TWO NON-LINEAR BIRTH AND DEATH PROCESSES

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1. Introduction

The random processes discussed here may be specified in the following way. A fixed population of N members is split into two distinct classes. Individuals move about randomly between the classes, and we are interested in the size of each class at any time, rather than in the behaviour of particular individuals. Let $i(t)$ and $N - i(t)$ be the numbers present in the respective classes at the time t. It is assumed that the process $\{i(t),\ t \geqq 0\}$ is Markovian, and that transitions between the states $j = 0, 1, \ldots N$, occur according to the conditional probabilities;

$$P[i(t+\delta t) = j+1 \mid i(t) = j] = \mu_j \delta t + 0(\delta t),$$
$$P[i(t+\delta t) = j-1 \mid i(t) = j] = \lambda_j \delta t + 0(\delta t).$$

and

$$P[i(t+\delta t) = j \mid i(t) = j] = 1 - (\lambda_j + \mu_j)\delta t + 0(\delta t).$$

The transition rates λ_j, μ_j are positive except that $\lambda_0 = \mu_N = 0$, so that any state can be reached from any other state. We suppose the initial position is given, $i(0) = n$ say, and consider the problem of finding the probability distribution $p_j(t) = P[i(t) = j]$; $j = 0, 1, \cdots N$, at every instant $t \geqq 0$, or its generating function $\Pi(x, t) = \sum_{j=0}^{N} p_j(t)x^j$.

In general the form of this distribution can be described in terms of the eigenvalues of the matrix of transition rates. Let $\omega_0, \omega_1, \cdots \omega_N$ be the roots of the equation $|Q - \omega I| = 0$, where I is the identity matrix of order $N+1$, and $q_{j,j-1} = -\lambda_j$, $q_{j,j} = \lambda_j + \mu_j$, $q_{j,j+1} = -\mu_j$; $j = 0, 1, \cdots N$. The remaining elements of Q are all zero. One of these roots is zero and the others are all real, positive and distinct. These results have been established in a paper by W. Ledermann and G. E. H. Reuter [1]. Thus we may arrange $\omega_0 = 0 < \omega_1 < \cdots < \omega_N$, and the required distribution has the form $p_j(t) = \sum_{k=0}^{N} p_j^{(k)} e^{-\omega_k t}$. For each ω_k, the coefficients $p_j^{(k)}$ form the corresponding left eigenvector of Q. The initial terms of this expansion are dominant when t is large, and in particular the first term gives the equilibrium distribution; $\lim_{t\to\infty} p_j(t) = p_j^{(0)}$. Then the relations $p_{j-1}^{(0)}\mu_{j-1} - p_j^{(0)}(\lambda_j + \mu_j) + p_{j+1}^{(0)}\lambda_{j+1} = 0$, together with $\sum_{j=0}^{N} p_j^{(0)} = 1$, determine this limiting distribution,

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$$p_j^{(0)} = \frac{\mu_0\mu_1\cdots\mu_{j-1}}{\lambda_1\lambda_2\cdots\lambda_j}\Big/ 1+\sum_{r=1}^{N}\frac{\mu_0\mu_1\cdots\mu_{r-1}}{\lambda_1\ \lambda_2\cdots\lambda_r}.$$

However, the explicit determination of the time-dependent probability distribution is possible only in a few special cases where $\omega_1, \omega_2, \cdots \omega_N$ can be found. Two such cases are considered here in which a direct solution of the characteristic equation can be avoided by considering instead, the differential equation satisfied by the generating function.

The first example has been investigated by P. A. P. Moran [2] as a model for a random process in genetics. The population consists of an even number N of gametes, each of which is of type A or $\bar{A}$. $i(m)$ is the number of A individuals at the time m; $m = 0, 1, 2, \cdots$. It is convenient to consider time as a discrete variable in the first place, although we shall be mainly concerned with the analogous continuous time process. If $i(m) = j$, the conditional distribution of $i(m+1)$ is determined by the rules:

(i) Immediately after time m, a single gamete, chosen at random, dies and is replaced, just before time $m+1$, by another whose type depends on mutation.

(ii) Let α be the probability that an A individual mutates to $\bar{A}$ during the interval $m < t < m+1$, and let $\bar{\alpha}$ be the probability that a single gamete of type $\bar{A}$ mutates to A. Then the replacement is of type A with probability $[j(1-\alpha)+(N-j)\bar{\alpha}]/N$, and is of type $\bar{A}$ with probability $[j\alpha+(N-j)(1-\bar{\alpha})]/N$. It is assumed that individual gametes behave independently.

