Note on Evolutionary Processes

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NOTE ON EVOLUTIONARY PROCESSES

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1. In 1939, W. FELLER [1] investigated the birth-and-death process associated with the "logistic" law of growth. This process differs from the ordinary birth and-death process only in the following point: the birth-rate λ and the death-rate μ are linearly dependent on the instantaneous population size. So these rates are

$$\lambda \equiv \alpha[N_2 - n(t)], \quad \mu \equiv \beta[n(t) - N_1], \quad (N_1 < N_2),$$

say, where $n(t)$ is the instantaneous population size at time t, and α, β, N_1 and N_2 are absolute constants.

A detailed discussion about this process has already been given by D. G. KENDALL [2]. In his paper, he showed that this process could not be solved explicitly by the p.g.f. method, and he obtained one limiting form of this process. Then the following question arises: Is there any stochastic process which has a similar property to this Feller's "logistic" process and which can be solved completely? In the discussion at the meeting "Symposium on stochastic process" (1949) (at this meeting, D. G. KENDALL's paper [2] was read), B. J. PRENDIVILLE [3] proposed one type of such processes and reported it to be solved completely. But we do not and can not know about his solution and how deeply he investigated his solution. So we want to investigate the PRENDIVILLE's process in an elementary way as possible as we can. In the following, these two processes shall be abbreviated as F-process and P-process, respectively.

The P-process is also the birth-and-death process and differs from the ordinary birth-and-death process in the following point: the birth and death rates are linearly dependent on the inverse of the instantaneous population size. So these rates are

$$\mu \equiv \alpha\left[\frac{N_2}{n(t)} - 1\right], \quad \mu \equiv \beta\left[1 - \frac{N_1}{n(t)}\right], \quad (N_1 < N_2),$$

where α, β, N_1 and N_2 are absolute constants.

2. We shall apply the PALM-BARTLETT's p.g.f. (probability generating function) method to the P-process and try to obtain its solution. As was stated in the last section, the birth and death rates have the following forms:

$$\lambda(n)=\alpha\left(\frac{N_2}{n}-1\right), \quad \mu(n)=\beta\left(1-\frac{N_1}{n}\right), \tag{1}$$
$$(0<N_1\leqq n\leqq N_2).$$

Now, $n(t)$ being the population size at time t, we shall put

$$\Pr\{n(t)=N\}=p_N(t),$$

i.e., $p_N(t)$ is the probability that the population size $n(t)$ has the value N at time t.

Then we can easily write down the differential equations for these $p_N(t)$:

$$\left\{\begin{aligned}
\frac{d}{dt}p_{N_1}(t) &= -\{\lambda(N_1)N_1+\mu(N_1)N_1\}p_{N_1}(t)\\
&\quad +\mu(N_1+1)(N_1+1)p_{N_1+1}(t),\\
\frac{d}{dt}p_N(t) &= -\{\lambda(N)N+\mu(N)N\}p_N(t)\\
&\quad +\mu(N+1)(N+1)p_{N+1}(t)\\
&\quad +\lambda(N-1)(N-1)p_{N-1}(t),\\
&\qquad\qquad (N=N_1+1,\cdots,N_2-1),\\
\frac{d}{dt}p_{N_2}(t) &= -\{\lambda(N_2)N_2+\mu(N_2)N_2\}p_{N_2}(t)\\
&\quad +\lambda(N_2-1)(N_2-1)p_{N_2-1}(t).
\end{aligned}\right. \tag{2}$$

The p.g.f. of $n(t)$ is denoted by $\varphi(z;t)$:

$$\varphi(z;t)=\sum_{n=N_1}^{N_2}p_n(t)z^n.$$

Then, using the above system of differential equations, we can obtain the partial differential equation which determines the function $\varphi(z;t)$. This is the following:

$$\frac{\partial\varphi}{\partial t}=(1-z)(\alpha z+\beta)\frac{\partial\varphi}{\partial z}+(z-1)\left(\alpha N_2+\frac{\beta N_1}{z}\right)\varphi. \tag{3}$$

The corresponding equation for the F-process has not yet been solved. This fact is discussed in details by D. G. KENDALL [2]. This equation is linear, but it has second-order partial derivatives and is of a mixed type.

