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LINEAR BIRTH AND DEATH PROCESSES WITH KILLING

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Abstract

We analyze a class of linear birth and death processes $X(t)$ with killing. The generator is of the form $\lambda_i = bi + \theta$, $\mu_i = ai$, $\gamma_i = ci$, where γ_i is the killing rate. Then $P\{\text{killed in } (t, t+h) \mid X(t) = i\} = \gamma_i h + o(h)$, $h \downarrow 0$. A variety of explicit results are found, and an example from population genetics is given.

BIRTH-DEATH PROCESSES; KILLING; POPULATION GENETICS

0. Introduction

Let $\{Y(t), t \geqq 0\}$ be a birth–death process on $S = \{0, 1, 2, \cdots\}$ with infinitesimal generator $A = (a_{ij})$ given by

$$(0.1)\qquad \begin{aligned} &a_{ij} = 0, \qquad |i-j| > 1 \\ &a_{i,i+1} = \lambda_i, \quad a_{i,i-1} = \mu_i, \quad a_{ii} = -(\lambda_i + \mu_i), \end{aligned}$$

where $\lambda_i > 0$ for $i \geqq 0$, $\mu_i > 0$ for $i \geqq 1$, and $\mu_0 \geqq 0$. If $\mu_0 > 0$, the process has an absorbing state at -1. It is established in [1] that in virtually all practical cases of birth–death processes the transition function $P_{ij}(t) = P\{Y(t) = j \mid Y(0) = i\}$ may be represented in the form

$$(0.2)\qquad P_{ij}(t) = \pi_j \int_0^\infty e^{-xt} Q_i(x) Q_j(x) d\rho(x), \qquad i, j \geqq 0$$

where ρ is a positive measure on $[0, \infty)$, and the system of polynomials $\{Q_n(x)\}$ satisfies

$$(0.3)\qquad \begin{aligned} &Q_0(x) \equiv 1 \\ -&xQ_0(x) = -(\lambda_0 + \mu_0)Q_0(x) + \lambda_0 Q_1(x) \\ -&xQ_n(x) = \mu_n Q_{n-1}(x) - (\lambda_n + \mu_n)Q_n(x) + \lambda_n Q_{n+1}(x), \qquad n \geqq 1, \end{aligned}$$

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and the orthogonality relations

$$\int_0^\infty Q_i(x)Q_j(x)d\rho(x) = \frac{\delta_{ij}}{\pi_j}, \qquad i, j \geqq 0$$

where

$$\pi_0 = 1, \quad \pi_n = \frac{\lambda_0\lambda_1 \cdots \lambda_{n-1}}{\mu_1\mu_2 \cdots \mu_n}, \qquad n \geqq 1.$$

In this note we study the properties of a class of birth–death processes with generator of the form

$$\begin{aligned} &a_{ij} = 0, \qquad |i-j| > 1 \\ &a_{i,i+1} = \lambda_i, \quad a_{i,i-1} = \mu_i, \quad a_{ii} = -(\lambda_i + \mu_i + \gamma_i), \end{aligned} \tag{0.4}$$

where $\gamma_i > 0$, $i > 0$. The parameter γ_i may be regarded as the rate of absorption, or killing into a fictitious state H, say;

$$P\{Y(t+h) = H \mid Y(t) = i\} = \gamma_i h + o(h), \qquad h \downarrow 0.$$

Our study of linear birth–death processes with killing was motivated in part by the following problem from population genetics. Consider a population of N individuals, each of which is classified as one of three possible genotypes AA, Aa, aa. A question of some interest, posed originally in [6], is: Given that the population currently comprises only the genotypes AA and Aa, how long does it take to produce the first homozygote aa? To put the problem in a simple framework, let $(X(t), Y(t))$ be the number of Aa, aa genotypes in the population at time t, and take $(X(0), Y(0)) = (i, 0)$ for $0 \leqq i \leqq N$. Then we want to ascertain the properties of the time T defined by $T = \inf\{t > 0 : Y(t) > 0\}$. Since $Y(t)$ is currently 0, we need only keep track of $X(t)$, and we add an extra state H to the state space $S = \{0, 1, \cdots, N\}$ to account for any cases in which $Y(\cdot) > 0$.