It follows that the transition probabilities $p_{j,k} = P[i(m+1) = k \mid i(m)=j]$ are given by

$$p_{j,j+1} = \frac{N-j}{N}\left[\frac{j}{N}(1-\alpha)+\frac{(N-j)}{N}\bar{\alpha}\right] = \frac{(1-\alpha-\bar{\alpha})}{N^2}j(N-j)+\frac{\bar{\alpha}}{N}(N-j),$$

$$p_{j,j-1} = \frac{j}{N}\left[\frac{j}{N}\alpha+\frac{(N-j)}{N}(1-\bar{\alpha})\right] = \frac{(1-\alpha-\bar{\alpha})}{N^2}j(N-j)+\frac{\alpha}{N}j,$$

$$p_{j,j} \quad = 1-p_{j,j+1}-p_{j,j-1}, \text{ for } j = 0, 1, \cdots N,$$

and the remaining elements are zero. The corresponding continuous time process is governed by transition rates of the form

$$\lambda_j = aj(N-j)+bj, \qquad \mu_j = aj(N-j)+c(N-j),$$

where the constants a, b and c are arbitrary, subject to the restriction that no transition rate is negative.

In an appendix to the above paper, E. J. Hannan shows that in the special case $\alpha = \bar{\alpha} = 0$, the eigenvalues of the matrix $(p_{j,k})$ are $1-k(k-1)/N^2$; $k = 0, 1, \cdots N$. From this it is deduced, that at least when α and $\bar{\alpha}$ are small, the eigenvalues with greatest moduli are 1, $1-(\alpha+\bar{\alpha})/N$, $1-2(\alpha+\bar{\alpha})/N-2(1-\alpha-\bar{\alpha})/N^2$. However, the study of the continuous time version of the process eliminates the difficulty of solving the characteristic equation, and there is no need to separate the special case $b=c=0$. In the present paper the eigenvalues are determined by considering the form of the equations satisfied by the factorial moments of the distribution. The method exploits the special property that the non-linear terms in the transition rates are balanced, so that $\lambda_j-\mu_j$ is linear in j. It follows from the results obtained in section 2, that in general the eigenvalues of (p_{jk}) are given by: $1-k(\alpha+\bar{\alpha})/N-k(k-1)(1-\alpha-\bar{\alpha})/N^2$ for $k=0,1,\cdots N$. Section 2 goes on further, to complete the determination of the probability generating function.

The process just described reduces, when $a=0$, to the well known process with linear transition rates. The example discussed in section 3 can also be regarded as a generalisation of this process. It has transition rates $\lambda_j=\lambda(\theta^j-1)$, $\mu_j=\mu(\theta^N-\theta^j)$, where θ is a positive constant. The linear process arises in the limit as θ approaches 1, if we choose λ and μ suitably, but it is assumed here that $\theta\neq 1$. Without loss of generality we suppose $\theta>1$, $\lambda>0$ and $\mu>0$. Again the probability generating function can be determined by solving a certain differential equation, and it is verified that the eigenvalues are

$$\omega_k=(\theta^k-1)(\lambda+\mu\theta^{N-k})=\lambda_k+\mu_{N-k};\qquad k=0,1,\cdots N.$$

Although the transition rates are non-linear, the eigenvalues are linearly related to them. Practical applications of this process are limited, but it is of theoretical interest since an explicit solution is available and because of this simple expression for the eigenvalues. The paper concludes with a more general discussion of the relationship between eigenvalues and transition rates. This considers the existence of further processes for which the eigenvalues have a similar form.

2. A Process With Balanced Non-linearities

Consider the process with transition rates $\lambda_j=aj(N-j)+bj$ and $\mu_j=aj(N-j)+c(N-j)$; $j=0,1,\cdots N$. If $b>0$, $c>0$ and $a>\text{Max}\,[-b/(N-1),-c/(N-1)]$ these rates are all positive except for $\lambda_0=\mu_N=0$, although the solution obtained below remains valid under the weaker condition that no transition rate is negative. For convenience it is further assumed that $a\neq 0$.

In general, the Kolmogorov forward equations for the probabilities $\{p_j(t)\}$ are;

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$$\frac{dp_j}{dt} = \lambda_{j+1}p_{j+1} - (\lambda_j + \mu_j)p_j + \mu_{j-1}p_{j-1}; \qquad j = 0, 1, \cdots N.$$

For the particular transition rates here, these relations lead to a single equation for the generating function $\Pi(x, t)$, [3].

$$\frac{\partial \Pi}{\partial t} + ax(1-x)^2 \frac{\partial^2 \Pi}{\partial x^2} - (1-x)[(a(N-1)-c)(1-x)+b+c]\frac{\partial \Pi}{\partial x} + cN(1-x)\Pi = 0.$$