3. Our principal aim is to solve the equation (3). This equation can be solved completely. Let us set the following initial condition:

$$[\varphi(z;t)]_{t=0}=z^n, \quad (N_1\leqq n\leqq N_2),$$

in other words, we assume that the population size has the value n at time $t=0$. The characteristic differential equation of (3) is

$$\frac{dt}{1}=\frac{dz}{(z-1)(\alpha z+\beta)}=\frac{d\varphi}{(z-1)\{\alpha N_2+(\beta N_1/z)\}\varphi}.$$

From this equation, we can obtain

$$\Phi\left(e^{-(\alpha+\beta)t}\frac{z-1}{\alpha z+\beta}\right)=\frac{z^{N_1}}{(\alpha z+\beta)^{N_1-N_2}}\cdot\frac{1}{\varphi},$$

where Φ is an arbitrary function. From the above initial condition, we can determine the form of this Φ, i.e.,

$$\Phi(u)=\frac{(1+\beta u)^{N_1-n}(1-\alpha u)^{n-N_2}}{(\alpha+\beta)^{N_1-N_2}}.$$

Therefore,

(4) $\varphi(z;t)$

$$=\frac{1}{(\alpha+\beta)^{N_2-N_1}}z^{N_1}\{(\alpha+\beta e^{-(\alpha+\beta)t})z+\beta(1-e^{-(\alpha+\beta)t})\}^{n-N_1}$$
$$\times\{\alpha(1-e^{-(\alpha+\beta)t})z+(\alpha e^{-(\alpha+\beta)t}+\beta)\}^{N_2-n}.$$

This is the p.g.f. of the P-process, and the expansion in powers of z of this φ gives the probability distribution for the population size at any time t. Accordingly, the complete solution of the P-process is now obtained.

4. Next, let us consider the "deterministic" equation for the P-process. If we denote the population size of the "deterministic" model by $\tilde{n}(t)$, we can easily obtain the differential equation for $\tilde{n}(t)$. This is

$$\frac{d\tilde{n}(t)}{dt}=(\alpha N_2+\beta N_1)-(\alpha+\beta)\tilde{n}(t). \tag{5}$$

The solution of this differential equation under the initial condition $\tilde{n}(0)=n$ is the following:

$$\tilde{n}(t)=\frac{1}{(\alpha+\beta)}[(\alpha N_2+\beta N_1)-\{(\alpha N_2+\beta N_1)-n(\alpha+\beta)\}e^{-(\alpha+\beta)t}]. \tag{6}$$

From this equation, we can see that $\tilde{n}(t)$ tends to a unique limiting value when t tends to infinity, and that this value is

$$\tilde{n}(\infty)=\frac{\alpha N_2+\beta N_1}{\alpha+\beta}. \tag{7}$$

This value is independent of the initial population size $\tilde{n}(0)$ and lies between N_1 and N_2.

For the F-process, as was stated by D. G. KENDALL [2], we can also obtain the explicit form of $\tilde{n}(t)$ and its limiting value $\tilde{n}(\infty)$ is also the same value as (7).

5. Before we make a similar consideration for the "stochastic" model, we shall firstly consider about the mean and variance of the P-process.

