



Inhomogeneous birth-death and birth–death–immigration processes and the logarithmic series distribution. Part 2

David Branson*

Department of Mathematics, University of Essex, Colchester CO4 3SQ, UK

Received 27 April 1998; received in revised form 21 September 1998

Abstract

A simple graphical argument described in a previous paper is used to show that the zero-modified geometric form of the population-size distribution of a time-inhomogeneous birth-and-death model is maintained when the death rates of individuals depend on their ages and times of birth. An explicit form for the population-size distribution is found. Certain models incorporating immigration, but again with general lifetime distributions, continue to lead to Fisher's logarithmic series distribution for the abundance of families of a particular size. It is shown that the zero-modified geometric form no longer holds if the model is extended to incorporate age-dependent birth rates. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Inhomogeneous birth–death process; Inhomogeneous birth–death–immigration process; Logarithmic series distribution

1. Introduction

In a previous paper, Branson (1991) discussed the generalized birth and death process in which birth and death rates (per head of population per unit of time) are any specified functions of time. Kendall (1948) had shown that, for such a model, the population size at any time, given one original ancestor, has a zero-modified geometric distribution; Branson showed how this result can be obtained by a simple graphical argument. The model, although time inhomogeneous, is age independent; that is, all individuals at a given time have the same birth and death rates, regardless of their age. In this paper we generalize the model in two respects: we retain the assumptions on birth rates, but now the death rate of an individual can depend on its age, and the lifetime distribution of an individual can depend on its time of birth. These assumptions of course render the population-size process non-Markovian, but, in Section 2, we employ the same graphical argument to demonstrate that the population-size distribution is

* Corresponding author Tel.: +44-1206-873033; fax: +44-1206-873043.

E-mail address: brand@essex.ac.uk (D. Branson)

still zero-modified geometric. In Section 3 we derive an explicit expression for the probability that a family founded at a particular time has j living members at a later specified instant.

Karlin and McGregor (1967) proved that if immigrants arrive at times that are the events of a Poisson process, and if the resulting families evolve independently following the laws of a continuous-time Markov chain, then the number of families with j living members at time t has a Poisson distribution with mean $m_j(t)$, say. They further showed that, for constant birth and death rates, $m_j(t)$ is proportional to ξ^j/j , where ξ is a known function of t , so that the means $m_j(t)$ satisfy Fisher's (1943) "logarithmic series distribution" (which is, in fact, a model for means rather than a probability distribution). Many interesting population properties, including, for example, Ewens', (1972) celebrated formula giving the allelic distribution in a population of genes, were shown by Watterson (1974a,b) to follow from the logarithmic series distribution. Branson (1991) demonstrated that the logarithmic series form of the Poisson means continues to hold if the birth, death and immigration rates vary with time, provided that the birth and immigration rates are proportional. In Section 4 we show that the logarithmic series form (and hence all its consequences) holds also in our more general context where the evolution of a family is no longer Markovian.

In Branson (1991) we discussed Kendall's result that the population size has a zero-modified geometric distribution if the birth and death rates are arbitrary functions of time. In Section 2 of this paper we extend the result to the case where the death rates of individuals depend on their ages and times of birth. The question arises whether the zero-modified geometric form still holds if the model is generalized still further to incorporate age-dependent birth rates. A simple example discussed in Section 5 shows that the answer to this question is no.

2. Birth and death processes

Suppose a family is founded by an individual born at time T . We illustrate the family's pattern of births and deaths up to time t by a binary planted plane tree, as in Fig. 1. Time runs up the page and the original ancestor's birth is represented by the root of the tree. At each subsequent birth (contrary to the convention of Branson (1991)) we angle the parent's branch to the right and the offspring's branch to the left. Vertices corresponding to individuals that are alive at time t are called *live vertices* and are distinguished by black discs. It is clear that, ignoring the relative times of births and deaths, there is a one-to-one correspondence between such trees and the possible patterns of family development over the interval $[T, t]$.