We concentrate on a model in which reproduction occurs by selfing. For further details of the problem, see also [3], [6]. We assume that reproduction events occur at the points of a Poisson process of rate λ. At such a point, suppose there are no aa individuals, i Aa and $N-i$ AA in the population. Following Moran [5], we chose one individual at random to die, and one to replace him as the result of selfing. The probabilities p_{AA}, p_{Aa}, p_{aa} that the replacement individual is of genotype AA, Aa, aa are given by

$$p_{AA} = 1 - \frac{3i}{4N}, \qquad p_{Aa} = \frac{i}{2N}, \qquad p_{aa} = \frac{i}{4N}. \tag{0.5}$$

The process $X(\cdot)$ is now identified as a birth–death process with killing on $S = \{0, 1, \cdots, N\} \cup \{H\}$, and the rates (0.4) are given by

$$\lambda_i = \lambda\left(1-\frac{i}{N}\right)p_{Aa}$$

(0.6) $$\mu_i = \lambda\frac{i}{N}p_{AA}$$

$$\gamma_i = \lambda p_{aa}.$$

Explicit results for this process are not easy to find, but there is an approximating process that is readily analyzed. We take $\lambda = N$ (corresponding to speeding up the timescale), and let $N\to\infty$. We obtain a process $\tilde{X}(\cdot)$ on $\{H\}\cup\{0,1,\cdots\}$ with transition rates

(0.7) $$\lambda_i = \tfrac{1}{2}i, \quad \mu_i = i, \quad \gamma_i = \tfrac{1}{4}i.$$

We described a number of explicit results for the process corresponding to (0.7) in Section 4.

1. Preliminaries

Although the methods we develop will apply in more general cases, we focus primary attention on a variety of linear processes, where explicit results are readily established. We start with the case of (0.1) where

(1.1) $$\lambda_i = (i+1)\lambda, \quad \mu_i = (i+\beta-1)\mu, \quad \lambda<\mu, \quad \beta>1.$$

Here $\mu_0>0$, so there is an absorbing state at -1. We denote the corresponding process by $\bar{X}(\cdot)=\{\bar{X}(t), t\geqq 0\}$. The properties of this process have been established in detail in [2]. We record the following results. Let

$$F(a,b;c;z)=\sum_{n\geqq 0}\frac{(a)_n(b)_n z^n}{n!(c)_n}, \qquad (a)_n=\frac{\Gamma(a+n)}{\Gamma(a)},$$

and define

(1.2) $$\varphi_n(x)=\varphi_n(x;\beta,\gamma)=F(-n,-x;\beta;1-(1/\gamma)),$$

for $\beta>0$, $0<\gamma<1$, and set $\varphi_{-1}\equiv 0$. The polynomials $(\beta)_n\varphi_n(x)$ are the classical Meixner polynomials. Now set

(1.3) $$\rho_n=(1-\gamma)^\beta(\beta)_n\frac{\gamma^n}{n!}, \qquad \gamma=\frac{\lambda}{\mu}.$$

Table 1C of [2] establishes that if $x_n=(n+\beta-1)(\mu-\lambda)$, then $\bar{P}_{ij}(t)=P\{\bar{X}(t)=j\mid \bar{X}(t)=i\}$ is given by

(1.4) $$\bar{P}_{ij}(t)=\left(\frac{\lambda}{\mu}\right)^j\frac{j!}{(\beta)_j}\sum_{n=0}^{\infty}e^{-x_n t}Q_i(x_n)Q_j(x_n)\rho_n$$

where

$$Q_n(x) = \frac{(\beta)_n}{n!}\varphi_n\left(\frac{x}{\mu-\lambda} - \beta + 1\right).$$

