ON THE GENERALIZED "BIRTH-AND-DEATH" PROCESS

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1. Introduction and Summary. The importance of stochastic processes in relation to problems of population growth was pointed out by W. Feller [1] in 1939. He considered among other examples the "birth-and-death" process in which the expected birth and death rates (per head of population per unit of time) were constants, λ_0 and μ_0, say. In this paper I shall give the complete solution of the equations governing the generalised birth-and-death process in which the birth and death rates $\lambda(t)$ and $\mu(t)$ may be any specified functions of the time t. The mathematical method employed starts from M. S. Bartlett's idea of replacing the differential-difference equations for the distribution of the population size by a partial differential equation for its generating function. For an account of this technique,[1] reference may be made to Bartlett's North Carolina lectures [2].

The formulae obtained lead to an expression for the probability of the ultimate extinction of the population, and to the necessary and sufficient condition for a birth-and-death process to be of "transient" type. For transient processes the distribution of the cumulative population is also considered, but here in general it is not found possible to do more than evaluate its mean and variance as functions of t, although a complete solution (including the determination of the asymptotic form of the distribution as t tends to infinity) is obtained for the simple process in which the birth and death rates are independent of the time.

It is shown that a birth-and-death process can be constructed to give an expected population size $\bar{n}_t$ which is any desired function of the time t, and among the many possible solutions the unique one is determined which makes the fluctuation, $\mathrm{Var}(n_t)$, a minimum for all t.

The general theory is illustrated with reference to two examples. The first of these is the $(\lambda_0, \mu_1 t)$ process introduced by N. Arley [3] in his study of the cascade showers associated with cosmic radiation; here the birth rate is constant and the death rate is a constant multiple of the "age", t, of the process. The $\bar{n}_t$-curve is then Gaussian in form, and the process is always of transient type.

The second example is provided by the family of "periodic" processes, in which the birth and death rates are periodic functions of the time t. These appear well adapted to describe the response of population growth (or epidemic spread) to the influence of the seasons.

2. The formulation and solution of the equations for the general (λ, μ) process. Let the integer-valued time-dependent random variable n_t measure at time t the

[1] It appears from some remarks by Arley and Borchsenius [5] that the generating function method was first employed in problems of this kind by Dr. C. Palm.

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size of a population, and suppose that in an element of time dt the only possible transitions (and their associated probabilities) are:

$$(1)\qquad \begin{aligned} n_{t+dt} &= n_t + 1, && \lambda(t)n_t dt + o(dt); \\ n_{t+dt} &= n_t, && 1 - \{\lambda(t) + \mu(t)\}n_t dt + o(dt); \\ n_{t+dt} &= n_t - 1, && \mu(t)n_t dt + o(dt). \end{aligned}$$

As an initial condition it will be supposed that the population is descended from a single "ancestor", so that $n_0 = 1$, and thus

$$(2)\qquad P_1(0) = 1, \qquad P_n(0) = 0 \qquad (n \neq 1).$$

It then follows that the $P_n(t)$ must satisfy the differential-difference equations

$$(3)\qquad \frac{\partial}{\partial t} P_n(t) = (n + 1)\mu P_{n+1}(t) + (n - 1)\lambda P_{n-1}(t) - n(\lambda + \mu)P_n(t),\ n \geq 1,$$

and

$$(4)\qquad \frac{\partial}{\partial t} P_0(t) = \mu P_1(t)$$

(where for convenience of writing I have ceased to indicate explicitly the dependence of λ and μ on the time). If $P_n(t)$ is defined to be zero when $n < 0$, the first of the above equations will then be true for all n, and accordingly the generating function

$$(5)\qquad \varphi(z, t) \equiv \sum_{n=-\infty}^{\infty} P_n(t)z^n$$

must satisfy the linear partial differential equation

$$(6)\qquad \frac{\partial\varphi}{\partial t} = (z - 1)(\lambda z - \mu)\frac{\partial\varphi}{\partial z};$$

the problem is to find the solution to this equation when it is coupled with the boundary condition $\varphi(z, 0) = z$.