The leftmost live vertex in a family tree (vertex F in Fig. 1) is called the *extreme vertex* and the path through the family tree from the root to the extreme vertex (RABCDEF) is called the *extreme path*. A tree that has j live vertices at time t is called a *j -tree*. For any j , there are countably many different j -trees distinguished by a label $r = 1, 2, 3, \dots$. The following result was established in Branson (1991) to which we refer the reader for details.

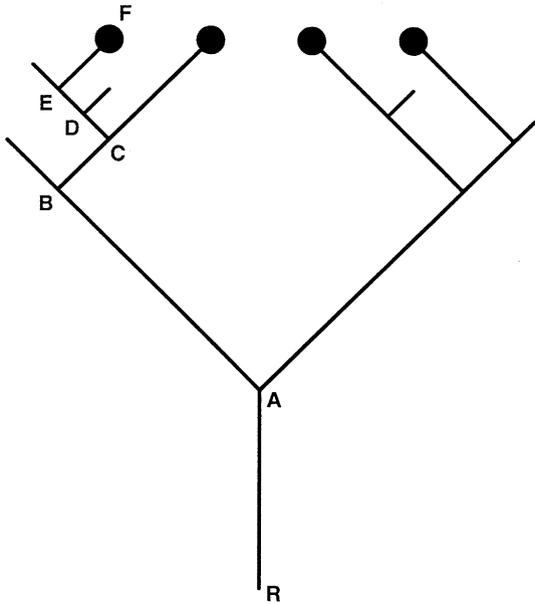


Fig. 1. A typical 4-tree, showing the live vertices as black discs.

Proposition. For $j \geq 1$, the complete set of $(j + 1)$ -trees is generated precisely once by taking every $(j$ -tree, 1-tree) pair, placing the root of the 1-tree in turn on (the interior of) each of the edges of the extreme path of the j -tree, aligning the trunk of the 1-tree to the left, and, if necessary, realigning to the right that part of the relevant edge of the j -tree which occurs later in time than the root of the 1-tree.

Let the lifetime of an individual born at time s have cumulative distribution function $F_s(t)$ and survivor function $R_s(t) = 1 - F_s(t)$. Such an individual gives birth to other individuals with rate $\lambda(t)$, where $\lambda(t)$ is independent of the parent’s age. All births and deaths occur independently, but all individuals at a given time have the same birth rate, and all individuals born at the same time have the same lifetime distribution. Thus, during an individual’s lifetime, the instants at which it gives birth constitute the events of an inhomogeneous Poisson process, but the time at which it dies may depend on both its age and its time of birth. Given that an individual was born at time s and survived until at least time t_1 , denote by $g(s, t_1, t_2)$ the probability that it survives until at least time t_2 , and gives birth to no offspring in the interval $[t_1, t_2]$. Then the assumptions above imply that

$$g(s, t_1, t_2) = \exp\left(-\int_{t_1}^{t_2} \lambda(\tau) d\tau\right) \frac{R_s(t_2 - s)}{R_s(t_1 - s)}. \tag{1}$$

Let $P_j(t_1, t)$ be the probability that a family founded at time t_1 has j members living at time t . Let $P_j(s, t_1, t)$ be the probability that the *subfamily* consisting of an individual that was born at time s (and survived until at least time t_1), together with all its descendants that were born subsequent to time t_1 , has j members living at time t ; such a subfamily can of course be described by a j -tree as before. Let $p_j(t_1, t; r)$

and $p_j(s, t_1, t; r)$ respectively be the corresponding probabilities relating to the pattern of births and deaths illustrated by the r th j -tree, so that

$$P_j(t_1, t) = \sum_r p_j(t_1, t; r), \quad P_j(s, t_1, t) = \sum_r p_j(s, t_1, t; r). \tag{2}$$

As we trace the extreme path through a j -tree ($j \geq 1$) from the root to the extreme vertex, the other vertices encountered are of two types: an l -vertex (r -vertex) is one from which the extreme path departs angled to the left (right). At an l -vertex the extreme path changes from a parent to its offspring whereas the extreme path represents the same individual either side of an r -vertex. In Fig. 1, the l -vertices are A, C and D and the r -vertices are B and E.

