ (homozygotes superior) and less than those of no selection case if $x<1$ (heterozygotes superior).

(c) Given initially Aa×Aa, the ultimate absorption probabilities into AA×AA and aa×aa are equal and are not affected by selection.

Given in Table 1 are the ultimate absorption probabilities into AA×AA ($\rho_{(1)}$) and into aa×aa ($\rho_{(2)}$) for $x=0, 0.5, 1.0, 1.5, 2, 2.5$ and 3.0 .

Table 1. *Ultimate absorption probabilities into AA×AA ($\rho_{(1)}$) and into aa×aa ($\rho_{(2)}$) for various values of x .*

	$x=0$.5	1.0	1.5	2.0	2.5	3.0	
AA × Aa	$\rho_{(1)}$	0.5	0.5714	0.6667	0.7368	0.7857	0.8205	0.8462
	$\rho_{(2)}$	0.5	0.4286	0.3333	0.2632	0.2143	0.1795	0.1538
aa × Aa	$\rho_{(1)}$	0.5	0.4286	0.3333	0.2632	0.2143	0.1795	0.1538
	$\rho_{(2)}$	0.5	0.5714	0.6667	0.7368	0.7857	0.8205	0.8462
Aa × AA	$\rho_{(1)}$	0.5	0.7143	0.8333	0.8947	0.9286	0.9487	0.9615
	$\rho_{(2)}$	0.5	0.2857	0.1667	0.1053	0.0714	0.0513	0.0385
Aa × aa	$\rho_{(1)}$	0.5	0.2857	0.1667	0.1053	0.0714	0.0513	0.0385
	$\rho_{(2)}$	0.5	0.7143	0.8333	0.8947	0.9286	0.9487	0.9615
Aa × Aa	$\rho_{(1)}$	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	$\rho_{(2)}$	0.5	0.5	0.5	0.5	0.5	0.5	0.5
aa × AA	$\rho_{(1)}$	0.5	0.5714	0.6667	0.7368	0.7857	0.8205	0.8462
	$\rho_{(2)}$	0.5	0.4286	0.3333	0.2632	0.2143	0.1795	0.1538
AA × aa	$\rho_{(1)}$	0.5	0.4286	0.3333	0.2632	0.2143	0.1795	0.1538
	$\rho_{(2)}$	0.5	0.5714	0.6667	0.7363	0.7857	0.8205	0.8462

Using (2.10), the vectors of absorption probabilities into AA×AA ($h_1^{(n)}$) and into aa×aa ($h_2^{(n)}$) at and before time n are obtained respectively as

$$h_1^{(n)} = \rho_{(1)} - \frac{1}{2(1+x)^n} \{\Delta_n + \tilde{r}_n\} \quad \text{and} \quad h_2^{(n)} = \rho_{(2)} - \frac{1}{2(1+x)^n} \{\Delta_n - \tilde{r}_n\},$$

where
$$\tilde{r}'_n = \frac{x^{(n+2)/2}}{1+x+x^2} (r_n \sqrt{x}, -r_n \sqrt{x}, r_{n-1}, -r_{n-1}, 0, (1+x)r_{n-1}, -(1+x)r_{n-1}),$$

$$\tilde{\Delta}'_n = \frac{1}{\Delta_1} (\Delta_{n+2}, \Delta_{n+2}, \Delta_{n+1}, \Delta_{n+1}, \Delta_{n+2}, (1+x)\Delta_{n+1}, (1+x)\Delta_{n+1}),$$

$$r_n = \begin{cases} \sqrt{x} & \text{if } n=0 \text{ and even } > 0 \\ (1+x) & \text{if } n \text{ is odd } > 0 \end{cases}, \quad \text{and}$$

$$\Delta_n = \delta_1^n - \delta_2^n.$$

To see the effect of selection on the absorption probabilities, we notice that $\Delta_n/\Delta_1 \geq 0$ and \uparrow with x for $x \geq 0$ if $n \geq 2$; and $\frac{r_n x^{(n+3)/2}}{1+x+x^2}, \frac{r_{n-1} x^{(n+2)/2}}{1+x+x^2}$ and $\frac{r_{n-1}(1+x)x^{(n+2)/2}}{1+x+x^2}$ are all \uparrow with x for $x \geq 0$ and $n \geq 1$, and ≥ 0 for all $x \geq 0$ and all $n \geq 1$. It follows that for each $n \geq 1$ fixed, the absorption probabilities into $AA \times AA$ given initially $AA \times Aa, Aa \times AA$ and $aa \times AA$ (or the absorption probabilities into $aa \times aa$ given initially $aa \times Aa, Aa \times aa$ and $AA \times aa$) increase steadily with x for $x \geq 0$. Moreover, since $\frac{\Delta_{n+2}}{\Delta_1} - r_n \frac{x^{(n+3)/2}}{1+x+x^2}, \frac{\Delta_{n+1}}{\Delta_1} - r_{n-1} \frac{x^{(n+2)/2}}{1+x+x^2}$ and $\frac{\Delta_{n+1}}{\Delta_1} - r_{n-1} \frac{(1+x)x^{(n+2)/2}}{1+x+x^2}$ increase first with x and then decrease with x for $x \geq 0$ and for each n fixed, so are the absorption probabilities into $aa \times aa$ given initially $AA \times Aa$ and $aa \times AA$ (or into $AA \times AA$ given initially $aa \times Aa, Aa \times aa$ and $AA \times aa$). For $x=0, \frac{\Delta_n}{\Delta_1} = 1$ and $\tilde{r}_n = 0$ for all $n \geq 1$ so that $\tilde{h}_1^{(n)} = \tilde{h}_2^{(n)} = 0$ for all n . Given in Table 2 are the numerical values of $x=0.5, 1, 1.5$ and $n=1, 2, \dots, 10$. It is observed that the absorption probabilities increase steadily with n for each $x \geq 0$ fixed as it is expected intuitively.