From now on we concentrate on the case $\beta = 2$. If we write $X(t) = \bar{X}(t) + 1$, then $\{X(t), t \geqq 0\}$ is the standard linear birth–death process on $S = \{0, 1, 2, \cdots\}$ with rates

$$\lambda_i = i\lambda, \quad \mu_i = i\mu, \quad i \geqq 0 \quad (\lambda < \mu) \tag{1.5}$$

and $P_{ij}(t) = \bar{P}_{i-1,j-1}(t)$, $i, j \geqq 1$. The explicit representation of $\bar{P}_{ij}(t)$ given in [2], pp. 654–5 is also useful, but we content ourselves with recording two standard formulas that can also be derived from [1] and [2].

$$G_i(z,t) = \sum_{j=0}^{\infty} P_{ij}(t)z^j = \left[\frac{(1-\sigma)+(\sigma-\gamma)z}{1-\sigma\gamma - z\gamma(1-\sigma)}\right]^i, \qquad i \geqq 1, \quad |z| < 1 \tag{1.6}$$

where $\sigma = \exp\{-(\mu-\lambda)t\}$. We note the notation of σ here differs from [2].

$$G_{ij} = \int_0^\infty P_{ij}(t)dt = \begin{cases} \gamma^j(1-\gamma^{-i})[j(\lambda-\mu)]^{-1}, & 0 < i \leqq j \\ [j(\lambda-\mu)]^{-1}(\gamma^j - 1), & i > j. \end{cases} \tag{1.7}$$

2. Linear birth–death with killing

We now focus on the special case of (0.4) in which the process $\tilde{X}(\cdot) = \{\tilde{X}(t), t \geqq 0\}$ has state space $\{H\} \cup \{0, 1, 2, \cdots\}$, and generator determined by

$$\lambda_i = bi, \quad \gamma_i = ci, \quad \mu_i = ai, \tag{2.1}$$

where $a, b, c > 0$.

In what follows, let v_0 and v_1 be the roots of the equation

$$bv + (a/v) = a + b + c; \qquad 0 < v_0 < 1 < v_1. \tag{2.2}$$

It is clear that either $\tilde{X}$ is absorbed at 0 or killed at H in finite time. Standard probabilistic arguments show that

$$q_i = P\{\tilde{X}(t) \text{ hits } 0 \text{ before } H \mid \tilde{X}(0) = i\} = v_0^i, \qquad i \geqq 0.$$

So we are led to look at the associated process $\{X(t), t \geqq 0\}$ obtained by conditioning on $\{0\}$ being reached first. The transition probabilities are given by

$$P_{ij}(t) = \tilde{P}_{ij}(t)v_0^j v_0^{-i}, \qquad i, j \geqq 0. \tag{2.3}$$

Observe that $P_{i,i+1}(h) = \tilde{P}_{i,i+1}(h)v_0 = ibv_0h + o(h)$ and $P_{i,i-1}(h) = (ia/v_0)h + o(h)$. Therefore, $X(\cdot)$ is a linear birth–death process with transition rates given by

$$\lambda_i = ibv_0; \quad \mu_i = \frac{ia}{v_0} = ibv_1, \qquad i \geqq 0. \tag{2.4}$$

(The last equation results since the product of the roots of (2.2) is $v_0 v_1 = a/b$.) Clearly, $\lambda_i = ibv_0 < \mu_i = ibv_1$. It follows immediately that $X(\cdot)$ is generated as a special case of (1.5). Hence, for $|z| \leqq 1$,

$$\tilde{G}_i(z,t) = \sum_{j=0}^{\infty} \tilde{P}_{ij}(t) z^j = \sum_{j=0}^{\infty} v_0^i v_0^{-j} P_{ij}(t) z^j = v_0^i G_i(z v_0^{-1}, t).$$