Then the substitution $y = x - 1$ reduces this to

$$(2.1) \qquad \frac{\partial \Pi}{\partial t} + ay^2(1+y)\frac{\partial^2 \Pi}{\partial y^2} + y[b+c-(a(N-1)-c)y]\frac{\partial \Pi}{\partial y} - cNy\Pi = 0$$

and the generating function becomes $\Pi = \sum_{k=0}^{N} M_k(t)y^k$. Although for convenience we have retained the symbol Π, this now represents the factorial moment generating function, whose coefficients are defined by $M_k(t) = \sum_{j=k}^{N} \binom{j}{k} p_j(t)$, for each k. In particular $M_0 = \sum_{j=0}^{N} p_j(t) = 1$ and $M_1(t)$ is the mean of the distribution. These factorial moments satisfy a set of first order difference equations, which result from comparing the coefficients of y^k in (2.1). We have

$$(2.2) \qquad \frac{dM_k}{dt} + k(a(k-1)+b+c)M_k = (N-k+1)(a(k-1)+c)M_{k-1}$$

for $k = 1, 2, \cdots N$. In principle, these equations can be solved successively, beginning with the equation for the mean, and it is clear that each solution would consist of a linear combination of the terms $\exp[-k(a(k-1)+b+c)t]$ $k = 0, 1, \cdots N$. However it follows from this, that the eigenvalues of the process must be $\omega_k = k(a(k-1)+b+c)$, for $k = 0, 1, \cdots N$. We remark that this property of the factorial moments depends critically on the fact that for each j, the coefficient of $j(N-j)$ is the same in each of the transition rates λ_j and μ_j.

We may now proceed to find the general solution of equation (2.1). This has the form $\Pi = \sum_{k=0}^{N} F_k(y) \exp[-k(a(k-1)+b+c)t]$ where each F_k is a polynomial of degree N in y. Further, the individual terms must satisfy (2.1). Thus

$$ay^2(1+y)\frac{d^2F_k}{dy^2}+y[b+c-(a(N-1)-c)y]\frac{dF_k}{dy}$$
$$-[k(a(k-1)+b+c)+cNy]F_k=0 \quad \text{for each } k.$$

If we write $F_k(y)=\sum_{m=0}^{N} a_{k,m}y^m$, then the coefficients $a_{k,m}$ are determined by,

$$(m-k)(a(m+k-1)+b+c)a_{k,m}=(N+1-m)(a(m-1)+c)a_{k,m-1}.$$

Now let $\rho=c/a$, $\sigma=(b+c)/a$, and replace $a_{k,k}$ by a_k. Then

$$F_k(y)=a_k\sum_{r=0}^{N-k}\frac{y^{k+r}\Gamma(N+1-k)\Gamma(\rho+k+r)\Gamma(\sigma+2k)}{\Gamma(r+1)\Gamma(N+1-k-r)\Gamma(\rho+k)\Gamma(\sigma+2k+r)};\quad k=0,1,\cdots N.$$

In order to complete the determination of the generating function, the constants a_k must be chosen to satisfy the initial conditions. At $t=0$, $i(0)=n$ and $\Pi=(1+y)^n=\sum_{k=0}^{N}F_k(y)$. Differentiate this m times and set $y=0$. Then if we interpret $\binom{n}{m}=0$ whenever $m>n$, it follows

$$\text{(2.3)}\qquad \sum_{k=0}^{m}\frac{a_k\Gamma(N+1-k)\Gamma(\rho+m)\Gamma(\sigma+2k)}{\Gamma(m+1-k)\Gamma(N+1-m)\Gamma(\rho+k)\Gamma(\sigma+k+m)}=\binom{n}{m}$$

for $m=0,1,\cdots N$. Thus $a_0=1$ and $a_1, a_2,\cdots a_N$ can be found successively.

Lemma. The solution of equations (2.3) is given by:

$$\text{(2.4)}\qquad a_k=\sum_{s=0}^{k}(-1)^s\binom{n}{k-s}\frac{\Gamma(N+1-k+s)\Gamma(\rho+k)\Gamma(\sigma+2k-s-1)}{\Gamma(s+1)\Gamma(N+1-k)\Gamma(\rho+k-s)\Gamma(\sigma+2k-1)};$$
$$k=0,1,\cdots N.$$

Proof. Consider the identity

$$\text{(2.5)}\qquad \sum_{s=0}^{k}(-1)^s\binom{k}{s}\frac{(\gamma+2s)}{(\gamma+s)(\gamma+s+1)\cdots(\gamma+s+k)}=\delta_{k,0},$$

for any real number γ and any integer $k\geqq 0$. This certainly holds when $k=0$, so we suppose $k>0$ and write,

$$T_m=\sum_{s=0}^{m}(-1)^s\binom{k}{s}\frac{(\gamma+2s)}{(\gamma+s)(\gamma+s+1)\cdots(\gamma+s+k)};\qquad m=0,1,\cdots k.$$

Now assume inductively that

$$T_m=(-1)^m\binom{k-1}{m}\frac{1}{(\gamma+m+1)(\gamma+m+2)\cdots(\gamma+m+k)}$$

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holds for a particular index $m < k$. The case "$m+1$" is easily verified by adding the last term of T_{m+1} to this expression. Then the induction is completed by examining T_0, and equation (2.5) follows immediately, since $T_k = 0$.