Using (2.12), we obtain the respective first time absorption vectors at time n into $AA \times AA$ ($\delta_1^{(n)}$) and into $aa \times aa$ ($\delta_2^{(n)}$) as:

$$\delta_1^{(1)'} = (0, 0, \frac{x}{1+x}, 0, 0, 0, 0),$$

$$\delta_2^{(1)'} = (0, 0, 0, \frac{x}{1+x}, 0, 0, 0) \quad \text{and for } n \geq 2,$$

$$\delta_1^{(n)} = \frac{x}{4(1+x)^n} \{2x\tilde{\Delta}_{n-3} + \tilde{\epsilon}_n\} \quad \text{and}$$

$$\delta_2^{(n)} = \frac{x}{4(1+x)^n} \{2x\tilde{\Delta}_{n-3} + \tilde{\epsilon}_n\}, \quad \text{where}$$

$$\tilde{\epsilon}'_n = x^{\frac{n-1}{2}} (\sqrt{x}\epsilon_n, -\sqrt{x}\epsilon_n, \epsilon_{n-1}, -\epsilon_{n-1}, 0, (1+x)\epsilon_{n-1}, -(1+x)\epsilon_{n-1})$$

with
$$\epsilon_n = \begin{cases} 2 & \text{if } n=0 \text{ or even } > 0 \\ 0 & \text{if } n \text{ odd } > 0 \end{cases}$$

Table 2. Absorption probabilities into AA×AA ($h_1^{(n)}$) and into aa×aa ($h_2^{(n)}$) at and before time n for $x=0.5, 1, 1.5$.

	AA×Aa	aa×Aa	Aa×AA	Aa×aa	Aa×Aa	aa×AA	AA×aa
$x=0.5$							
$n=1$	$h_1^{(n)}$	0.0	0.0	0.3333	0.0	0.0	0.0
	$h_2^{(n)}$	0.0	0.0	0.0	0.3333	0.0	0.0
$n=2$	$h_1^{(n)}$	0.1111	0.0	0.3333	0.0	0.0556	0.0
	$h_2^{(n)}$	0.0	0.1111	0.0	0.3333	0.0556	0.0
$n=3$	$h_1^{(n)}$	0.1481	0.0370	0.4074	0.0	0.0926	0.1111
	$h_2^{(n)}$	0.0370	0.1481	0.0	0.4074	0.0926	0.1111
$n=4$	$h_1^{(n)}$	0.1975	0.0617	0.4321	0.0247	0.1296	0.1481
	$h_2^{(n)}$	0.0617	0.1975	0.0247	0.4321	0.1296	0.1481
$n=5$	$h_1^{(n)}$	0.2305	0.0947	0.4650	0.0412	0.1626	0.1975
	$h_2^{(n)}$	0.0947	0.2305	0.0412	0.4650	0.1626	0.1975
$n=6$	$h_1^{(n)}$	0.2634	0.1221	0.4870	0.0631	0.1927	0.2305
	$h_2^{(n)}$	0.1221	0.2634	0.0631	0.4870	0.1927	0.2305
$n=7$	$h_1^{(n)}$	0.2908	0.1495	0.5089	0.0814	0.2202	0.2634
	$h_2^{(n)}$	0.1495	0.2908	0.0814	0.5089	0.2202	0.2634
$n=8$	$h_1^{(n)}$	0.3164	0.1739	0.5272	0.0997	0.2452	0.2908
	$h_2^{(n)}$	0.1739	0.3164	0.0997	0.5272	0.2452	0.2908
$n=9$	$h_1^{(n)}$	0.3392	0.1967	0.5443	0.1159	0.2679	0.3164
	$h_2^{(n)}$	0.1967	0.3392	0.1159	0.5443	0.2679	0.3164
$n=10$	$h_1^{(n)}$	0.3600	0.2173	0.5595	0.1311	0.2887	0.3392
	$h_2^{(n)}$	0.2173	0.3600	0.1311	0.5595	0.2887	0.3392
$x=1$							
$n=1$	$h_1^{(n)}$	0.0	0.0	0.5	0.0	0.0	0.0
	$h_2^{(n)}$	0.0	0.0	0.0	0.5	0.0	0.0
$n=2$	$h_1^{(n)}$	0.25	0.0	0.5	0.0	0.125	0.0
	$h_2^{(n)}$	0.0	0.25	0.0	0.5	0.125	0.0
$n=3$	$h_1^{(n)}$	0.3125	0.0625	0.625	0.0	0.1875	0.25
	$h_2^{(n)}$	0.0625	0.3125	0.0	0.625	0.1875	0.25
$n=4$	$h_1^{(n)}$	0.4063	0.0938	0.6563	0.0313	0.25	0.3125
	$h_2^{(n)}$	0.0938	0.4063	0.0313	0.6563	0.25	0.3125
$n=5$	$h_1^{(n)}$	0.4531	0.1406	0.7031	0.0469	0.2965	0.4063
	$h_2^{(n)}$	0.1406	0.4531	0.0469	0.7031	0.2965	0.4063
$n=6$	$h_1^{(n)}$	0.5	0.1719	0.7266	0.0703	0.3359	0.4531
	$h_2^{(n)}$	0.1719	0.5	0.0703	0.7266	0.3359	0.4531
$n=7$	$h_1^{(n)}$	0.5313	0.2031	0.75	0.0859	0.3672	0.5
	$h_2^{(n)}$	0.2031	0.5313	0.0859	0.75	0.3672	0.5
$n=8$	$h_1^{(n)}$	0.5586	0.2266	0.7656	0.1016	0.3926	0.5313
	$h_2^{(n)}$	0.2266	0.5586	0.1016	0.7656	0.3926	0.5313
$n=9$	$h_1^{(n)}$	0.5791	0.2471	0.7793	0.1133	0.4131	0.5586
	$h_2^{(n)}$	0.2471	0.5791	0.1133	0.7793	0.4131	0.5586