Suppose that the r th j -tree has m l -vertices which we label $(1, 0), (2, 0), \dots, (m, 0)$. The root and extreme vertex are labelled $(0, 0)$ and $(m + 1, 0)$ respectively. Between l -vertices $(i, 0)$ and $(i + 1, 0)$ there are, say, n_i r -vertices labelled $(i, 1), (i, 2), \dots, (i, n_i)$, $i = 0, \dots, m$. Then, for $j \geq 1$, the probability of the evolution described by the r th j -tree is given by

$$\begin{aligned} p_j(T, t; r) = & \int G_{01} \lambda(t_{10}) p_{j_1}(T, t_{10}, t, r_{10}) dt_{10} \\ & \times G_{12} \lambda(t_{20}) p_{j_2}(t_{10}, t_{20}, t, r_{20}) dt_{20} \dots \\ & \times G_{m-1, m} \lambda(t_{m0}) p_{j_m}(t_{m-1, 0}, t_{m0}, t, r_{m0}) dt_{m0} G_{m, m+1} \end{aligned} \tag{3}$$

where the factor p_{j_i} gives the probability of the pattern of descent, from a parent of age $(t_{i0} - t_{i-1, 0})$, represented by the branch sprouting to the right of the extreme path from the l -vertex $(i, 0)$, and

$$\begin{aligned} G_{i, i+1} = & g(t_{i0}, t_{i0}, t_{i1}) \lambda(t_{i1}) p_0(t_{i1}, t, r_{i1}) dt_{i1} \\ & \times g(t_{i0}, t_{i1}, t_{i2}) \lambda(t_{i2}) p_0(t_{i2}, t, r_{i2}) dt_{i2} \dots \\ & \times g(t_{i0}, t_{i, n_i-1}, t_{i, n_i}) \lambda(t_{i, n_i}) p_0(t_{i, n_i}, t, r_{i, n_i}) dt_{i, n_i} g(t_{i0}, t_{i, n_i}, t_{i+1, 0}). \end{aligned} \tag{4}$$

Here the g functions are given by (1) and the p_0 factors give the probability of the branches, headed by new-born individuals, sprouting to the left of the extreme path at r -vertices. Note that, from the definition of the extreme vertex, all the branches sprouting to the left from r -vertices must be 0-trees as they must be extinct by time t . The labels on the integration variables t_{ik} match the labels on the corresponding vertices, and the integrations are taken over the regions

$$t_{i0} < t_{i1} < t_{i2} < \dots < t_{i, n_i} < t_{i+1, 0}, \quad i = 0, \dots, m, \tag{5}$$

$$T = t_{00} < t_{10} < t_{20} < \dots < t_{m0} < t_{m+1, 0} = t. \tag{6}$$

The proposition above implies that, to obtain $P_{j+1}(T, t)$, we sum the terms obtained by replacing, in turn, each of the $g(t_{i0}, t_{ik}, t_{i, k+1})$ factors in (3), $k = 0, \dots, n_i$, $i = 0, \dots, m$, by

$$\int_{t_{ik}}^{t_{i, k+1}} g(t_{i0}, t_{ik}, \sigma) \lambda(\sigma) P_1(\sigma, t) d\sigma g(t_{i0}, \sigma, t_{i, k+1})$$

(for notational convenience we identify t_{i,n_i+1} with $t_{i+1,0}$), and by summing over r . (The sum over 1-trees has already been performed in the factor $P_1(\sigma, t)$.) It is easy to verify from Eq. (1) that

$$g(t_{i_0}, t_{ik}, \sigma)g(t_{i_0}, \sigma, t_{i,k+1}) = g(t_{i_0}, t_{ik}, t_{i,k+1})$$

so we see from (2) and (3) that, for $j \geq 1$,

$$\begin{aligned} P_{j+1}(T, t) &= \sum_r p_j(T, t; r) \sum_{i=0}^m \sum_{k=0}^{n_i} \int_{t_{ik}}^{t_{i,k+1}} \lambda(\sigma) P_1(\sigma, t) d\sigma \\ &= P_j(T, t) \int_T^t \lambda(\sigma) P_1(\sigma, t) d\sigma \\ &= P_j(T, t) \eta(T, t) \end{aligned}$$