The equation (6) is of Lagrange's type, and can be solved in the usual manner. The auxiliary equation is

$$(7)\qquad \frac{dz}{dt} = -\mu + (\lambda + \mu)z - \lambda z^2,$$

and while in particular examples it might be convenient to attack this equation directly, progress in general is more easily made by observing that (7) is of Riccati's form, for which a general theory is available.[2] The fundamental property of a Riccati equation is that the general solution is a homographic

[2] See, for example, G. N. Watson [4], pp. 93–94.

function of the constant of integration, so that

$$z = \frac{f_1 + Cf_2}{f_3 + Cf_4},$$

and equally

$$C = \frac{zf_3 - f_1}{f_2 - zf_4},$$

where f_1, f_2, f_3 and f_4 are all functions of the time t. Thus the general solution of (6) is of the form

$$\varphi(z, t) = \Phi\left\{\frac{zf_3 - f_1}{f_2 - zf_4}\right\},$$

and from the boundary condition $\varphi(z, 0) = z$ it then follows that

$$\varphi(z, t) = \frac{g_1(t) + zg_2(t)}{g_3(t) + zg_4(t)}.$$

On expansion, one obtains

(8) $$P_0(t) = \xi_t \text{ and } P_n(t) = \{1 - P_0(t)\}(1 - \eta_t)\eta_t^{n-1} \qquad (n \geqslant 1),$$

where ξ_t and η_t are functions of the time t. Thus, *for the general* (λ, μ) *process, the population size at any time is distributed in a geometric series with a modified zero term*

The next stage of the solution is to determine the functions ξ_t and η_t. From (8),

(9) $$\varphi(z, t) = \frac{\xi + (1 - \xi - \eta)z}{1 - \eta z},$$

and if this expression for φ be substituted in (6) it will be found[3] that

$$(\eta\xi' - \xi\eta') + \eta' = \lambda(1 - \xi)(1 - \eta),$$

and

$$\xi' = \mu(1 - \xi)(1 - \eta).$$

Now let $U = 1 - \xi$ and $V = 1 - \eta$, so that

$$U'/U = -\mu V,$$

and

$$V' = (\mu - \lambda)V - \mu V^2.$$

The last equation is of Bernoulli's type and can be solved by writing

$$W = 1/V,$$

[3] Here $\xi' \equiv d\xi/dt$, etc.

so that

$$W' + (\mu - \lambda)W = \mu.$$

Initially $\xi = \eta = 0$, and $U = V = W = 1$; the solution of the W-equation is therefore

$$W = e^{-\rho}\left\{1 + \int_0^t e^{\rho(\tau)}\mu(\tau)d\tau\right\}, \tag{10a}$$

where the function ρ is defined by

$$\rho(t) = \int_0^t \{\mu(\tau) - \lambda(\tau)\}d\tau. \tag{11}$$

Integration by parts gives two other formulae for W which will prove useful; they are

$$W = 1 + e^{-\rho}\int_0^t e^{\rho(\tau)}\lambda(\tau)d\tau, \tag{10b}$$

and

$$W = \tfrac{1}{2}(1 + e^{-\rho}) + \tfrac{1}{2}e^{-\rho}\int_0^t e^{\rho(\tau)}\{\lambda(\tau) + \mu(\tau)\}d\tau. \tag{10c}$$

The quantities U and V, and hence also ξ and η can now be expressed in terms of ρ and W, for

$$\frac{U'}{U} = -\mu V = -\frac{\mu}{W} = -\frac{W'}{W} - \rho',$$

and so

$$\xi_t = 1 - \frac{e^{-\rho}}{W} \quad\text{and}\quad \eta_t = 1 - \frac{1}{W}. \tag{12}$$

These results, together with (8), suffice to determine completely the $P_n(t)$ as functions of the time t.

It is easy to deduce formulae for the mean and variance of n_t (these could also be obtained directly from (6)). For the mean,

$$\bar{n}_t = \frac{1 - \xi_t}{1 - \eta_t} = e^{-\rho(t)}, \tag{13}$$

while for the variance,

$$\begin{aligned}\text{Var}\,(n_t) &= \frac{(1 - \xi)(\xi + \eta)}{(1 - \eta)^2} = e^{-\rho}(2W - 1 - e^{-\rho}) \\ &= e^{-2\rho}\int_0^t e^{\rho(\tau)}\{\lambda(\tau) + \mu(\tau)\}d\tau.\end{aligned} \tag{14c}$$

Alternatively, using the other forms for W, one can write

$$\text{(14a)} \qquad \text{Var}(n_t) = e^{-\rho}\left\{e^{-\rho} - 1 + 2e^{-\rho}\int_0^t e^{\rho(\tau)}\mu(\tau)\,d\tau\right\},$$

$$\text{(14b)} \qquad = e^{-\rho}\left\{1 - e^{-\rho} + 2e^{-\rho}\int_0^t e^{\rho(\tau)}\lambda(\tau)\,d\tau\right\}.$$

If the initial population $n_0 = N > 1$, these formulae for $\bar{n}_t$ and $\text{Var}(n_t)$ are to be multiplied by N.