From the equation (3), we can obtain the following differential equation for the mean population size $\mu_1(t)$ at time t:

$$(8) \qquad \frac{d\mu_1(t)}{dt} = (\alpha N_2 + \beta N_1) - (\alpha+\beta)\mu_1(t), \quad [\mu_1(t)]_{t=0} = n.$$

This equation has the same form as the equation (5). Accordingly, its solution has the same form as the expression (5):

$$(9) \quad \mu_1(t) = \frac{1}{(\alpha+\beta)}[(\alpha N_2 + \beta N_1) - \{(\alpha N_2 + \beta N_1) - n(\alpha+\beta)\} e^{-(\alpha+\beta)t}].$$

In the second place, let us consider the variance of the population size $n(t)$ at time t. From (3), we can get the differential equation

$$(10) \qquad \frac{d\omega(t)}{dt} = -2\beta N_1 + 2(\alpha N_2 + \beta N_1 - \alpha)\mu_1(t) - 2(\alpha+\beta)\omega(t),$$
$$[\omega(t)]_{t=0} = n^2 - n,$$

where $\omega(t) = \mu_2(t) - \mu_1(t)$, and $\mu_2(t)$ is the second-order moment of the population size at time t. Its solution is

$$(11) \qquad \omega(t) = \left\{-\frac{N}{\alpha+\beta} + \frac{(\alpha N_2+\beta N_1)^2 - \alpha(\alpha N_2 + \beta N_1)}{(\alpha+\beta)^2}\right\}$$
$$+ \left\{\frac{2n(\alpha N_2 + \beta N_1) - 2n\alpha}{\alpha+\beta} - \frac{2(\alpha N_2 + \beta N_1)^2 - 2\alpha(\alpha N_2 + \beta N_1)}{(\alpha+\beta)^2}\right\} e^{-(\alpha+\beta)t}$$
$$+ \left\{n^2 - n + \frac{\beta N_1 - 2n(\alpha N_2 + \beta N_1) + 2n\alpha}{\alpha+\beta} + \frac{(\alpha N_2 + \beta N_1)^2 - \alpha(\alpha N_2 + \beta N_1)}{(\alpha+\beta)^2}\right\} e^{-2(\alpha+\beta)t}.$$

Therefore, the variance of $n(t)$ is

$$(12) \quad \text{var}\,(t) = \left\{\frac{N}{\alpha+\beta} - \frac{\alpha(\alpha N_2 + \beta N_1)}{(\alpha+\beta)^2}\right\}$$
$$+ \left\{n - \frac{\alpha N_2 + \beta N_1 + 2n\alpha}{\alpha+\beta} + \frac{2\alpha(\alpha N_2 + \beta N_1)}{(\alpha+\beta)^2}\right\} e^{-(\alpha+\beta)t}$$
$$+ \left\{-n + \frac{\beta N_1 + 2n\alpha}{\alpha+\beta} - \frac{\alpha(\alpha N_2 + \beta N_1)}{(\alpha+\beta)^2}\right\} e^{-2(\alpha+\beta)t}.$$

Of course, these moments can be also obtained directly from the form (4) of the $\varphi(z; t)$.

On the other hand, for the F-process, the differential equation is

$$\frac{d\mu_1(t)}{dt}=(\alpha N_2+\beta N_2)\mu_1(t)-(\alpha+\beta)\mu_2(t).$$

This equation can not be solved, because it contains an unknown function $\mu_2(t)$. Therefore in this case, we can not obtain the simple relation between the developement of the "deterministic" process and the mean developement of the "stochastic" process, which holds in the case of the P-process. This is the essential character of the F-process. This fact was firstly discussed in details by W. FELLER [1] (and see also D. G. KENDALL [2]).