where

$$\eta(T, t) = \int_T^t \lambda(\sigma) P_1(\sigma, t) d\sigma. \tag{7}$$

Hence, by induction,

$$P_j(T, t) = P_1(T, t) [\eta(T, t)]^{j-1}, \quad j = 1, 2, 3, \dots \tag{8}$$

This equation assumes that the original ancestor was born at time T , but, of course, it also holds in the case where it was born before time T if we just replace the original ancestor’s lifetime distribution by its remaining lifetime distribution at T . Eq. (8) establishes our desired result, namely, that, with a single ancestor at time T , the probability that a population has j members at a later time t is given by a zero-modified geometric distribution. In the next section we obtain an explicit expression for this probability.

3. Calculation of probabilities

If we sum both sides of (8) from 1 to infinity we obtain

$$\bar{P}(T, t) = 1 - P_0(T, t) = P_1(T, t) [1 - \eta(T, t)]^{-1}, \tag{9}$$

where we have denoted by $\bar{P}(T, t)$ the probability that a family founded at time T survives until time t . We can find this probability explicitly by summing the probabilities corresponding to all family trees that possess an extreme path. Eqs. (3) and (4) refer to a particular family tree with an extreme path, and we can sum over all such trees by modifying their right-hand sides in the following ways.

- (i) In the right-hand side of (3) we must sum over all r_{i_0} and all $j_i, i = 1, \dots, m$, in order to take account of all possible developments sprouting to the right from the l -vertices. The effect of this is to replace each factor p_{j_i} by 1.
- (ii) In the right-hand side of (4) we must sum over all $r_{ik}, k = 1, \dots, n_i$, in order to take account of all possible 0-trees sprouting to the left from the r -vertices. Using (2) we see that the effect of this is to replace each factor $p_0(t_{ik}, t, r_{ik})$ by $P_0(t_{ik}, t)$.

(iii) We must sum over all possible numbers of r -vertices and l -vertices, i.e. we must sum over $n_i, i = 0, \dots, m$, and over m .

These modifications give

$$\bar{P}(T, t) = \sum_{m=0}^{\infty} \sum_{n_0=0}^{\infty} \dots \sum_{n_m=0}^{\infty} \int \bar{G}_{01} \lambda(t_{10}) dt_{10} \bar{G}_{12} \lambda(t_{20}) dt_{20} \dots \bar{G}_{m-1,m} \lambda(t_{m0}) dt_{m0} \bar{G}_{m,m+1} \tag{10}$$

where

$$\begin{aligned} \bar{G}_{i,i+1} &= g(t_{i0}, t_{i0}, t_{i1}) \lambda(t_{i1}) P_0(t_{i1}, t) dt_{i1} \\ &\times g(t_{i0}, t_{i1}, t_{i2}) \lambda(t_{i2}) P_0(t_{i2}, t) dt_{i2} \dots \\ &\times g(t_{i0}, t_{i, n_i-1}, t_{i, n_i}) \lambda(t_{i, n_i}) P_0(t_{i, n_i}, t) dt_{i, n_i} g(t_{i0}, t_{i, n_i}, t_{i+1, 0}). \end{aligned} \tag{11}$$

Using (1) we can write (11) as

$$\begin{aligned} \bar{G}_{i,i+1} &= \exp\left(-\int_{t_{i0}}^{t_{i+1,0}} \lambda(\tau) d\tau\right) R_{t_{i0}}(t_{i+1,0} - t_{i0}) \\ &\times \lambda(t_{i1}) P_0(t_{i1}, t) dt_{i1} \lambda(t_{i2}) P_0(t_{i2}, t) dt_{i2} \dots \lambda(t_{i, n_i}) P_0(t_{i, n_i}, t) dt_{i, n_i}. \end{aligned}$$