Using the identifications $\lambda = bv_0$, $\mu = a/v_0$, $\gamma = \lambda/\mu = v_0/v_1$, we have

$$\tilde{G}_i(z,t) = \left[\frac{v_0 v_1(1-\sigma) + z(v_1\sigma - v_0)}{v_1 - \sigma v_0 - z(1-\sigma)}\right]^i, \tag{2.5}$$

where in this case $\sigma = \exp\{-b(v_1 - v_0)t\}$. We also record from (1.7) that $\tilde{G}_{ij} = \int_0^\infty \tilde{P}_{ij}(t)dt = v_0^i v_0^{-j} G_{ij}$ is given by

$$\tilde{G}_{ij} = \begin{cases} [jb(v_1 - v_0)]^{-1} v_1^{-j}(v_1^i - v_0^i), & 0 < i \leqq j \\ [jb(v_1 - v_0)]^{-1} v_0^i(v_0^{-j} - v_1^{-j}), & i \geqq j. \end{cases} \tag{2.6}$$

We shall now discuss some of the properties of the killing process. Denote by T_H the hitting time of H. Since $P_i\{T_H > t\} = P_i\{0 \leqq \tilde{X}(t) < \infty\} = \tilde{G}_i(1,t)$, (where P_i, E_i denote probabilities and expectations given $\tilde{X}(0) = i$), we have

$$P_i\{T_H > t\} = \left[\frac{v_0(v_1 - 1) + v_1\sigma(1 - v_0)}{(v_1 - 1) + \sigma(1 - v_0)}\right]^i, \qquad i \geqq 1. \tag{2.7}$$

(2.7) establishes, letting $t \to \infty$ and hence $\sigma \to 0$, that $P_i\{T_H < \infty\} = 1 - v_0^i$, which confirms that indeed $\tilde{X}(\cdot)$ ends at $\{0\}$ or $\{H\}$. The mean termination time is given by $E_i[T] = E_i(T_0 \wedge T_H) = \sum_{j=1}^\infty \tilde{G}_{ij}$.

In what follows, we shall consider only those sample paths that end at $\{H\}$ rather than $\{0\}$. Denote this process by $X^*(t)$, with transition functions $P_{ij}^*(t)$, $i, j \geqq 1$. Since in this process $\{H\}$ is hit with probability 1, it makes sense to define the killing position $K = X^*(T_H)$. We shall derive the distribution of K in the following lemma.

Lemma 1. Let $\{X(t), t \geqq 0\}$ be a birth–death process with infinitesimal parameters (0.4). Assume $P_i\{T_H < \infty\} = 1$ for all $i \in S$. Then $P_i\{K = j\} = G_{ij}\gamma_j$, $i, j \in S$.

Proof. $P_i\{X(t) = j,\ t < T_H \leqq t + h\} = P_{ij}(t)\gamma_j h + o(h)$, $h \downarrow 0$. So $P_i\{K = j\} = \int_0^\infty P_{ij}(t)\gamma_j dt \equiv \gamma_j G_{ij}$.

For the process at hand, the relevant Green's function G_{ij}^* is given by

$$G_{ij}^* = \int_0^\infty P_{ij}^*(t)dt = \frac{1 - v_0^j}{1 - v_0^i}\int_0^\infty \tilde{P}_{ij}(t)dt = \frac{1 - v_0^j}{1 - v_0^i}\tilde{G}_{ij},$$

and since $\gamma_j = cj(1-v_0^j)^{-1}$ (the rate of killing given eventual killing) we find that

$$P_i\{K=j\} = cj\tilde{G}_{ij}(1-v_0^i)^{-1} = \begin{cases} c[b(v_1-v_0)]^{-1}(1-v_0^i)^{-1}v_1^{-j}(v_1^i - v_0^i), & 0<i\leqq j \\ c[b(v_1-v_0)]^{-1}(1-v_0^i)^{-1}v_0^i(v_0^{-j}-v_1^{-j}), & i\geqq j. \end{cases} \tag{2.8}$$

When $i=1$, we see that $P_1\{K=j\} = (1-1/v_1)(1/v_1)^{j-1}$, $j\geqq 1$.

To describe the behavior of $\tilde{X}(\cdot)$ and $X^*(\cdot)$ before killing takes place, we shall study the asymptotic conditional distributions given by

$$\begin{aligned} \tilde{a}_j &= \lim_{t\to\infty} P_i\{\tilde{X}(t)=j \mid T_0 \wedge T_H > t\}, \\ a_j^* &= \lim_{t\to\infty} P_i\{X^*(t)=j \mid T_H > t\}. \end{aligned} \tag{2.9}$$

These are straightforward to compute from (2.5), via the following lemma.