We can now verify (2.4) by direct substitution into the left side of equation (2.3). The expression obtained can be written

$$\sum_{r=0}^{m}\left[\binom{n}{r}\frac{\Gamma(N+1-r)\Gamma(\rho+m)}{\Gamma(N+1-m)\Gamma(m+1-r)\Gamma(\rho+r)}\right.$$
$$\left.\times\sum_{s=0}^{m-r}(-1)^s\binom{m-r}{s}\frac{(\sigma+2r-1+2s)}{(\sigma+2r+s-1)(\sigma+2r+s)\cdots(\sigma+2r-1+s+m-r)}\right]$$

where k has been replaced by $r+s$. But by (2.5), for the case $\gamma = \sigma + 2r - 1$, the second summation reduces to $\delta_{m,r}$, and hence the whole expression is equal to $\binom{n}{m}$, as required.

The following results have been established. The probability generating function is given in terms of the initial state $i(0) = n$, by

$$\Pi(x, t) = \sum_{k=0}^{N} F_k(x-1)\exp\left[-k(a(k-1)+b+c)t\right],$$

where each

$$F_k(y) = a_k\sum_{r=0}^{N-k}\frac{y^{k+r}\Gamma(N+1-k)\Gamma(\rho+k+r)\Gamma(\sigma+2k)}{\Gamma(r+1)\Gamma(N+1-k-r)\Gamma(\rho+k)\Gamma(\sigma+2k+r)}$$

and $\rho = c/a$, $\sigma = (b+c)/a$.

$$a_k = \sum_{s=0}^{k}(-1)^s\binom{n}{k-s}\frac{\Gamma(N+1-k+s)\Gamma(\rho+k)\Gamma(\sigma+2k-s-1)}{\Gamma(s+1)\Gamma(N+1-k)\Gamma(\rho+k-s)\Gamma(\sigma+2k-1)}$$

for $k = 0, 1, \cdots N$.

Formulae for the probabilities $\{p_j(t)\}$ can be deduced from this. In particular it is not difficult to show that the equilibrium distribution reduces to

$$p_j(\infty) = \binom{N}{j}\frac{\Gamma(\rho+j)\Gamma(\sigma)\Gamma(\sigma-\rho+N-j)}{\Gamma(\rho)\Gamma(\sigma+N)\Gamma(\sigma-\rho)}; \qquad j = 0, 1, \cdots N.$$

However the formulae obtained for the time dependent probabilities are extremely complicated. As it might be expected from the manner in which the generating function was determined, a more convenient way of describing this distribution is in terms of its factorial moments. We have

$$M_k(t) = \sum_{r=0}^{k}\left[\frac{a_r\Gamma(N+1-r)\Gamma(\rho+k)\Gamma(\sigma+2r)}{\Gamma(k-r+1)\Gamma(N+1-k)\Gamma(\rho+r)\Gamma(\sigma+r+k)}\right.$$
$$\left.\times\exp\left[-r(a(r-1)+b+c)t\right]\right]$$

by picking out the coefficient of y^k in $\Pi(1+y, t)$. For example, the mean $M_1(t) = cN/(b+c) + (n - cN/(b+c))\, e^{-(b+c)t}$, which does not depend on the parameter a. Thus the non-linear terms in the original transition rates affect only the moments of higher order. We recall that by equation (2.2), the mean is determined by $dM_1/dt + (b+c)M_1 = cN$ where $M_1(0) = n$, and this is precisely the same as the deterministic equation of the process. The variance, which does depend on a, can be found from the expression for $M_2(t)$.

3. A Process With Linear Eigenvalues

The particular random process studied in this section has transition rates $\lambda_j = \lambda(\theta^j - 1)$, $\mu_j = \mu(\theta^N - \theta^j)$; $j = 0, 1, \cdots N$, where λ and μ are arbitrary positive constants and $\theta > 1$. As in the previous example the probability generating function, $\Pi(x, t) = \sum_{j=0}^{N} p_j(t) x^j$ satisfies a differential equation, obtained by combining the relations which hold between the probabilities. Here however, the equation has a different character. It relates $\Pi(\theta x, t)$ to $\Pi(x, t)$ and $\partial \Pi(x, t)/\partial t$. We have

$$\frac{\partial \Pi(x,t)}{\partial t} + \frac{(1-x)}{x}\left[(\lambda+\mu\theta^N x)\Pi(x,t) - (\lambda+\mu x)\Pi(\theta x, t)\right] = 0. \tag{3.1}$$

Nevertheless its solution can be found by a method similar to that used in section 2. We seek particular solutions of the form $\Pi = f(x)\, e^{-\omega t}$, where $f(x)$ is a polynomial of degree, at most N. Such polynomials exist only when ω is an eigenvalue of the process.