If we substitute this into (10) and integrate it with respect to $t_{i1}, t_{i2}, \dots, t_{i, n_i}$, where the integration region is given by (5), we obtain

$$\exp\left(-\int_{t_{i0}}^{t_{i+1,0}} \lambda(\tau) d\tau\right) R_{t_{i0}}(t_{i+1,0} - t_{i0}) \frac{[\int_{t_{i0}}^{t_{i+1,0}} \lambda(\tau) P_0(\tau, t) d\tau]^{n_i}}{n_i!}.$$

Performing the summation over n_i and combining the exponentials gives

$$\exp\left(-\int_{t_{i0}}^{t_{i+1,0}} \lambda(\tau) \bar{P}(\tau, t) d\tau\right) R_{t_{i0}}(t_{i+1,0} - t_{i0}).$$

Finally, we can combine the exponentials corresponding to different values of i to obtain

$$\bar{P}(T, t) = \exp\left(-\int_T^t \lambda(\tau) \bar{P}(\tau, t) d\tau\right) H(T, t) \tag{12}$$

where

$$\begin{aligned} H(T, t) &= \sum_{m=0}^{\infty} \int R_T(t_{10} - T) \lambda(t_{10}) dt_{10} R_{t_{10}}(t_{20} - t_{10}) \lambda(t_{20}) dt_{20} \dots \\ &\times R_{t_{m-1,0}}(t_{m0} - t_{m-1,0}) \lambda(t_{m0}) dt_{m0} R_{t_{m0}}(t - t_{m0}); \end{aligned} \tag{13}$$

the integration region is again given by (6). To solve Eq. (12) for $\bar{P}(T, t)$, we first rearrange it to give

$$\bar{P}(T, t) \exp\left(\int_T^t \lambda(\tau) \bar{P}(\tau, t) d\tau\right) = H(T, t). \tag{14}$$

If we multiply both sides of this equation by $\lambda(T)$ and integrate with respect to T we obtain

$$\exp\left(\int_T^t \lambda(\tau) \bar{P}(\tau, t) d\tau\right) = 1 + \int_T^t \lambda(\tau) H(\tau, t) d\tau. \tag{15}$$

Dividing Eq. (14) by Eq. (15) gives

$$\bar{P}(T, t) = \frac{H(T, t)}{1 + \int_T^t \lambda(\tau)H(\tau, t) d\tau}. \tag{16}$$

Having found an explicit expression for $\bar{P}(T, t)$, we can now derive the other probabilities involved. Differentiating Eq. (7) gives

$$\partial\eta(T, t)/\partial T = -\lambda(T)P_1(T, t)$$

and combining this with Eq. (9) we find

$$-\frac{\partial\eta(T, t)}{\partial T} \frac{1}{1 - \eta(T, t)} = \lambda(T)\bar{P}(T, t).$$

Integrating both sides with respect to T and exponentiating gives

$$\begin{aligned} \eta(T, t) &= 1 - \exp\left(-\int_T^t \lambda(\tau)\bar{P}(\tau, t) d\tau\right) \\ &= 1 - \frac{1}{1 + \int_T^t \lambda(\tau)H(\tau, t) d\tau}, \end{aligned} \tag{17}$$

where the second equality follows from (15). So now, using (8), (9), (16) and (17) we can express $P_j(T, t)$ in terms of lifetime distributions and birth rates:

$$\begin{aligned} P_0(T, t) &= 1 - \frac{H(T, t)}{1 + \int_T^t \lambda(\tau)H(\tau, t) d\tau}, \\ P_j(T, t) &= \frac{H(T, t)}{(1 + \int_T^t \lambda(\tau)H(\tau, t) d\tau)^2} \left(1 - \frac{1}{1 + \int_T^t \lambda(\tau)H(\tau, t) d\tau}\right)^{j-1}, \quad j \geq 1, \end{aligned}$$

where $H(T, t)$ is given by (13).