Lemma 2. $\lim_{t\to\infty}\sigma^{-1}(\tilde{G}_i(z,t)-v_0^i) = -v_0^{i-1}A(z)$, $i\geqq 1$, where $\sigma = \exp\{-b(v_1-v_0)t\}$ and $A(z) = (v_1-v_0)(v_0-z)/(v_1-z)$, $0\leqq z<v_1$.

Proof. From (2.5), we can write

$$\tilde{G}_i(z,t) = \left\{v_0 - \sigma A(z)\left[1-\sigma\left(\frac{v_0-z}{v_1-z}\right)\right]^{-1}\right\}^i.$$

Hence

$$\begin{aligned} \tilde{G}_i(z,t) - v_0^i &= \sum_{k=0}^{i}\binom{i}{k}\left\{-\sigma A(z)\left(1-\sigma\left(\frac{v_0-z}{v_1-z}\right)\right)^{-1}\right\}^k v_0^{i-k} - v_0^i \\ &= \sum_{k=1}^{i}\binom{i}{k}\left[-\sigma A(z)\left\{1-\sigma\left(\frac{v_0-z}{v_1-z}\right)\right\}^{-1}\right]^k v_0^{i-k}. \end{aligned}$$

The result now follows immediately as $\sigma\to 0$ when $t\to\infty$.

To establish the first of (2.9), we use Lemma 2 to see that for $0\leqq z\leqq 1$,

$$\begin{aligned} \sum_{j=1}^{\infty} P_i\{\tilde{X}(t)=j \mid T>t\}z^j &= \frac{\tilde{G}_i(z,t)-\tilde{G}_i(0,t)}{\tilde{G}_i(1,t)-\tilde{G}_i(0,t)} \\ &\to \frac{-A(z)+A(0)}{-A(1)+A(0)} \qquad \text{as } t\to\infty. \end{aligned}$$

The limit is precisely the probability generating function of $\tilde{a}_j$, which leads on simplification to

$$\tilde{a}_j = \left(1-\frac{1}{v_1}\right)\left(\frac{1}{v_1}\right)^{j-1}, \qquad j\geqq 1.$$

Using similar considerations, we see that for $0\leqq z\leqq 1$

$$\sum_{j=1}^{\infty} P_i\{X^*(t)=j \mid T_H > t\}z^j = \left[\sum_{k=1}^{\infty} P_{ik}^*(t)\right]^{-1} \sum_{j=1}^{\infty} \frac{(1-v_0^j)}{(1-v_0^i)} \tilde{P}_{ij}(t)z^j$$
$$= \frac{\tilde{G}_i(z,t)-\tilde{G}_i(zv_0,t)}{\tilde{G}_i(1,t)-\tilde{G}_i(v_0,t)}.$$

So another application of Lemma 2 shows that $\{a_j^*, j \geqq 1\}$ has probability generating function given by

$$\sum_{j=1}^{\infty} a_j^* z^j = \frac{-A(z)+A(zv_0)}{-A(1)+A(v_0)}.$$

The probabilities $\{a_j^*\}$ are given by

$$a_j^* = \frac{v_1-v_0}{v_1(1-v_0)}\left(1-\frac{1}{v_1}\right)\left(\frac{1}{v_1}\right)^{j-1} - \frac{v_0(v_1-1)}{v_1(1-v_0)}\left(1-\frac{v_0}{v_1}\right)\left(\frac{v_0}{v_1}\right)^{j-1}, \qquad j \geqq 1.$$

3. Linear birth–death process with immigration and killing

In this section, we concentrate on the birth–death process $\tilde{X}(t)$ with killing on state space $\{0,1,\cdots\}\cup\{H\}$ with infinitesimal transition rates given by

$$\tilde{a}_{i,i+1} = bi+\theta, \quad \tilde{a}_{i,i-1} = ai, \quad \tilde{a}_{ii} = -[i(a+b+c)+\theta] \tag{3.1}$$

where $a, b, c, \theta > 0$.