6. Now, let us investigate the behaviour of the p.g.f. $\varphi(z;t)$ of the P-process as t approaches infinity. Using (4), we obtain

$$\begin{aligned}\text{(13)}\qquad \varphi(z;\infty)&=\lim_{t\to\infty}\varphi(z;t)\\ &=\frac{1}{(\alpha+\beta)^{N_2-N_1}}z^{N_1}(\alpha z+\beta)^{N_2-N_1}\\ &=\frac{1}{(\alpha+\beta)^{N_2-N_1}}\sum_{\nu=0}^{N_2-N_1}\binom{N_2-N_1}{\nu}\alpha^{\nu}\beta^{(N_2-N_1)-\nu}z^{\nu+N_1}.\end{aligned}$$

This function $\varphi(z;\infty)$ will generate probabilities which will represent the ultimate "stable" distribution of the values of the population size. And, as the probability that the ultimate population size is equal to $N_1+\nu$, we obtain

$$\text{(14)}\qquad P_{N_1+\nu}=\frac{1}{(\alpha+\beta)^{N_2-N_1}}\binom{N_2-N_1}{\nu}\alpha^{\nu}\beta^{(N_2-N_1)-\nu},\quad (\nu=0,1,2,\cdots,N_2-N_1).$$

Also, from the form of this $\varphi(z;\infty)$, the mean value of this distribution is

$$\frac{\alpha N_2+\beta N_1}{\alpha+\beta},$$

and this value is equal to the limiting value (7) in the "deterministic" model.

On the other hand, for the F-process, D. G. KENDALL [2] obtained the following result:

$$P_{N_1+\nu}=\frac{C}{N_1+\nu}\binom{N_2-N_1}{\nu}\alpha^{\nu}\beta^{(N_2-N_1)-\nu},\quad (\nu=0,1,2,\cdots,N_2-N_1),$$

where the constant C is to be adjusted to make

$$\sum_{n=N_1}^{N_2}P_n=1.$$

Thus, from this point of view, there is a close relation between the F-process and the P-process. D. G. KENDALL [4] has spended a few words to explain the more general situation.

7. Finally, let us consider one limiting form for the P-process. For the F-process, D. G. KENDALL [2] has already obtained this limiting form. It occurs when

$$\begin{aligned} &N_2 \to \infty, \quad \alpha \to 0, \quad \alpha N_2 = \lambda_0, \\ &N_1 = 1, \quad \beta = \mu_1 . \end{aligned}$$

We also consider this case. Accordingly, we have the following birth and death rates:

$$\lambda \equiv \frac{\lambda_0}{n(t)}, \quad \mu \equiv \mu_1\left[1 - \frac{1}{n(t)}\right]. \tag{15}$$

The population size $n(t)$ can then range through all the values given by the positive integers. Our limiting form is

$$P_\nu = e^{-(\lambda_0/\mu_1)} \frac{1}{(\nu-1)!}\left(\frac{\lambda_0}{\mu_1}\right)^{\nu-1}, \quad (\nu = 1, 2, 3, \cdots). \tag{16}$$

This is the modification of the Poisson distribution. Its mean value is

$$\sum_{\nu=1}^{\infty} \nu P_\nu = 1 + \frac{\lambda_0}{\mu_1}, \tag{17}$$

and from (7) the limiting population size of the "deterministic" model in this case is

$$\lim \frac{\alpha N_2 + \beta N_1}{\alpha + \beta} = 1 + \frac{\lambda_0}{\mu_1}. \tag{18}$$

Namely, in the P-process, these two values coincide.

On the other hand, as was stated by D. G. KENDALL, in the case of the F-process, the corresponding P_ν's have the modified Poissonian form $(e^{\lambda_0/\mu_1} - 1)^{-1}(\lambda_0/\mu_1)^\nu/\nu!$, $(\nu = 1, 2, 3, \cdots)$, and its mean value is $(1 - e^{-(\lambda_0/\mu_1)})^{-1} \times (\lambda_0/\mu_1)$, so that the limiting population size of the "deterministic" model is greater than the corresponding value of the "stochastic" model.

8. From these considerations, the P-process is not a process which has a character, pointed out by W. FELLER, that it does not show the simple relation which might have been expected between the developement of the "deterministic" process and the mean developement of the "stochastic" process. So, the P-process shows a sort of the "logistic" law of growth, but it has not a structure parallel to the structure of the F-process.

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