	AA × Aa	aa × Aa	Aa × AA	Aa × aa	Aa × Aa	aa × AA	AA × aa
$n=10$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.5962	0.2632	0.7896	0.1235	0.4297	0.5791
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.2632	0.5962	0.1235	0.7896	0.4297	0.2471
$x=1.5$							
$n=1$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.0	0.0	0.6	0.0	0.0	0.0
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.0	0.0	0.0	0.6	0.0	0.0
$n=2$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.36	0.0	0.6	0.0	0.18	0.0
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.0	0.36	0.0	0.6	0.18	0.0
$n=3$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.432	0.072	0.744	0.0	0.252	0.36
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.072	0.432	0.0	0.744	0.252	0.36
$n=4$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.5472	0.1008	0.7728	0.0288	0.324	0.432
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.1008	0.5472	0.0288	0.7728	0.324	0.432
$n=5$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.5933	0.1469	0.8189	0.0403	0.3701	0.5472
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.1469	0.5933	0.0403	0.8189	0.3701	0.1008
$n=6$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.6394	0.1722	0.8373	0.0588	0.4058	0.5933
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.1722	0.6394	0.0588	0.8373	0.4058	0.1469
$n=7$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.6647	0.1976	0.8557	0.0689	0.4311	0.6394
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.1976	0.6647	0.0689	0.8557	0.4311	0.1722
$n=8$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.6850	0.2138	0.8659	0.0790	0.4498	0.6647
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.2138	0.6850	0.0790	0.8659	0.4498	0.1976
$n=9$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.6995	0.2274	0.8744	0.0855	0.4634	0.6850
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.2274	0.6995	0.0855	0.8744	0.4634	0.2138
$n=10$	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.71	0.2367	0.8798	0.0909	0.4733	0.6995
	$\begin{cases} h_1^{(n)} \\ h_2^{(n)} \end{cases}$	0.2367	0.71	0.0909	0.8798	0.4733	0.2274

From above it is obvious that $\delta_1^{(n)} = \delta_2^{(n)} = 0$ if $x=0$ while the change of the first time absorption probabilities with respect to x and n is determined by the functions ϵ_n and Δ_n/Δ_1 and by the initially given mating types. For each n fixed, the general picture appears to be that the first time absorption probabilities increase first with x and then decrease as x increases. For each x fixed, the first time absorption probabilities in general progress downward as n increases in a zigzag manner such that it may not decrease in any two adjacent times; it decreases however in each of the subsequences $\{2m\}$, and $\{2m+1\}$, $m=0, 1, 2, \dots$. Furthermore, from the definition of ϵ_n , it follows that at any even time the first time absorption probabilities into $AA \times AA$ and into $aa \times aa$ are equal if given initially the mating types $Aa \times AA$, $Aa \times aa$, $Aa \times AA$, $aa \times AA$ and $AA \times aa$ while at any odd time, the first time absorption probabilities into the two absorbing classes are equal if given initially the mating types $AA \times Aa$ and $aa \times Aa$. Given in table 3 are the respective first time absorption probabilities into $AA \times AA$ and $aa \times aa$ for $x=0.5, 1, 1.5$ and 2 and for $n=2, 3, 4, 5, 6, 7, 8$.

Table 3. First time absorption probabilities into AA×AA ($\delta_1^{(n)}$) and into aa×aa ($\delta_2^{(n)}$) at time n for $x=0.5, 1, 1.5, 2.0$ and $n=2, 3, 4, 5, 6, 7, 8$.