It is now a simple matter to apply these formulae to the Arley $(\lambda_0, \mu_1 t)$ process. It will be found that

$$\rho = \tfrac{1}{2}\mu_1 t^2 - \lambda_0 t.$$

and

$$W = 1 + \lambda_0 e^{-\frac{1}{2}\mu_1 t^2 + \lambda_0 t}\int_0^t e^{\frac{1}{2}\mu_1 \tau^2 - \lambda_0 \tau}\,d\tau.$$

The mean growth of the process therefore follows the Gaussian law

$$\bar{n}_t = e^{\lambda_0 t - \frac{1}{2}\mu_1 t^2},$$

while for the variance (using (14*b*), since λ is a constant) one finds

$$\text{Var}(n_t) = \bar{n}_t(1 - \bar{n}_t) + 2\lambda_0 \bar{n}_t^2 \int_0^t e^{\frac{1}{2}\mu_1 \tau^2 - \lambda_0 \tau}\,d\tau,$$

in agreement with Arley [3] and Bartlett [2]. The distribution of n_t at time t follows on inserting the above values of ρ and W into (8) and (12).

3. The chances of extinction. The simplest special case is that in which (λ, μ) have the *constant* values (λ_0, μ_0); this is the process introduced by Feller [1] and later discussed by several writers.[4] The formulae (13) and (14*c*) give at once the results

$$\text{(15)} \qquad \bar{n}_t = e^{(\lambda_0 - \mu_0)t} \quad \text{and} \quad \text{Var}(n_t) = \frac{\lambda_0 + \mu_0}{\lambda_0 - \mu_0}\,\bar{n}_t(\bar{n}_t - 1),$$

due to Feller, while since

$$W = \frac{\lambda_0 \bar{n}_t - \mu_0}{\lambda_0 - \mu_0},$$

equations (8) and (12) give

$$\text{(16)} \qquad P_0(t) = \frac{\mu_0(\bar{n}_t - 1)}{\lambda_0 \bar{n}_t - \mu_0} \quad \text{and} \quad P_n(t) = \{1 - P_0(t)\}(1 - \eta_t)\eta_t^{n-1} \ (n \geqq 1),$$

[4] See Arley [3], Arley and Borchsenius [5], Bartlett [2] and Kendall [6]. Palm's formulae (16) are stated without proof by Arley and Borchsenius, but it appears from their remarks that he used a generating-function method probably identical with that later employed by Bartlett and myself.

where

$$\eta_t = \frac{\lambda_0}{\mu_0} P_0(t) = \frac{\lambda_0(\bar{n}_t - 1)}{\lambda_0 \bar{n}_t - \mu_0}.$$

These formulae were first given by C. Palm.[5] They actually hold only if $\lambda_0 \neq \mu_0$; in the case of equality, $W = 1 + \lambda_0 t$, and then

$$\bar{n}_t = 1, \qquad \mathrm{Var}(n_t) = 2\lambda_0 t,$$

$$(17) \qquad P_0(t) = \frac{\lambda_0 t}{1 + \lambda_0 t} \quad \text{and} \quad P_n(t) = \{1 - P_0(t)\}(1 - \eta_t)\eta_t^{n-1} \qquad (n \geqq 1),$$

where $\eta_t = P_0(t)$.

One particularly interesting point is that

$$P_0(t) \to 1 \text{ as } t \to \infty \text{ if } \lambda_0 \leqq \mu_0,$$

so that the population is "almost certain" to die out, even though in the critical case ($\lambda_0 = \mu_0$) the *expected* population size $\bar{n}_t$ has a constant value. The same is true for any initial size of population; the new expression for $P_0(t)$ is then simply equal to the former one raised to the power $n_0 = N$, and therefore tends to unity as before. This phenomenon of extinction was first noticed in a similar problem[6] by Francis Galton and H. W. Watson; an account of their work is given in Appendix *F* of Galton's book [7].

The formulae of the last section now make possible a discussion of the chances of extinction for the general (λ, μ) process. When $n_0 = 1$,

$$(18) \qquad P_0(t) = \frac{\int_0^t e^{\rho} \mu \, d\tau}{1 + \int_0^t e^{\rho} \mu \, d\tau},$$

and so *the necessary and sufficient condition for the ultimate extinction of the population is that the integral*

$$(19) \qquad I = \int_0^\infty e^{\rho(\tau)} \mu(\tau) \, d\tau$$

should be divergent.