Consider the set of quantities $R_j(t) = \Pi(\theta^{-j}, t)$ for $j = 0, 1, \cdots N$. It follows by taking the appropriate combinations of the Kolmogorov forward equations, that for each index $j = 1, 2, \cdots N$ we have:

$$\frac{dR_j}{dt} + (\theta^j - 1)(\lambda + \mu\theta^{N-j})R_j = (\theta^j - 1)(\lambda + \mu\theta^{-j})R_{j-1},$$

and $R_0 = 1$. These relations have a similar form to equations (2.2) and the quantities $R_j(t)$ play the same role as did the factorial moments in the previous example. In particular, it is clear that the required eigenvalues are given by $\omega_k = (\theta^k - 1)(\lambda + \mu\theta^{N-k})$ for $k = 0, 1, \cdots N$. Suppose now that $f_k(x)\, e^{-\omega_k t}$ is a solution of equation (3.1). It follows that

$$(1 - \theta^k x)(\lambda + \mu\theta^{N-k} x) f_k(x) = (1 - x)(\lambda + \mu x) f_k(\theta x)$$

holds for all values of x. We replace x by θx and use this relation repeatedly. Then the condition that $f_k(x)$ must be a polynomial, implies

$$f_k(x) = c_k(1-x)(1-\theta x)\cdots(1-\theta^{k-1}x) \times(\lambda+\mu\theta^{N-k-1}x)(\lambda+\mu\theta^{N-k-2}x)\cdots(\lambda+\mu x).$$

These are the required polynomials, for $k = 0, 1, \cdots N$. Hence the general solution of equation (3.1) is

$$\Pi(x, t) = \sum_{k=0}^{N} f_k(x) \exp[-(\theta^k-1)(\lambda+\mu\theta^{N-k})t].$$

It remains to determine the constants $\{c_k\}$ from the boundary conditions on $\Pi(x, t)$.

Suppose that initially the process is in state n; $0 \leqq n \leqq N$. Thus

$$\Pi(x, 0) = \sum_{k=0}^{N} f_k(x) = x^n.$$

We can obtain a triangular system of equations for $c_N, c_{N-1}, \cdots c_0$, in that order, by setting $x = -\theta^{-j}\lambda/\mu$ for $j = 0, 1, \cdots N$, in succession; but since the eigenvalues are arranged in increasing order, it is preferable to use the alternative approach suggested by the factors of $f_k(x)$. Let $a_r = 1-\theta^{-r}$ and $b_r = \lambda+\mu\theta^{N-r}$ for any integer r. When $x = \theta^{-j}$, the above equation becomes

$$\sum_{k=0}^{j} c_k a_j a_{j-1}\cdots a_{j-k+1} b_{j+k+1} b_{j+k+2}\cdots b_{j+N} = \theta^{-nj} \tag{3.2}$$

which holds for $j = 0, 1, \cdots N$. For example, it follows immediately that $c_0 = (b_1 b_2 \cdots b_N)^{-1}$ which does not depend on n. We shall prove that the complete solution of this system of equations is as follows:

$$c_k = \sum_{r=0}^{k} (-1)^r \frac{\theta^{n(r-k)}\theta^{-\frac{1}{2}r(r-1)} b_{2k}}{(a_1 a_2\cdots a_r)(a_1 a_2\cdots a_{k-r})(b_{2k-r} b_{2k-r+1}\cdots b_{k-r+N})}, \quad k = 0, 1, \cdots N. \tag{3.3}$$

PROOF. Let

$$S_v^{(k)} = \sum_{r=0}^{v} (-1)^r \frac{\theta^{-\frac{1}{2}r(r-1)} b_{2m+2r}(a_{r+1}a_{r+2}\cdots a_k)(b_{2m+1}b_{2m+2}\cdots b_{2m+r-1})}{(a_1 a_2\cdots a_{k-r})(b_{2m+k+1}b_{2m+k+2}\cdots b_{2m+k+r})}$$

where m is a fixed integer and $0 \leqq v \leqq k$. In this summation, the term for which $r = 0$ is to be interpreted as unity. We need the identity $S_k^{(k)} = \delta_{k,0}$. Suppose $k > 0$, and assume inductively that for some particular value of $v < k$,

$$S_{v-1}^{(k)} = (-1)^{v-1} \frac{\theta^{-\frac{1}{2}v(v-1)}(a_{k-v+1}a_{k-v+2}\cdots a_{k-1})(b_{2m+1}b_{2m+2}\cdots b_{2m+v-1})}{(a_1 a_2\cdots a_{v-1})(b_{2m+k+1}b_{2m+k+2}\cdots b_{2m+k+v-1})} \tag{3.4}$$

holds. It follows

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$$S_v^{(k)} = (-1)^v \times \frac{\theta^{-\frac{1}{2}v(v-1)}(a_{k-v+1}a_{k-v+2}\cdots a_{k-1})(b_{2m+1}b_{2m+2}\cdots b_{2m+v-1})[a_k b_{2m+2v} - a_v b_{2m+k+v}]}{(a_1 a_2 \cdots a_v)(b_{2m+k+1}b_{2m+k+2}\cdots b_{2m+k+v})}$$

But the definitions of a_r and b_r imply

$$a_k b_{2m+2v} - a_v b_{2m+k+v} = \theta^{-v} a_{k-v} b_{2m+v}.$$

Thus equation (3.4) remains valid when v is replaced by $v+1$. Finally $S_0^{(k)} = 1$, and the induction is proved. In particular

$$S_{k-1}^{(k)} = (-1)^{k-1} \frac{\theta^{-\frac{1}{2}k(k-1)} b_{2m+1}b_{2m+2}\cdots b_{2m+k-1}}{b_{2m+k+1}b_{2m+k+2}\cdots b_{2m+2k-1}},$$

which is the negative of the last term in the sum $S_k^{(k)}$, and hence $S_k^{(k)} = 0$. This holds for every $k > 0$, and certainly $S_0^{(0)} = 1$.