$\delta_1^{(n)}$	AA × Aa	aa × Aa	Aa × AA	Aa × aa	Aa × Aa	aa × AA	AA × aa
$n=2$							
$x=0.5$	0.1111	0.0000	0.0000	0.0000	0.0556	0.0000	0.0000
$x=1.0$	0.2500	0.0000	0.0000	0.0000	0.1250	0.0000	0.0000
$x=1.5$	0.3600	0.0000	0.0000	0.0000	0.1800	0.0000	0.0000
$x=2.0$	0.4444	0.0000	0.0000	0.0000	0.2222	0.0000	0.0000
$n=3$							
$x=0.5$	0.0370	0.0370	0.0741	0.0000	0.0370	0.1111	0.0000
$x=1.0$	0.0625	0.0625	0.1250	0.0000	0.0625	0.2500	0.0000
$x=1.5$	0.0720	0.0720	0.1440	0.0000	0.0720	0.3600	0.0000
$x=2.0$	0.0741	0.0741	0.1481	0.0000	0.0741	0.4444	0.0000
$n=4$							
$x=0.5$	0.0494	0.0247	0.0247	0.0247	0.0370	0.0370	0.0370
$x=1.0$	0.0937	0.0312	0.0313	0.0313	0.0625	0.0625	0.0625
$x=1.5$	0.1152	0.0288	0.0288	0.0288	0.0720	0.0720	0.0720
$x=2.0$	0.1235	0.0247	0.0247	0.0247	0.0741	0.0741	0.0741
$n=5$							
$x=0.5$	0.0329	0.0329	0.0329	0.0165	0.0329	0.0494	0.0247
$x=1.0$	0.0469	0.0466	0.0469	0.0156	0.0469	0.0937	0.0312
$x=1.5$	0.0461	0.0461	0.0461	0.0115	0.0461	0.1152	0.0288
$x=2.0$	0.0412	0.0412	0.0412	0.0082	0.0412	0.1235	0.0247
$n=6$							
$x=0.5$	0.0329	0.0274	0.0219	0.0219	0.0302	0.0329	0.0329
$x=1.0$	0.0469	0.0312	0.0234	0.0234	0.0391	0.0469	0.0469
$x=1.5$	0.0461	0.0253	0.0184	0.0184	0.0357	0.0461	0.0461
$x=2.0$	0.0412	0.0192	0.0137	0.0137	0.0302	0.0412	0.0412
$n=7$							
$x=0.5$	0.0274	0.0274	0.0219	0.0183	0.0274	0.0329	0.0274
$x=1.0$	0.0312	0.0312	0.0234	0.0156	0.0312	0.0469	0.0312
$x=1.5$	0.0253	0.0253	0.0184	0.0101	0.0253	0.0461	0.0253
$x=2.0$	0.0192	0.0192	0.0137	0.0064	0.0192	0.0412	0.0192
$n=8$							
$x=0.5$	0.0256	0.0244	0.0183	0.0183	0.0250	0.0274	0.0274
$x=1.0$	0.0273	0.0234	0.0156	0.0156	0.0254	0.0312	0.0312
$x=1.5$	0.0212	0.0162	0.0101	0.0101	0.0187	0.0253	0.0253
$x=2.0$	0.0135	0.0107	0.0064	0.0064	0.0131	0.0192	0.0192
$n=2$							
$x=0.5$	0.0000	0.1111	0.0000	0.0000	0.0556	0.0000	0.0000

$\delta_2^{(n)}$	AA × Aa	aa × Aa	Aa × AA	Aa × aa	Aa × Aa	aa × AA	AA × aa
$x=1.0$	0.0000	0.2500	0.0000	0.0000	0.1250	0.0000	0.0000
$x=1.5$	0.0000	0.3600	0.0000	0.0000	0.1800	0.0000	0.0000
$x=2.0$	0.0000	0.4444	0.0000	0.0000	0.2222	0.0000	0.0000
$n=3$							
$x=0.5$	0.0370	0.0370	0.0000	0.0741	0.0370	0.0000	0.1111
$x=1.0$	0.0625	0.0625	0.0000	0.1250	0.0625	0.0000	0.2500
$x=1.5$	0.0720	0.0720	0.0000	0.1440	0.0720	0.0000	0.3600
$x=2.0$	0.0741	0.0741	0.0000	0.1481	0.0741	0.0000	0.4444
$n=4$							
$x=0.5$	0.0247	0.0494	0.0247	0.0247	0.0370	0.0370	0.0370
$x=1.0$	0.0312	0.0937	0.0313	0.0313	0.0625	0.0625	0.0625
$x=1.5$	0.0288	0.1152	0.0288	0.0288	0.0720	0.0720	0.0720
$x=2.0$	0.0247	0.1235	0.0247	0.0247	0.0741	0.0741	0.0741
$n=5$							
$x=0.5$	0.0329	0.0329	0.0165	0.0329	0.0329	0.0247	0.0494
$x=1.0$	0.0469	0.0469	0.0156	0.0569	0.0469	0.0312	0.0937
$x=1.5$	0.0461	0.0461	0.0115	0.0461	0.0461	0.0288	0.1152
$x=2.0$	0.0412	0.0412	0.0082	0.0412	0.0412	0.0247	0.1235
$n=6$							
$x=0.5$	0.0274	0.0329	0.0219	0.0219	0.0302	0.0329	0.0329
$x=1.0$	0.0312	0.0469	0.0234	0.0234	0.0391	0.0469	0.0469
$x=1.5$	0.0253	0.0461	0.0184	0.0184	0.0357	0.0461	0.0461
$x=2.0$	0.0192	0.0412	0.0137	0.0137	0.0302	0.0412	0.0412
$n=7$							
$x=0.5$	0.0274	0.0274	0.0183	0.0219	0.0274	0.0274	0.0329
$x=1.0$	0.0312	0.0312	0.0156	0.0234	0.0312	0.0312	0.0469
$x=1.5$	0.0253	0.0253	0.0101	0.0184	0.0253	0.0253	0.0461
$x=2.0$	0.0192	0.0192	0.0064	0.0137	0.0192	0.0192	0.0412
$n=8$							
$x=0.5$	0.0244	0.0256	0.0183	0.0183	0.0250	0.0274	0.0274
$x=1.0$	0.0234	0.0273	0.0156	0.0156	0.0254	0.0312	0.0312
$x=1.5$	0.0162	0.0212	0.0101	0.0101	0.0187	0.0293	0.0253
$x=2.0$	0.0107	0.0155	0.0064	0.0064	0.0131	0.0192	0.0192

(c) The mean absorption times \underline{U} and the variances \underline{V} of first absorption times.