It will be noticed that the integrand of (19) is non-negative, and so the integral must either diverge to plus infinity, or have a finite value. Hence in any case *the population always has a definite chance of extinction, given by* $I/(1 + I)$. For a population descended from N initial ancestors, the $P_n(t)$ are generated by the function

$$(20) \qquad \left\{ \frac{\xi + (1 - \xi - \eta)z}{1 - \eta z} \right\}^N,$$

[6] The extinction of family-names. Further references will be found in my paper [6].

so that

$$P_0(t) = \xi_t^N,$$

and the chance of ultimate extinction is

$$\left(\frac{I}{1+I}\right)^N, \tag{21}$$

which is or is not equal to unity for all N indifferently.

Extinction is impossible, in the sense of being an event of zero probability, if and only if μ is identically zero, so that the process is one of reproduction only. It is also worth noting that a necessary but not sufficient condition for almost certain extinction is the divergence of the integral

$$\int_0^\infty \mu(\tau)d\tau. \tag{22}$$

For if (22) had a finite value, $\rho(t)$ would be bounded for all t, and so (19) could not be divergent. In general, when $I = \infty$ and the population is almost certainly doomed to extinction, I shall speak of the process as *transient.*

For a transient process it is of interest to consider the random variable T, defined to be the "age" of the process at the moment of extinction. Since

$$P_0(t) \equiv \text{Probability } \{T \leq t\},$$

the probability distribution of T is $P_0'(T)dT$, or

$$\frac{e^{\rho(T)}\mu(T)dT}{\left\{1 + \int_0^T e^{\rho(\tau)}\mu(\tau)d\tau\right\}^2}, \qquad 0 < T < \infty. \tag{23}$$

For example, in the simplest birth-and-death process, when λ and μ are equal constants, the distribution of T is

$$\frac{\lambda_0\, dT}{(1 + \lambda_0 T)^2}, \qquad 0 < T < \infty. \tag{24}$$

This is for an initial population $n_0 = 1$; more generally, when $n_0 = N > 1$, the distribution of T is

$$NP_0'(T)\{P_0(T)\}^{N-1}dT.$$

The *median life-time* T_m is determined by the relation

$$\int_0^{T_m} e^{\rho(\tau)}\mu(\tau)d\tau = 1. \tag{25}$$

For the simple process, $T_m = 1/\lambda_0$ when $\lambda_0 = \mu_0$, and more generally

$$T_m = \frac{1}{\mu_0 - \lambda_0} \cdot \log\left(2 - \frac{\lambda_0}{\mu_0}\right) \qquad (\lambda_0 \neq \mu_0) \tag{26}$$

if $n_0 = 1$. When $n_0 = N > 1$, the formula for T_m becomes

$$\int_0^{T_m} e^{\rho(\tau)} \mu(\tau) d\tau = 1/(2^{1/N} - 1) \sim \frac{N}{\log 2}. \tag{27}$$

For the balanced process (λ_0, λ_0) it therefore follows that

$$T_m(N) = T_m(1)/(2^{1/N} - 1) \sim 1.44 \, N \, T_m(1), \tag{28}$$

as N tends to infinity. If the process is unbalanced, however, so that $\lambda_0 < \mu_0$, this asymptotic proportionality to N does not hold, and instead

$$T_m = \frac{1}{\mu_0 - \lambda_0} \log \left\{ \frac{2^{1/N} \mu_0 - \lambda_0}{(2^{1/N} - 1)\mu_0} \right\} \sim \frac{\log N}{\mu_0 - \lambda_0}, \tag{29}$$

as N tends to infinity.

4. The cumulative population. There is associated with a birth-and-death process another random variable, M_t, which is of importance in some applications. This is defined as follows: initially $M_0 = n_0$, while for $t > 0$, M_t shares all the *positive* jumps of n_t.

For example, if n_t represents the number of cases of a disease in a population at time t, M_t will be the total number of cases which have been recorded up to that time. If the process is transient, so that the epidemic is almost certainly extinguished in the course of time, M_∞ will then be a measure of its overall severity.

Again, if n_t represents the *viable count* of a population of bacteria[6] with a birth rate $\lambda(t)$ and a death rate $\mu(t)$, M_t will be equal to the *total count* in which living and dead organisms are not distinguished.