We are now in a position to verify equations (3.3). The expression obtained on substituting from (3.3) into the left hand side of (3.2) can be arranged as follows:

$$\sum_{m=0}^{j}\Bigg[\frac{\theta^{-mn}(a_{j-m+1}a_{j-m+2}\cdots a_j)(b_{N+m+1}b_{N+m+2}\cdots b_{N+j})}{(a_1 a_2\cdots a_m)(b_{2m+1}b_{2m+2}\cdots b_{m+j})} \times \left\{\sum_{r=0}^{j-m}(-1)^r \frac{\theta^{-\frac{1}{2}r(r-1)} b_{2m+2r}(a_{r+1}a_{r+2}\cdots a_{j-m})(b_{2m+1}b_{2m+2}\cdots b_{2m+r-1})}{(a_1 a_2\cdots a_{j-m-r})(b_{j+m+1}b_{j+m+2}\cdots b_{j+m+r})}\right\}\Bigg].$$

However the second sum is simply $S_{j-m}^{(j-m)} = \delta_{j,m}$ and consequently the whole expression reduces to θ^{-nj}. This completes the proof.

Consider a particle which moves continuously in the interval $[0, N]$ with a velocity equal to the difference between the right and left transition rates, at any point. Let $y(t)$ denote its position. Then $dy/dt = \mu(\theta^N - \theta^y) - \lambda(\theta^y - 1)$. The solution of this equation, when $y(0) = n$ is given by,

$$\theta^{-y(t)} = \frac{\lambda+\mu}{\lambda+\mu\theta^N} + \left(\theta^{-n} - \frac{\lambda+\mu}{\lambda+\mu\theta^N}\right)\theta^{-(\lambda+\mu\theta^N)t}.$$

On the other hand, the mean of the distribution is

$$E[i(t)] = \sum_{r=0}^{N-1}\frac{\mu\theta^r}{\lambda+\mu\theta^r} - \sum_{k=1}^{N} c_k a_{-1}a_{-2}\cdots a_{1-k}b_{k+1}b_{k+2}\cdots b_N e^{-\omega_k t},$$

which is fundamentally different in character.

For example the deterministic variable $y(t)$ is a monotone function of t, but this is not in general true of the mean, which also has a different limit as t tends to infinity. The moments of higher order have extremely complicated expressions.

For this process, the natural set of quantities which characterise the distribution is $\{R_j(t) = \Pi(\theta^{-j}, t);\ j = 1, 2, \cdots N\}$.

These are exponentially weighted sums of the probabilities,

$$R_j(t) = \sum_{k=0}^{N} \theta^{-jk} p_k(t).$$

We have

$$R_j(t) = \sum_{k=0}^{j} c_k a_j a_{j-1} \cdots a_{j-k+1} b_{j+k+1} b_{j+k+2} \cdots b_{j+N} e^{-\omega_k t},$$

which depends only on the first $j+1$ eigenvalues. For example

$$R_1(t) = E[\theta^{-i(t)}] = \frac{\lambda\theta+\mu}{\lambda\theta+\mu\theta^N} + \left(\theta^{-n} - \frac{\lambda\theta+\mu}{\lambda\theta+\mu\theta^N}\right) \exp[-(\theta-1)(\lambda+\mu\theta^{N-1})t],$$

which is comparable to the above expression for $\theta^{-\nu(t)}$. In practise these parameters would be awkward to deal with. However the probability generating function itself is not unmanageable. In particular, since $0 < \omega_1 < \omega_2 \cdots < \omega_N$, the asymptotic properties of the distribution can be obtained by considering the initial terms of its expansion. By substituting the values of c_0 and c_1, we have, in the original notation:

$$\begin{aligned}\Pi(x, t) = {} & \frac{(\lambda+\mu x)(\lambda+\mu\theta x)\cdots(\lambda+\mu\theta^{N-1}x)}{(\lambda+\mu)(\lambda+\mu\theta)\cdots(\lambda+\mu\theta^{N-1})} \\ & + \left[\left(\frac{\theta^{-n}}{\lambda\theta+\mu} - \frac{1}{\lambda\theta+\mu\theta^N}\right)\frac{\theta^2(1-x)(\lambda+\mu x)(\lambda+\mu\theta x)\cdots(\lambda+\mu\theta^{N-2}x)}{(\theta-1)(\lambda+\mu)(\lambda+\mu\theta)\cdots(\lambda+\mu\theta^{N-3})}\right. \\ & \left.\times \exp[-(\theta-1)(\lambda+\mu\theta^{N-1})t]\right] + 0(e^{-\omega_2 t}).\end{aligned}$$

4. Remarks on the Eigenvalues

The eigenvalues of the process considered in the preceding section are linearly related to its transition rates; $\omega_k = \lambda_k + \mu_{N-k};\ k = 0, 1, \cdots N$. In fact, as we shall prove, the process is uniquely determined by this property.