Using (2.14) and (2.15), the vectors of mean absorption times (\underline{U}) and of the variances of first absorption times (\underline{V}) are obtained respectively as:

$$\underline{U} = \left(\frac{1+x}{x} + \left(\frac{1+x}{x} \right)^2, \frac{1+x}{x} + \left(\frac{1+x}{x} \right)^2, \left(\frac{1+x}{x} \right)^2, \left(\frac{1+x}{x} \right)^2, \frac{1+x}{x} + \left(\frac{1+x}{x} \right)^2, 1 + \frac{1+x}{x} + \left(\frac{1+x}{x} \right)^2, 1 + \frac{1+x}{x} + \left(\frac{1+x}{x} \right)^2 \right)$$

and

$$\tilde{V}' = \frac{1}{x^4} (g_1(x), g_1(x), g_2(x), g_2(x), g_1(x), g_1(x), g_1(x)),$$

where

$$g_1(x) = 1 + 6x + 10x^2 + 5x^3 \text{ and } g_2(x) = 1 + 6x + 9x^2 + 4x^3.$$

It is easily seen that $\frac{1+x}{x}$, $\frac{1}{x^4}g_1(x)$ and $\frac{1}{x^4}g_2(x) \downarrow$ as x increases for $x \geq 0$. Hence,

$$\tilde{U}' \downarrow (2, 2, 1, 1, 2, 3, 3) \text{ and}$$

$\tilde{V}' \downarrow 0'$ as $x \rightarrow \infty$. Furthermore, the means and variances are greater than (less than) those of no selection case if $x < 1$ ($x > 1$).

It might be of interest to point out that it takes one more generation for $aa \times AA$ (or $AA \times aa$) than $AA \times Aa$ (or $aa \times Aa$) to reach fixation. This follows from the trivial result that with probability 1 $aa \times AA \rightarrow AA \times Aa$ ($AA \times aa \rightarrow aa \times Aa$) in one generation.

This may also account for the equality of variances of first time absorption probabilities. Given in Table 4 are the mean absorption times and variances of first absorption times for $x=0, 0.5, 1, 1.5, 2, 2.5, 4.0$.

Table 4. Mean absorption times (U) and variance (V) of first absorption times

\tilde{u}	$x=0.5$	1.0	1.5	2.0	2.5	4.0
AA × Aa	12	6	4.4444	3.75	3.36	2.8125
aa × Aa	12	6	4.4444	4.75	3.36	2.8125
Aa × AA	9	4	2.7778	2.25	1.96	1.5625
Aa × aa	9	4	2.7778	2.25	1.96	1.5625
Aa × Aa	12	6	4.4444	3.75	3.36	2.8125
aa × AA	13	7	5.4444	4.75	4.36	3.8125
AA × aa	13	7	5.4444	4.75	4.36	3.8125
\tilde{v}	$x=0.5$	1.0	1.5	2.0	2.5	4.0
AA × Aa	114	22	9.7531	5.8125	4.0096	1.9727
aa × Aa	114	22	9.7531	5.8125	4.0096	1.9727
Aa × AA	108	20	8.6420	5.0625	3.4496	1.6602
Aa × aa	108	20	8.6420	5.0625	3.4496	1.6602
Aa × Aa	114	22	9.7531	5.8125	4.0096	1.9727
aa × AA	114	22	9.7531	5.8125	4.0096	1.9727
AA × aa	114	22	9.7531	5.8125	4.0096	1.9727

(d) The absolute probabilities distributions of $X(n)$.

Given the initial frequencies as \tilde{a}_0 , the absolute probability distribution at time n is

$$\tilde{a}'_n = \tilde{a}'_0 \begin{pmatrix} 1 & 0 & \vdots & 0 \\ 0 & 1 & \vdots & 0 \\ \hline \rho^{(1)} & \rho^{(2)} & \vdots & 0 \end{pmatrix} - \sum_{i=1}^5 \lambda_i^n \tilde{a}'_0 \begin{pmatrix} 0 & 0 & \vdots & 0 \\ 0 & 0 & \vdots & 0 \\ \hline \frac{1}{1-\lambda_i} A_i R_1 & \frac{1}{1-\lambda_i} A_i R_2 & \vdots & -A_i \end{pmatrix}$$

Let $f_{ij}(n) = P_r[X(n) = j | X(0) = i]$, i transient state. Then, given $\tilde{a}'_0 = (a_{01}, a_{02}, a_{03}, a_{04}, \dots, a_{09})$, the absolute probability distribution at time n is

$$\tilde{a}'_n = (a_{01} + b_1, a_{02} + b_2, b_3, b_4, b_5, b_6, b_7, b_8, b_9),$$

where

$$b_j = \sum_{i=3}^9 b_{0i} f_{ij}(n).$$

Given in Table 5 are the absolute probability distributions at time n given various transient states ($f_{ij}(n)$'s). This may be used to derive the absolute probability distributions of $X(n)$. This may also be used to compute the correlations of relatives as has been done in Horner (1956). As the procedure is rather straightforward, we will not go into detail, however.