The following observation simplifies the analysis. Let $v = v_0$ be the smaller solution of Equation (2.2), and define

$$a^* = a/v, \quad b^* = vb, \quad \theta^* = \theta v, \quad \kappa = \theta(1-v). \tag{3.2}$$

Recall from (2.4) that $a^* > b^*$. Let $X(t)$ be a birth–death process with rates

$$\lambda_i = ib^* + \theta^*, \quad \mu_i = ia^*, \qquad i \geqq 0 \tag{3.3}$$

and let $P_{ij}(t)$ be its transition functions. Define

$$\tilde{P}_{ij}(t) = v^{-j}v^i P_{ij}(t)e^{-\kappa t}, \qquad i,j \geqq 0. \tag{3.4}$$

Lemma 3. The functions $\{\tilde{P}_{ij}(t), t>0\}$ satisfy

$$\tilde{P}_{ij}'(t) = ai\tilde{P}_{i-1,j}(t) - \{i(a+b+c)+\theta\}\tilde{P}_{ij}(t) + (bi+\theta)\tilde{P}_{i+1,j}(t), \qquad i,j \geqq 0$$

and $\tilde{P}_{ij}(t) = P\{\tilde{X}(t)=j \mid \tilde{X}(0)=i\}$.

Proof. $\tilde{P}_{ij}'(t) = v^{-j}v^i P_{ij}'(t)e^{-\kappa t} - \kappa\tilde{P}_{ij}(t)$, $i,j \geqq 0$.

Now use the backward equation satisfied by $\{P_{ij}(t), t>0\}$ to see that

$$\tilde{P}_{ij}'(t) = e^{-\kappa t}v^{-j}v^i[a^*iP_{i-1,j}(t) + (b^*i+\theta^*)P_{i+1,j}(t)$$
$$-((a^*+b^*)i+\theta^*)P_{ij}(t)] - \kappa\tilde{P}_{ij}(t)$$
$$= ai\tilde{P}_{i-1,j}(t) + (bi+\theta)\tilde{P}_{i+1,j}(t) - \{(a+b+c)i+\theta\}\tilde{P}_{ij}(t).$$

Since $\{\tilde{P}_{ij}(t), t \geqq 0\}$ satisfy the requisite equations for $\{\tilde{X}(t), t \geqq 0\}$, and because the infinitesimal rates are linear they determine a unique process. We may then take $\tilde{P}_{ij}(t) = P\{\tilde{X}(t) = j \mid \tilde{X}(0) = i\}$, and the proof is complete.

It is worth while noting that if in (3.2) we specify $v = v_1$ (the larger solution of (2.2)) the resulting $\tilde{X}(t)$ is identical to that determined from $v = v_0$.

The $X(\cdot)$ generated by (3.2) and (3.3) is a linear birth–death process with immigration which has been extensively studied. In particular, the spectral decomposition (0.2) is given in [2], Table 1F. From [2],

$$P_{ij}(t) = \pi_j \int_0^\infty e^{-xt} Q_i(x) Q_j(x) d\rho(x) \tag{3.5}$$

with

$$\sigma = \exp\{-b(v_1 - v_0)t\}, \quad \pi_j = \left(\frac{v_0}{v_1}\right)^j \frac{(\beta)_j}{j!}, \quad \beta = \frac{\theta}{b}, \quad \gamma = \frac{v_0}{v_1} \tag{3.6}$$

where the measure $\rho(\cdot)$ has masses of size ρ_n (cf. Equation (1.3)) at points $x_n = nb(v_1 - v_0)$, $n = 0, 1, 2, \cdots$, and $Q_n(x) = \varphi_n(x/b(v_1 - v_0), \beta, \gamma$ (cf. (1.2)). (3.5) reduces then to

$$P_{ij}(t) = \pi_j \sum_{n=0}^\infty \sigma^n \varphi_i(n) \varphi_j(n) \rho_n. \tag{3.7}$$

The spectral representation

$$\tilde{P}_{ij}(t) = \tilde{\pi}_j \int_0^\infty e^{-yt} \tilde{Q}_i(y) \tilde{Q}_j(y) d\tilde{\rho}(y)$$

is now accessible.