In order to discuss the joint variation of n_t and M_t it is necessary to introduce the new generating function

$$\psi(z, w, t) = \sum_{n=0}^{\infty} \sum_{M=0}^{\infty} P_{n,M}(t) z^n w^M. \tag{30}$$

Here the $P_{n,M}(t)$ give the joint frequency-distribution of n_t and M_t at time t. By the usual argument the differential equation satisfied by the function ψ will be found to be

$$\frac{\partial \psi}{\partial t} = \{\lambda w z^2 - (\lambda + \mu) z + \mu\} \frac{\partial \psi}{\partial z}, \tag{31}$$

and the associated boundary condition (if initially $n_0 = M_0 = 1$) is

$$\psi(z, w, 0) = zw. \tag{32}$$

I have been unable to solve this equation for general $\lambda(t)$ and $\mu(t)$; the solution when λ and μ are constants will be given in the next section. It is however

[6] For some general remarks about birth-and-death processes in relation to bacterial growth, reference may be made to my paper [6].

possible to find general expressions for the mean and variance of M_t; for this purpose it is more convenient[7] to work with the cumulant-generating function

$$K(u, v, t) = \log \psi(e^u, e^v, t). \tag{33}$$

This satisfies the differential equation

$$\frac{\partial K}{\partial t} = \{\lambda(e^{u+v} - 1) - \mu(1 - e^{-u})\} \frac{\partial K}{\partial u}, \tag{34}$$

and of course

$$K = u\bar{n}_t + v\bar{M}_t + \tfrac{1}{2}u^2 \operatorname{Var}(n_t) + \tfrac{1}{2}v^2 \operatorname{Var}(M_t) + uv \operatorname{Cov}(n_t, M_t) + \cdots. \tag{35}$$

Expanding both sides of the equation in powers of u and v, and equating coefficients, one obtains the differential equations

$$\frac{d}{dt} \bar{n}_t = (\lambda - \mu)\bar{n}_t, \tag{36}$$

$$\frac{d}{dt} \operatorname{Var}(n_t) = (\lambda + \mu)\bar{n}_t + 2(\lambda - \mu) \operatorname{Var}(n_t), \tag{37}$$

$$\frac{d}{dt} \bar{M}_t = \lambda\bar{n}_t, \tag{38}$$

$$\frac{d}{dt} \operatorname{Var}(M_t) = \lambda\bar{n}_t + 2\lambda \operatorname{Cov}(n_t, M_t), \tag{39}$$

and

$$\frac{d}{dt} \operatorname{Cov}(n_t, M_t) = \lambda\bar{n}_t + \lambda \operatorname{Var}(n_t) + (\lambda - \mu) \operatorname{Cov}(n_t, M_t). \tag{40}$$

The solutions to the first two equations have of course already been given in section 2; from the third it follows that the mean value of M_t is

$$\bar{M}_t = 1 + \int_0^t e^{-\rho(\tau)}\lambda(\tau)d\tau. \tag{41}$$

The solution of the fifth equation is

$$\operatorname{Cov}(n_t, M_t) = \bar{n}_t \int_0^t \left\{1 + \frac{\operatorname{Var}(n_\tau)}{\bar{n}_\tau}\right\} \lambda(\tau)d\tau, \tag{42}$$

and so the variance of M_t is

$$\operatorname{Var}(M_t) = \int_0^t \{\bar{n}_\tau + 2 \operatorname{Cov}(n_\tau, M_\tau)\}\lambda(\tau)d\tau. \tag{43}$$

[7] Compare Bartlett [2].

In illustration of these formulae, consider first the Arley $(\lambda_0, \mu_1 t)$ process; from (41)

$$(44) \qquad \bar{M}_t = 1 + \lambda_0 \int_0^t e^{\lambda_0 \tau - \frac{1}{2}\mu_1 \tau^2} d\tau,$$

but the complete expression for Var (M_t) will be a multiple integral which does not appear to admit of much simplification.