Table 5. Absolute probability distribution at time n given the transient states

	AA × Aa	aa × Aa
AA × AA	$\frac{1}{2} \left[1 + \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n} \times \left[\frac{\Delta_{n+2}}{\Delta_1} + \frac{\gamma_n(\sqrt{x})^{n+3}}{1+x+x^2} \right]$	$\frac{1}{2} \left[1 - \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n} \times \left[\frac{\Delta_{n+2}}{\Delta_1} - \frac{\gamma_n(\sqrt{x})^{n+3}}{1+x+x^2} \right]$
aa × aa	$\frac{1}{2} \left[1 - \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n} \times \left[\frac{\Delta_{n+2}}{\Delta_1} - \frac{\gamma_n(\sqrt{x})^{n+3}}{1+x+x^2} \right]$	$\frac{1}{2} \left[1 + \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n} \times \left[\frac{\Delta_{n+2}}{\Delta_1} + \frac{\gamma_n(\sqrt{x})^{n+3}}{1+x+x^2} \right]$
AA × Aa	$\frac{1}{4(1+x)^n} \left[(\sqrt{x})^n \varepsilon_n + \frac{2x}{\Delta_1} \Delta_{n-1} \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_{n-1} - (\sqrt{x})^n \varepsilon_n \right]$
aa × Aa	$\frac{1}{4(1+x)^n} \left[-(\sqrt{x})^n \varepsilon_n + \frac{2x}{\Delta_1} \Delta_{n-1} \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_{n-1} + (\sqrt{x})^n \varepsilon_n \right]$
Aa × AA	$\frac{1}{4(1+x)^n} \left[(\sqrt{x})^{n+1} \varepsilon_{n-1} + \frac{2x}{\Delta_1} \Delta_n \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_n - (\sqrt{x})^{n+1} \varepsilon_{n-1} \right]$
Aa × aa	$\frac{1}{4(1+x)^n} \left[-(\sqrt{x})^{n+1} \varepsilon_{n-1} + \frac{2x}{\Delta_1} \Delta_n \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_n + (\sqrt{x})^{n+1} \varepsilon_{n-1} \right]$
Aa × Aa	$\frac{1}{4(1+x)^n} \times \frac{4\Delta_n}{\Delta_1}$	$\frac{1}{4(1+x)^n} \times \frac{4\Delta_n}{\Delta_1}$
aa × AA	0	0
AA × aa	0	0

	Aa × AA	Aa × aa
AA × AA	$\frac{1}{2} \left[1 + \frac{x+x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n} \times$ $\left[\frac{\Delta_{n+1}}{\Delta_1} + \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$	$\frac{1}{2} \left[1 - \frac{x+x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n}$ $\left[\frac{\Delta_{n+1}}{\Delta_1} - \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$
aa × aa	$\frac{1}{2} \left[1 - \frac{x+x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n} \times$ $\left[\frac{\Delta_{n+1}}{\Delta_1} - \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$	$\frac{1}{2} \left[1 + \frac{x+x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^n} \times$ $\left[\frac{\Delta_{n+1}}{\Delta_1} + \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$
AA × Aa	$\frac{1}{4(1+x)^n} \left[\frac{2\Delta_{n-2}}{\Delta_1} x + \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_{n-2} - \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$
aa × Aa	$\frac{1}{4(1+x)^n} \left[\frac{2\Delta_{n-2}}{\Delta_1} x - \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_{n-2} + \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$
Aa × AA	$\frac{1}{4(1+x)^n} \left[\frac{2\Delta_{n-1}}{\Delta_1} x + \varepsilon_n(\sqrt{x})^n \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_{n-1} - \varepsilon_n(\sqrt{x})^n \right]$
Aa × aa	$\frac{1}{4(1+x)^n} \left[\frac{2\Delta_{n-1}}{\Delta_1} x - \varepsilon_n(\sqrt{x})^n \right]$	$\frac{1}{4(1+x)^n} \left[\frac{2x}{\Delta_1} \Delta_{n-1} + \varepsilon_n(\sqrt{x})^n \right]$
Aa × Aa	$\frac{1}{4(1+x)^n} \times \frac{4\Delta_{n-1}}{\Delta_1}$	$\frac{1}{4(1+x)^n} \times \frac{4\Delta_{n-1}}{\Delta_1}$
aa × AA	0	0
AA × aa	0	0

	Aa × Aa	aa × AA
AA × AA	$\frac{1}{2} \left[1 - \frac{1}{(1+x)^n} \frac{\Delta_{n+2}}{\Delta_1} \right]$	$\frac{1}{2} \left[1 + \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^{n-1}} \times$ $\left[\frac{\Delta_{n+1}}{\Delta_1} + \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$
aa × aa	$\frac{1}{2} \left[1 - \frac{1}{(1+x)^n} \frac{\Delta_{n+2}}{\Delta_1} \right]$	$\frac{1}{2} \left[1 - \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^{n-1}} \times$ $\left[\frac{\Delta_{n+1}}{\Delta_1} - \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$
AA × Aa	$\frac{2x}{\Delta_1} \Delta_{n-1}$	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-2} + \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$
aa × Aa	$\frac{2x}{\Delta_1} \Delta_{n-1}$	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-2} - \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$
Aa × AA	$\frac{2x}{\Delta_1} \Delta_n$	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-1} + \varepsilon_n(\sqrt{x})^n \right]$
Aa × aa	$\frac{2x}{\Delta_1} \Delta_n$	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-1} - \varepsilon_n(\sqrt{x})^n \right]$
Aa × Aa	$\frac{4\Delta_n}{\Delta_1}$	$\frac{1}{4(1+x)^{n-1}} \times \frac{4\Delta_{n-1}}{\Delta_1}$
aa × AA	0	0
AA × aa	0	0