In fact

$$\tilde{P}_{ij}(t) = v_0^i v_0^{-j} e^{-\kappa t} P_{ij}(t),$$

and from (3.5) we get

$$\begin{aligned}\tilde{P}_{ij}(t) &= v_0^i v_0^{-j} e^{-\kappa t} \pi_j \int_0^\infty e^{-xt} Q_i(x) Q_j(x) d\rho(x) \\ &= \frac{\pi_j}{v_0^{2j}} \int_0^\infty e^{-(\kappa + x)t} [v_0^i Q_i(x)][v_0^j Q_j(x)] d\rho(x) \\ &= \tilde{\pi}_j \int_\kappa^\infty e^{-yt} [v_0^i Q_i(y - \kappa)][v_0^j Q_j(y - \kappa)] d\rho(y - \kappa).\end{aligned}$$

The spectral measure $\tilde{\rho}$ is given by $\tilde{\rho}(E) = \rho(E - \kappa)$, that is $\tilde{\rho}$ concentrates mass ρ_n of (1.3) at $\kappa + nb(v_1 - v_0)$, $n = 0, 1, 2, \cdots$, and

$$\tilde{Q}_i(x) = v_0^i Q_i(x - \kappa), \qquad i \geqq 0. \tag{3.8}$$

Now $X(\cdot)$ is positive recurrent and $\lim_{t\to\infty} e^{\kappa t}\tilde{P}_{ij}(t) = v_0^i v_0^{-j}\pi_j\rho_0$. Further, the sequences $m_i = \pi_i v_0^{-i}$ $(i \geqq 0)$, $\xi_i = v_0^i$ $(i \geqq 0)$ satisfy the invariance properties

$$\sum_i m_i \tilde{P}_{ij}(t) = e^{-\kappa t} m_j, \qquad j \geqq 0 \tag{3.9}$$

$$\sum_j \tilde{P}_{ij}(t)\xi_j = e^{-\kappa t}\xi_i, \qquad i \geqq 0.$$

It follows in particular that $Z(t) = e^{t\kappa} v_0^{X(t)}$ is a martingale.

The spectral representation yields in a simple way the recurrence properties of $\tilde{X}(t)$; see also [4]. The explicit form for $\tilde{P}_{ij}(t)$ now follows from (3.4) and [2], p. 655. Hence, we have

$$G_i(z,t) = \sum_{j=0}^{\infty} P_{ij}(t) z^j$$

$$= \left[\frac{1-\sigma - z(\gamma-\sigma)}{1-\sigma\gamma - \gamma z(1-\sigma)}\right]^i \left[\frac{1-\gamma\sigma-\gamma z(1-\sigma)}{1-\gamma}\right]^{-\beta}, \qquad i \geqq 0, \tag{3.10}$$

where

$$\sigma = e^{-b(v_1 - v_0)t}, \quad \gamma = \frac{v_0}{v_1}, \quad \beta = \frac{\theta}{b}$$

and so

$$\tilde{G}_i(z,t) = \sum_{j=0}^{\infty} \tilde{P}_{ij}(t) z^j$$

$$= \sum_{j=0}^{\infty} v_0^{-j} v_0^i P_{ij}(t) e^{\kappa t} z^j$$

$$= v_0^i e^{-\kappa t} G_i(z v_0^{-1}, t).$$

Again, denoting by T the killing time, we have

$$P_i\{T > t\} = \tilde{G}_i(1,t) = v_0^i e^{-\kappa t} G_i(v_0^{-1}, t), \qquad i \geqq 0;$$

$$= e^{-\kappa t}\left[\frac{v_0(v_1-1)+v_1\sigma(1-v_0)}{v_1 - 1 + \sigma(1-v_0)}\right]^i \left[\frac{(v_1-1)+\sigma(1-v_0)}{v_1 - v_0}\right]^{-\beta}, \qquad i \geqq 0. \tag{3.11}$$