The process with arbitrary left and right transition rates λ_j and μ_j, can be regarded as a superposition of a birth process and a death process. Let $\lambda_j = \alpha u_j$ and let $\mu_j = \beta v_{N-j};\ j = 0, 1, \cdots N$, where $u_0 = v_0 = 0$; $u_1 \cdots u_N$, $v_1 \cdots v_N$, are fixed positive constants, and $\alpha \geqq 0$, $\beta \geqq 0$ are arbitrary. For simplicity we further suppose that $u_1, u_2, \cdots u_N$, are distinct and similarly for $v_1, v_2, \cdots v_N$. The pure birth process arises when $\alpha = 0$. Again, if $\beta = 0$, only transitions to the left are possible, and we have a death process. The eigenvalues of the complete process are the roots $\omega_0, \omega_1, \cdots \omega_N$ of the equation $|\alpha U + \beta V - \omega I| = 0$, where

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$$\alpha U+\beta V=\begin{pmatrix} \alpha u_0+\beta v_N & -\beta v_N & 0 & \cdots\cdots 0 & 0 \\ -\alpha u_1 & \alpha u_1+\beta v_{N-1} & -\beta v_{N-1} & 0 & 0 \\ 0 & -\alpha u_2 & \alpha u_2+\beta v_{N-2} & 0 & 0 \\ \vdots & & & \ddots & \vdots \\ 0 & 0 & 0 & \alpha u_{N-1}+\beta v_1 & -\beta v_1 \\ 0 & 0 & 0\ \cdots\cdots & -\alpha u_N & \alpha u_N+\beta v_0 \end{pmatrix}.$$

Consider these eigenvalues as functions of α and β. In the case $\alpha = 0$ the roots are simply $\beta v_0, \beta v_1, \cdots \beta v_N$, and similarly when $\beta = 0$, but in general, these functions are irrational. The question arises, under what conditions on the parameters $u_1, \cdots u_N$, $v_1, \cdots v_N$, do the eigenvalues have a simple form, for arbitrary α and β.

It becomes clear on examining the characteristic equation for small values of N, that the only suitable form is linear. For example, in the case $N = 2$, it is easily verified that ω_0, ω_1, ω_2 are rational functions of α and β if and only if $u_1/u_2 + v_1/v_2 = 1$ and then $\omega_k = \alpha u_k + \beta v_k$ for $k = 0, 1, 2$. Consequently, we restrict attention to the relations $\omega_k = \alpha u_k + \beta v_k$; $k = 0, 1, \cdots N$, when N is arbitrary. The required conditions are established in the following theorem.

THEOREM. $|\alpha U + \beta V - \omega I| \equiv \prod_{k=0}^{N} (\alpha u_k + \beta v_k - \omega)$, if and only if there exists a positive constant θ, such that $u_j = u_1 (\theta^j - 1)/(\theta - 1)$ and $v_j = v_1(1-\theta^{-j})/(1-\theta^{-1})$, for $j = 1, 2, \cdots N$.

PROOF. The first statement has already been verified in section 3. It remains to prove the only if assertion.

(i) Let A and B be any square matrices of order m, with distinct eigenvalues $\xi_1, \xi_2, \cdots \xi_m$, and $\eta_1, \eta_2, \cdots \eta_m$, respectively. The following condition is necessary for the identity $|\alpha A+\beta B-\omega I| \equiv \prod_{j=1}^{m}(\alpha\xi_j+\beta\eta_j-\omega)$. When A is reduced by an orthogonal transformation to the form diag $[\xi_1, \xi_2, \cdots \xi_m]$ the corresponding reduction of B has the elements $\eta_1, \eta_2, \cdots \eta_m$, in that order, on its diagonal. Suppose that on applying the transformation, B is replaced by (b_{jk}). The above identity continues to hold, and in particular we may set $\omega = \alpha\xi_1$. Then it follows by comparing the coefficients of $\alpha^{m-1}\beta$, that $b_{11} = \eta_1$, and similarly $b_{jj} = \eta_j$ for $j = 2, 3, \cdots m$.