For the simple (λ_0, μ_0) process, however, when $\lambda_0 < \mu_0$, it readily follows that

$$(45) \qquad \bar{M}_t = \frac{\mu_0 - \lambda_0 \bar{n}_t}{\mu_0 - \lambda_0},$$

$$(46) \qquad \text{Cov}\,(n_t, M_t) = \frac{\lambda_0 \bar{n}_t}{\mu_0 - \lambda_0}\left\{2\mu_0 t - \frac{\mu_0 + \lambda_0}{\mu_0 - \lambda_0}(1 - \bar{n}_t)\right\},$$

and

$$(47) \quad \text{Var}\,(M_t) = \frac{\lambda_0(\mu_0 + \lambda_0)}{(\mu_0 - \lambda_0)^2}(1 - \bar{n}_t) - \frac{4\lambda_0^2 \mu_0 t \bar{n}_t}{(\mu_0 - \lambda_0)^2} + \frac{\lambda_0^2(\mu_0 + \lambda_0)}{(\mu_0 - \lambda_0)^3}(1 - \bar{n}_t^2).$$

Thus in the limit, as $t \to \infty$, the mean and variance of M_∞ are

$$(48) \qquad \bar{M}_\infty = \frac{\mu_0}{\mu_0 - \lambda_0}, \quad \text{and} \quad \text{Var}\,(M_\infty) = \frac{\lambda_0 \mu_0(\lambda_0 + \mu_0)}{(\mu_0 - \lambda_0)^3},$$

the covariance of course tending to zero. If the process is balanced, so that $\lambda_0 = \mu_0$ and $\bar{n}_t = 1$, the integral for M_t has the value $1 + \lambda_0 t$, which increases without limit as t tends to infinity. This will always be so for a balanced process if the integral

$$\int_0^\infty \lambda(\tau) d\tau$$

is divergent.

If the initial population n_0 is equal to $N > 1$, and if all its members are counted into M_0, the only modification necessary to the above formulae is that in each case the right-hand side is to be multiplied by N.

5. The asymptotic distribution of the cumulative population for a simple transient birth-and-death process. The equation (31), which appears in the general case to be intractable even if one only requires the asymptotic distribution determined by $\psi(1, w, \infty)$, can be solved completely in the specially simple case when the birth and death rates $\lambda(t)$ and $\mu(t)$ have the constant values λ_0 and μ_0.

Let α and β be the roots of the quadratic

$$(49) \qquad \lambda_0 w z^2 - (\lambda_0 + \mu_0) z + \mu_0 = 0,$$

so chosen that $0 < \alpha < 1 < \beta$; then the general solution of (31) will be found by the usual method to be

$$\psi = \Psi\left\{\frac{z-\alpha}{\beta - z} e^{-\lambda_0 w(\beta-\alpha)t}\right\}.$$

The boundary condition $\psi(z, w, 0) = zw$ therefore gives

$$\psi = w\left(\frac{\alpha(\beta - z) + \beta(z-\alpha)e^{-\lambda_0 w(\beta-\alpha)t}}{(\beta - z) + (z - \alpha)e^{-\lambda_0 w(\beta-\alpha)t}}\right), \tag{50}$$

and it may be noted that if $n_0 = M_0 = N > 1$, this formula for ψ would have to be raised to the Nth power. It will suffice, however, to discuss the simplest case when $n_0 = M_0 = 1$.

Let the process be transient, so that $\lambda_0 \leq \mu_0$; then the asymptotic frequency distribution of M_t when $t \to \infty$ is determined by the generating function

$$\psi(1, w, \infty) = w\alpha = \frac{\lambda_0 + \mu_0 - \sqrt{\{(\lambda_0+\mu_0)^2 - 4\lambda_0\mu_0 w\}}}{2\lambda_0}, \tag{51}$$

and here it is the positive square root which must be taken. The probability distribution of M_∞ is thus

$$Q_M = \frac{\lambda_0 + \mu_0}{2\lambda_0} \frac{(2M)!}{2^{2M}(M!)^2} \frac{x^M}{2M-1}, \qquad (M = 1, 2, 3, \cdots), \tag{52}$$

where

$$x = \frac{4\lambda_0\mu_0}{(\lambda_0 + \mu_0)^2}. \tag{53}$$

The first few terms are

$$\frac{\mu_0}{\lambda_0 + \mu_0}\{1, \tfrac{1}{4}x, \tfrac{1}{8}x^2, \tfrac{5}{64}x^3, \cdots\}, \tag{54}$$

and it is easy to verify that the mean and variance of this distribution agree with the values given in the last section. When $\lambda_0 = \mu_0$, $x = 1$, and then the terms in (54) fall off to zero like $M^{-3/2}$, $\bar{M}_\infty$ being infinite (in accordance with the remarks at the end of section 4).

6. The determination of the process when its mean growth, $\bar{n}_t$, is given. Since $\bar{n}_t = e^{-\rho(t)}$, it follows that

$$\lambda(t) - \mu(t) = \frac{d}{dt}\log \bar{n}_t, \tag{55}$$

and thus if $\bar{n}_t$ is required to be a given function of the time, the birth and death rates must be chosen in accordance with (55); the only other condition is that for all t, $\lambda(t) \geq 0$ and $\mu(t) \geq 0$.