4. Birth, death and immigration processes

Suppose now that immigrants appear during the period $T \geq 0$ at times which are the events of an inhomogeneous Poisson process with rate $\nu(T)$. Each immigrant is the original ancestor of an independent family that evolves as described in the previous sections. We call the time of an immigrant’s arrival a “type j ” event if that immigrant’s subsequent family has j members living at time t . It follows from the independent increments property of the Poisson process and the independent evolution of each family that type j events form an inhomogeneous Poisson process with rate $\nu(T)P_j(T, t)$ and that processes of different types are independent. Denote by $m_j(t)$ the mean number of type j families. Then it can be shown, exactly as in Branson (1991), that if the birth and immigration rates are proportional, that is, if $\nu(T) = \theta\lambda(T)$ for some constant θ , then

$$m_j(t) = \theta[\eta(0, t)]^j/j,$$

so that the means $m_j(t)$ possess the “logarithmic series distribution” property. The implications of this result are discussed in Branson (1991).

5. Age-dependent birth rates

We now return to a consideration of birth and death processes without immigration, but generalized to allow time-dependent birth rates. Specifically, we investigate the following model.

- (i) Any individual gives birth to offspring at a constant rate λ so long as the individual's age is less than a ; thereafter the individual is sterile.
- (ii) All individuals live for at least a time b (where b is greater than $3a$), but we make no further assumptions concerning their lifetime distributions.

These assumptions imply that the number of offspring of any individual is a Poisson variate with mean λa . Consider the size at time t of the family descended from an individual born at time T , where $3a < t - T < b$. It follows from this inequality and from assumption (ii) that there have been no deaths by time t . Therefore the population size at time t is equal to one if the original ancestor has no offspring during its fertile period of length a . Hence

$$P_1(T, t) = \exp(-\lambda a). \quad (18)$$

There are two individuals in the population at time t if the original ancestor has one child who has no offspring, so

$$\begin{aligned} P_2(T, t) &= [\lambda a \exp(-\lambda a)] [\exp(-\lambda a)] \\ &= \lambda a \exp(-2\lambda a). \end{aligned} \quad (19)$$

The population size at time t is equal to three if *either* the original ancestor has two children who have no offspring, *or* the original ancestor has one child who in turn has one child who has no offspring:

$$\begin{aligned} P_3(T, t) &= \left[\frac{(\lambda a)^2}{2} \exp(-\lambda a) \right] [\exp(-\lambda a)]^2 + [\lambda a \exp(-\lambda a)]^2 [\exp(-\lambda a)] \\ &= \frac{3}{2} (\lambda a)^2 \exp(-3\lambda a). \end{aligned} \quad (20)$$

It is clear from (18), (19) and (20) that $P_1(T, t)$, $P_2(T, t)$ and $P_3(T, t)$ do not follow the pattern of the zero-modified geometric distribution given in (8). This shows that the class of models whose population size has a zero-modified geometric distribution cannot be extended to include age-dependent birth rates.

Acknowledgements

I should like to thank the associate editor for a helpful suggestion.

References

- Branson, D., 1991. Inhomogeneous birth-death and birth-death-immigration processes and the logarithmic series distribution. *Stochastic Process. Appl.* 39, 131–137.
- Ewens, W.J., 1972. The sampling theory of selectively neutral alleles. *Theoret. Population. Biol.* 3, 87–112.

- Fisher, R.A., 1943. A theoretical distribution for the apparent abundance of different species. *J. Anim. Ecol.* 12, 54–57.
- Karlin, S., McGregor, J., 1967. The number of mutant forms maintained in a population. In: Le Cam, L.M., Neyman, J. (Eds.), *Proceedings of the Fifth Berkeley Symposium on Mathematical and Statistic Probability*, Vol. IV, University of California Press, Berkeley, CA, pp. 415–438.
- Kendall, D.G., 1948. On the generalized “birth-and-death” process. *Ann. Math. Statist.* 19, 1–15.
- Watterson, G.A., 1974a. The sampling theory of selectively neutral alleles. *Adv. Appl. Probab.* 6, 463–488.
- Watterson, G.A., 1974b. Models for the logarithmic species abundance distributions. *Theoret. Population Biol.* 6, 217–250.