AA × aa	
AA × AA	$\frac{1}{2} \left[1 - \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^{n-1}} \left[\frac{\Delta_{n+1}}{\Delta_1} - \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$
aa × aa	$\frac{1}{2} \left[1 + \frac{x^2}{1+x+x^2} \right] - \frac{1}{2(1+x)^{n-1}} \left[\frac{\Delta_{n+1}}{\Delta_1} + \frac{\gamma_{n-1}(\sqrt{x})^{n+2}}{1+x+x^2} \right]$
AA × Aa	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-2} - \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$
aa × Aa	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-2} + \varepsilon_{n-1}(\sqrt{x})^{n-1} \right]$
Aa × AA	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-1} - \varepsilon_n(\sqrt{x})^n \right]$
Aa × aa	$\frac{1}{4(1+x)^{n-1}} \left[\frac{2x}{\Delta_1} \Delta_{n-1} + \varepsilon_n(\sqrt{x})^n \right]$
Aa × Aa	$\frac{1}{4(1+x)^{n-1}} \times \frac{4\Delta_{n-1}}{\Delta_1}$
aa × AA	0
AA × aa	0

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Lireature Cited

Bosso, J. A., O. M. Sorarrain, and E. E. A. Favret. 1969 Applications of finite absorbent Markov chains to sib mating populations with selection. *Biometrics* 25: 17-26.
 Horner, T. W. 1956. Parent-offspring and full-sib correlations under a parent-offspring mating system, *Genetics* 41: 460-468.
 Karlin, S. 1966. A First Course in Stochastic Processes. Academic press, New York.
 Karin, S. 1968. Equilibrium behavior of population genetic models with non-random mating. *J. Appl. Prob.* 5: 231-313.
 Nelder, J. A. 1952. Some genotypic frequencies and variance components occurring in biometrical genetics. *Heredity* 6: 387-394.

Appendix 1

Lemma 1. Let A be a $n \times n$ matrix. If A is diagonal, then

$$A = \sum_{j=1}^l \lambda_j A_j, \text{ where } \lambda_1, \lambda_2, \dots, \lambda_l \text{ are the distinct eigenvalues of } A; \sum_{j=1}^l A_j = I_n, A_j^2 = A_j, \text{ and } A_i A_j = 0, i \neq j. \text{ Furthermore, } A_j = \prod_{i \neq j} \frac{1}{(\lambda_j - \lambda_i)} (A - \lambda_i I_n), j = 1, 2, \dots, l.$$

Proof. There exists a nonsingular matrix P such that

$$P^{-1}AP = \text{Diag } (\underbrace{\lambda_1, \lambda_1, \dots, \lambda_1}_{r_1}, \underbrace{\lambda_2, \lambda_2, \dots, \lambda_2}_{r_2}, \dots, \underbrace{\lambda_l, \dots, \lambda_l}_{r_l}), = \lambda_1 E_1 + \lambda_2 E_2 + \dots + \lambda_l E_l$$

where $\text{Diag}(x_1, x_2, \dots, x_n)$ denotes a $n \times n$ diagonal matrix with diagonal elements x_1, x_2, \dots, x_n , and

$$E_i = \text{Diag}(0, \dots, 0; \underbrace{1, 1, \dots, 1}_{r_i}; 0, \dots, 0), \quad i=1, 2, \dots, l$$

Then,

$A = \sum_{j=1}^l \lambda_j P E_j P^{-1} = \sum_{j=1}^l \lambda_j A_j$, where $A_j = P E_j P^{-1}$. It is easy to check that $\sum_{j=1}^l A_j = I_n$, $A_j^2 = A_j$ and $A_i A_j = 0$ for $i \neq j$.

Furthermore, by pre- and post-multiplying $\prod_{i \neq j} \frac{1}{(\lambda_j - \lambda_i)} (A - \lambda_i I_n)$ by P^{-1} and P respectively, it is straightforward to show that

$$P^{-1} \left\{ \prod_{i \neq j} \frac{1}{(\lambda_j - \lambda_i)} (A - \lambda_i I_n) \right\} P = E_j \text{ so that } A_j = \prod_{i \neq j} \frac{1}{(\lambda_j - \lambda_i)} (A - \lambda_i I_n), \quad j=1, 2, \dots, l.$$

QED

Lemma 2. Let $Q = \begin{bmatrix} Q_{11} & 0 \\ Q_{12} & 0 \end{bmatrix}$ be $n \times n$ and Q_{11} $r \times r$ diagonal. Then Q is

diagonal and $Q^n = \sum_{j=2}^k \mu_j \begin{bmatrix} B_j & 0 \\ \frac{1}{\mu_j} Q_{12} B_j & 0 \end{bmatrix}$, where $\mu_2, \mu_3, \dots, \mu_k$ are the distinct

non-zero eigenvalues of Q_{11} , and $B_j = \prod_{i \neq j} \frac{1}{(\mu_j - \mu_i)} (Q_{11} - \mu_i I_r)$.