For the case $i = 0$, we find

$$E_0[T] = \int_0^\infty \tilde{G}_0(1,t)dt$$

$$= \left(\frac{v_1 - v_0}{v_1 - 1}\right)^{\beta} \frac{1}{\theta(1-v_0)} F\left(\beta, \beta\left(\frac{1-v_0}{v_1 - v_0}\right); \beta\left(\frac{1-v_0}{v_1-v_0}\right) + 1; \frac{v_0 - 1}{v_1 - 1}\right).$$

Lemma 1 shows in principle how to find the distribution of the detection position, once the Green's function

$$\tilde{G}_{ij} = \int_0^\infty \tilde{P}_{ij}(t)dt = v_0^i v_0^{-j}\int_0^\infty e^{-\kappa t} P_{ij}(t)dt$$

is computed. This seems difficult to do in an explicit way. However, the asymptotic conditional distribution is easy to find. The method of Section 2 shows that

$$\sum_{j=0}^{\infty} P_i\{\tilde{X}(t)=j \mid T>t\}z^j = \frac{\tilde{G}_i(z,t)}{\tilde{G}_i(1,t)} \to \left[\frac{1-zv_0}{1-v_0}\right]^{-\beta}$$

as $t \to \infty$. Hence the asymptotic conditional distribution $\{a_j, j \geqq 0\}$ is negative binomial, with

$$a_j = \lim_{t\to\infty} P_i\{\tilde{X}(t)=j \mid T>t\} = (1-v_0)^{\beta} v_0^j \frac{(\beta)_j}{j!} \qquad j \geqq 0,$$

where $\beta = \theta/b$. The mean is $\Sigma\, ja_j = (1-v_0)^{-1}\beta v_0$.

We remark that the generating function $\tilde{G}_i(z,t)$ can be found using a simple compounding argument based on Poisson immigrations of rate θ, and the linear birth–death process studied in Section 2. However, direct evaluation of the spectral representation leads to more detailed results. The general theory established in [1] can be used to evaluate first-passage problems. Here is another example. Let q_i be the probability that $\tilde{X}(\cdot)$ reaches $\{0\}$ before $\{H\}$. Then

$$q_i = \tilde{Q}_i(0) = v_0^i Q_i(-\kappa) = v_0^i \varphi_i\left(\frac{-\kappa}{b(v_1-v_0)}\right).$$

4. An example from population genetics

We highlight in this concluding section several explicit results for the birth–death process with rates (0.7). This is a special case of the process studied in Section 2 (2.1) with $b = 1/2$, $a = 1$, $c = 1/4$. We get $v_0 = 0.7192$, $v_1 = 2.7808$, and it follows that the probability that formation of any aa-individuals occurs before fixation of the A allele is $1 - q_i = 1 - (0.7192)^i$, $i \geqq 0$. This will give a good approximation to the underlying process (0.6) when N is large. In a genetic context, we are most interested in the behavior of the process when $\tilde{X}(0) = 1$, corresponding to the appearance of a single mutant a-allele. For the general case of Section 2, we have from (2.6)

$$E_1(T) = E_1(T_0 \wedge T_H) = \sum_{j=1}^{\infty} \tilde{G}_{ij} = -\frac{1}{b}\ln\left(1-\frac{1}{v_1}\right). \tag{4.1}$$

This reduces to $E_1(T) = 0.891$ in the present case, and corresponds to a value of $0.891N$ for the process (0.6) with $\lambda = 1$. In a similar way, we find

$$E_1(T_H \mid T_H < \infty) = \sum_{j=1}^{\infty} G_{ij}^* = -\frac{1}{b(v_1-v_0)}\ln\left(\frac{v_1-1}{v_1-v_0}\right). \tag{4.2}$$

This gives a value of $E_1(T_H \mid T_H < \infty) = 1.043$, or $1.043N$ for (0.6) with $\lambda = 1$.

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