Arley has pointed out that the simple process ($\lambda(t) = c$, $\mu(t) = 0$) gives a smaller *fluctuation*, Var (n_t), than any other simple process with the same mean growth, say (λ_0, μ_0) where $\lambda_0 - \mu_0 = c$. This suggests that one should consider the more general question: *if $\bar{n}_t$ is given for all* t, *for which choice of the functions* $\lambda(t)$ *and* $\mu(t)$ *will the fluctuation* Var (n_t) *be a minimum?*

Suppose then that the whole region $t > 0$ consists of three sets of intervals, E_1, E_2 and E_3, and that within an interval of the set E_j,

$\bar{n}_t$ is a decreasing function if $j = 1$,

$\bar{n}_t$ is an increasing function if $j = 2$,

and $\bar{n}_t$ is a constant if $j = 3$.

Then one can write

$$\begin{aligned}\text{Var}(n_t) &= e^{-2\rho}\Sigma_1[e^{\rho(\tau)}] + 2e^{-2\rho}\int_{E_1} e^{\rho(\tau)}\lambda(\tau)d\tau \\ &+ e^{-2\rho}\Sigma_2[-e^{\rho(\tau)}] + 2e^{-2\rho}\int_{E_2} e^{\rho(\tau)}\mu(\tau)d\tau \\ &+ e^{-2\rho}\int_{E_3} e^{\rho(\tau)}\{\lambda(\tau) + \mu(\tau)\}d\tau.\end{aligned}$$

Here the terms involving λ and μ explicitly are all non-negative, and so Var (n_t) will be a minimum for the (unique) choice of λ and μ which makes them all vanish, namely:

$$\begin{aligned}&\text{in } E_1, \lambda(t) = 0 \quad \text{and } \mu(t) = -\bar{n}_t'/\bar{n}_t; \\ &\text{in } E_2, \lambda(t) = \bar{n}_t'/\bar{n}_t \text{ and } \mu(t) = 0; \\ &\text{in } E_3, \lambda(t) = \mu(t) = 0.\end{aligned} \tag{56}$$

However, when one is looking for a (λ, μ) process with a given $\bar{n}_t$ function, this minimum-fluctuation solution would frequently be an artificial one. For example, suppose it is required that $\bar{n}_t$ shall be a Gaussian curve, reducing to unity when $t = 0$; then

$$\bar{n}_t = e^{\lambda_0 t - \frac{1}{2}\mu_1 t^2}, \tag{57}$$

say, and $\lambda(t) - \mu(t) = \lambda_0 - \mu_1 t$; the most natural solution is then the Arley process,

$$\lambda(t) = \lambda_0, \qquad \mu(t) = \mu_1 t.$$

It is of interest that a (λ, μ) process can be found for which the expected growth follows a logistic law,

$$\bar{n}_t = \frac{\alpha}{1 + (\alpha - 1)e^{-\beta t}} \qquad (\alpha > 1, \beta > 0). \tag{58}$$

According to (55) one must have

$$\lambda(t) - \mu(t) = \frac{(\alpha - 1)\beta}{e^{\beta t} + (\alpha - 1)}.$$

The minimum-fluctuation solution is thus the purely reproductive process

$$\lambda(t) = \frac{(\alpha - 1)\beta}{e^{\beta t} + (\alpha - 1)}, \qquad \mu(t) = 0, \tag{59}$$

which satisfies the relation

$$\lambda(t) = \beta\left(1 - \frac{\bar{n}_t}{\alpha}\right), \tag{60}$$

as might have been expected, since the Verhulst-Pearl-Reed differential equation (which forms the *deterministic* basis for the logistic law) is

$$\frac{1}{n}\frac{dn}{dt} = \beta\left(1 - \frac{n}{\alpha}\right). \tag{61}$$

7. "Periodic" birth-and-death processes. As a further example of the general theory it is worth considering the "periodic" processes for which the expected growth $\bar{n}_t$ is a function of the time which repeats itself with the period $\tilde{\omega}$. It will then follow that $\rho(t)$ and so also $\lambda(t) - \mu(t)$ have the period $\tilde{\omega}$, while $\rho(t)$ must be zero whenever t is an integer multiple of $\tilde{\omega}$. The only cases of interest are those in which λ and μ are separately periodic, and then it can be seen from (14c) that