Proof. The result follows immediately from $Q^n = \begin{bmatrix} Q_{11}^n & 0 \\ Q_{12} Q_{11}^{n-1} & 0 \end{bmatrix}$ and lemma 1.

QED

Appendix 2

Section 2 is concerned only with finite Markov chain. It is, however, interesting to point out some connections between results of finite Markov chains with stationary transition probabilities and arbitrary Markov chains with stationary transition probabilities. For this purpose we put

ρ_{ij} = ultimate absorption probability into the j th closed set C_j given initially $X(0) = i \in T$,

$\delta_{ij}(n)$ = probability of first time absorption into C_j at time n given initially $X(0) = i \in T$.

Then it is easily seen that ρ_{ij} and $\delta_{ij}(n)$ satisfy respectively,

$$\rho_{ij} = \sum_{v \in T} P_{iv} \rho_{vj} + \sum_{h \in C_j} P_{ih}, \quad j=1, 2, \dots, k, \quad i \in T,$$

$$\delta_{ij}(n) = \sum_{v \in T} P_{iv}(n-1) \sum_{h \in C_j} P_{vh}, \quad i \in T, \quad j=1, 2, \dots, k, \text{ where } P_{ij} \text{ and } P_{iv}(n-1) \text{ are}$$

the one-step and $(n-1)$ step transition probabilities respectively.

Thus, the probability of first time absorption into persistent states at time n given initially $X(0) = i \in T$ is

$$\begin{aligned} \delta_i(n) &= \sum_{j=1}^k \delta_{ij}(n) = \sum_{v \in T} P_{iv}(n-1) \sum_{j=1}^k \sum_{h \in U_j} P_{vh} \\ &= \sum_{v \in T} P_{iv}(n-1) \{1 - \sum_{h \in T} P_{vh}\} = \rho_i^{(n-1)} - \rho_i^{(n)} \end{aligned}$$

where

$$\rho_i^{(n)} = P_r[X(n) \in T \mid X(0) = i], \quad i \in T.$$

If $\delta_i(n)$ is a p. d. f. over n , then $\delta_i(n)$ may be utilized to compute the mean absorption times μ_i and other moments of first absorption times of $i \in T$. From the above formulor of $\delta_i(n)$, it is easy to see that $\delta_i(n)$ is a p. d. f. over n if and only if $\lim_{n \rightarrow \infty} \rho_i^{(n)} = 0$ (the limit exists as $\rho_i^{(n)} \leq \rho_i^{(n-1)}$), that is, the probability is zero that the chain will stay forever in T given $X(0) = i \in T$. We now show in fact that the μ_i 's satisfy

$$\mu_i = 1 + \sum_{v \in T} P_{iv} \mu_v, \quad i \in T,$$

which is a well-known formulor for mean absorption times.

We have, for every $i \in T$,

$$\mu_i = \sum_{n=1}^{\infty} n \delta_i(n) = \sum_{n=1}^{\infty} n [\rho_i^{(n-1)} - \rho_i^{(n)}] = \sum_{n=0}^{\infty} \rho_i^{(n)} = 1 + \sum_{n=1}^{\infty} \rho_i^{(n)},$$

and $\rho_i^{(n)} = P_r[X(n) \in T \mid X(0) = i] = \sum_{v \in T} P_{iv} P_r[X(n) \in T \mid X(1) = v] = \sum_{v \in T} P_{iv} \rho_v^{(n-1)}$.

Hence $\sum_{n=1}^{\infty} \rho_i^{(n)} = \sum_{v \in T} P_{iv} \sum_{n=0}^{\infty} \rho_v^{(n)} = \sum_{v \in T} P_{iv} \mu_v$, for every $i \in T$ so that, $\mu_i = 1 + \sum_{n=1}^{\infty} \rho_i^{(n)} = 1 + \sum_{v \in T} P_{iv} \mu_v$, for all $i \in T$.

有限馬可夫鏈在遺傳學上的應用

論親子配偶系統中淘汰的影響力

譚 外 元

美國華盛頓州立大學數學系

1. 本文首先對於時間穩定之有限馬可夫鏈 (Stationary finite Markov Chain) 提供一些數學公式藉以計算 (a) 過渡元素 (Transient states) 於時間 n 及以前之被吸收入某一給定之閉合集 (Closed set) 之機率; (b) 過渡元素最終之被吸收入某一給定閉合集之機率; (c) 過渡元素初次於時間 n 之被吸收入某一給定閉合集之機率; (d) 過渡元素之平均吸收入持久元素 (Persistent states) 之平均吸收時間及 (e) 過渡元素之被吸收入持久元素之變方 (Variance)。

2. 本文其次研究親子配偶系統中淘汰 (Selection) 之影響力; 利用上述之公式以研究淘汰對於過渡型式 (Transient types) 之被吸收入二種配偶型 (Mating types) $AA \times AA$ 及 $aa \times aa$ 之各項機率, 平均吸收時間及吸入時間之變方之效應。本文亦求出於時間 n 時各配偶型之機率分布。本文所採用之方法基本為行列之譜開展 (Spectral expansion); 故淘汰之效應基本上可由轉渡行列 (Transition matrix) 之固有根 (Latent roots 或 eigenvalues) 表明之。