(ii) We apply this necessary condition to the case $A = U$, $B = V$; given that $|\alpha U + \beta V - \omega I| \equiv \prod_{k=0}^{N} (a u_k + \beta v_k - \omega)$. Since U is a triangular matrix, and $u_1, u_2, \cdots u_N$ are distinct, the eigenvectors needed for constructing the linear transformation which reduces U to diag $[u_0, u_1, \cdots u_N]$ are not difficult to obtain. This transformation must then be applied to V, and the new diagonal elements equated to $v_0, v_1, \cdots v_N$, in order. These calculations lead directly to the equations

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$$(4.1)\qquad \frac{v_j}{u_j} = \frac{v_{N+1-j}}{u_j - u_{j-1}} - \frac{v_{N-j}}{u_{j+1} - u_j}; \quad \text{for } j = 1, 2, \cdots N.$$

Since U and V may be interchanged, we also have

$$(4.2)\qquad \frac{u_j}{v_j} = \frac{u_{N+1-j}}{v_j - v_{j-1}} - \frac{u_{N-j}}{v_{j+1} - v_j}; \quad j = 1, 2, \cdots N.$$

A number of elementary manipulations must be applied to these formulae before the required results are obtained, but only the more important steps will be mentioned. We suppose throughout the remainder of the proof that $N = 2n$, is an even integer. A similar argument applies in the case when N is odd.

(iii) We deduce that

$$(4.3)\qquad \frac{u_{n+r+1} - u_{n+r}}{u_{n+r} - u_{n+r-1}} = \frac{v_{n-r}u_{n+1-r}}{u_{n-r}v_{n+1-r}} = \frac{v_{n+r} - v_{n+r-1}}{v_{n+r+1} - v_{n+r}},$$

for every integer r in the range $|r| \leqq n - 1$. We proceed by induction on r. The case $r = 0$ follows from equations (4.1) and (4.2), when $j = n$. Now suppose (4.3) holds for every value of r in $|r| \leqq k - 1$, where $0 < k < n$. Then by multiplying together the corresponding parts of (4.3) for the cases $r = -(k-1), -(k-2), \cdots (k-2), (k-1)$, we obtain

$$\frac{u_{n+k} - u_{n+k-1}}{u_{n+1-k} - u_{n-k}} = \frac{u_{n+k}v_{n+1-k}}{v_{n+k}u_{n+1-k}} = \frac{v_{n+1-k} - v_{n-k}}{v_{n+k} - v_{n+k-1}}.$$

The first part of this equation shows that

$$\frac{v_{n+k}}{u_{n+k}} = \frac{v_{n+1-k}}{u_{n+1-k}} \frac{(u_{n+1-k} - u_{n-k})}{(u_{n+k} - u_{n+k-1})}.$$

Now set $j = n + k$ in (4.1) and we have

$$\frac{v_{n+k}}{u_{n+k}} = \frac{v_{n+1-k}}{u_{n+k} - u_{n+k-1}} - \frac{v_{n-k}}{u_{n+k+1} - u_{n+k}}.$$

Then it follows from the last two statements that

$$\frac{u_{n+k+1} - u_{n+k}}{u_{n+k} - u_{n+k-1}} = \frac{v_{n-k}u_{n+1-k}}{u_{n-k}v_{n+1-k}}.$$

This remains true when u and v are interchanged, and hence equation (4.3) is valid when $r = k$. Similarly, the case $r = -k$ is established, and the induction is proved.

(iv) Let $u_{j+1} - u_j = \theta_j$ and $v_{j+1} - v_j = c/\theta_j$ for $j = 0, 1, \cdots N - 1$. By (4.3), c does not depend on j. The final step in the proof consists of

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showing that θ_{j+1}/θ_j is also constant. We may suppose without loss of generality that $u_n = v_n = 1$. Let $\theta = \theta_n/\theta_{n-1}$. Then equation (4.3) implies, when $r = 0$; $c = (1 + \theta_n - \theta)\theta_n/\theta$. Next, the case $r = 1$ gives us $\theta_{n+1}/\theta_n = (\theta_{n-1} - c)/[\theta_{n-1}(1 - \theta_{n-1})] = \theta$. We can continue the argument by using the cases $r = -1, 2, -2$, and so on, until it is established that $\theta_{j+1}/\theta_j = \theta$ for every $j = 0, 1, \cdots N-2$. The restriction $u_n = v_n = 1$, may now be removed.

We have shown that $\theta_j = \theta_0\theta^j$ when $j = 0, 1, \cdots N-1$. Thus $u_j = \theta_0(1-\theta^j)/(1-\theta)$, $v_j = c(1-\theta^{-j})/[\theta_0(1-\theta^{-1})]$, except when $\theta = 1$, when there are obvious modifications. Alternatively: $u_j = u_1(\theta^j-1)/(\theta-1)$ and $v_j = v_1(1-\theta^{-j})/(1-\theta^{-1})$, which proves the theorem.

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Note added in proof: For a more direct determination of the eigenvalues for Moran's model, the reader is referred to: J. Gani. On the stochastic matrix in a genetic model of Moran. *Biometrika. Vol. 48, 1961, p. 203.*

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