$$\bar{n} = n_0 \text{ and } \operatorname{Var}(n) = kn_0 \int_0^{\tilde{\omega}} e^{\rho(\tau)}\{\lambda(\tau) + \mu(\tau)\}d\tau, \tag{62}$$

whenever $t = k\tilde{\omega}$, for every positive integer k. Thus, although the *expected* value of n_t repeats itself regularly, in practice this "periodicity" would be obscured by the rapid increase, with increasing t, in the magnitude of the random fluctuations (as measured by Var (n_t)). Moreover, since

$$\int_0^{k\tilde{\omega}} e^{\rho(\tau)}\mu(\tau)d\tau = k\int_0^{\tilde{\omega}} e^{\rho(\tau)}\mu(\tau)d\tau,$$

it is clear that the process is necessarily transient, there being unit probability that n_t will ultimately be reduced to zero.

Periodic birth-and-death processes are likely to be of importance in biology; it should be pointed out, however, that this type of process describes the stochastic modification of a *regular* periodicity imposed on the model *from outside*, and it is not to be confused with other stochastic models which themselves generate irregular (non-phase-keeping) oscillations. The models discussed in this section are in fact suitable for the quantitative description of seasonal influences.

Before going into further detail it is natural to specialise the model by assuming that the functions λ and μ are at most *simply* harmonic. If $n_0 = 1$, and since there is to be no damping, one will then have

$$\bar{n}_t = e^{\alpha\{\sin\nu(t+\epsilon) - \sin\nu\epsilon\}} \qquad (\alpha > 0), \tag{63}$$

where $\nu\tilde{\omega} = 2\pi$, and α and ϵ are amplitude and phase constants, respectively. The functions λ and μ are now to be determined from the relation

$$\lambda - \mu = \alpha\nu \cos \nu(t + \epsilon),$$

and this can be done in many ways. The minimum-fluctuation solution would here be artificial, and it is more natural to select two other solutions,

$$(64) \qquad \lambda = \alpha\nu\{1 + \cos \nu(t + \epsilon)\}, \qquad \mu = \alpha\nu,$$

and

$$(65) \qquad \lambda = \alpha\nu, \qquad \mu = \alpha\nu\{1 - \cos \nu(t + \epsilon)\},$$

for further consideration. In the first of these the death rate is constant and the birth rate executes simple-harmonic oscillations, while in the second it is the birth rate which is constant, and the death rate which oscillates. It can be seen that, of all solutions of these two types, (64) and (65) are those with the least value for Var (n_t). From formulae (14*a*) and (14*b*) it will be found that, for either process,

$$(66) \qquad \text{Var } (n) = 4\pi k\alpha I_0(\alpha)e^{\alpha \sin \nu\epsilon} \text{ when } t = k\tilde{\omega}$$

where $I_0(\alpha)$ is the Bessel function of zero order, of the first kind and of imaginary argument. (It will be noticed that, whenever t is an integer multiple of $\tilde{\omega}$, the distribution of the population size n_t is the same for the two models.) For small oscillations, when $t = k\tilde{\omega}$,

$$(67) \qquad \text{Var } (n) \sim 4\pi k\alpha \text{ as } \alpha \to 0$$

since $I_0(0) = 1$, while for large oscillations

$$(68) \qquad \text{Var } (n) \sim 2k(2\pi\alpha)^{\frac{1}{2}}/\bar{n}_{\min} \text{ as } \alpha \to \infty.$$

(Here $\bar{n}_{\min}$ is the minimum value of $\bar{n}_t$.)

The calculation of $P_0(\tilde{\omega})$ presents some points of interest. For either model it proves to be

$$(69) \qquad \frac{2\pi\alpha I_0(\alpha)e^{\alpha \sin \nu\epsilon}}{1 + 2\pi\alpha I_0(\alpha)e^{\alpha \sin \nu\epsilon}};$$

this is the probability that a population element, known to be descended from a single individual at time $t = 0$, will have become extinct one year later (if one identifies the oscillations with a seasonal effect). It will be seen that $P_0(\tilde{\omega})$ will be least when $\sin \nu\epsilon = -1$, and greatest when $\sin \nu\epsilon = +1$; i.e. when $\bar{n}_t$ is expected to have a minimum, or a maximum, at $t = 0$, respectively. Accordingly it follows that the progeny of a new member of the population is most likely to survive till the following year if the "ancestor" commences its "membership" at a time of year when the population would normally have its minimum value.

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