

SENSITIVITY OF A BIRTH PROCESS TO CHANGES IN THE GENERATION TIME DISTRIBUTION

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1. Introduction

This paper describes some studies on the age dependent binary branching process. These studies are partly theoretical and partly numerical. We shall first describe the model and then mention two problems which suggested this investigation.

The model is one that is sometimes used to represent the growth of cellular populations under favorable conditions, in which there are no deaths, and the life of each individual terminates by a process of fission giving rise to two new individuals. The life length of an individual is the period from its inception by binary fission of its parent to the instant of its own fission. This period varies randomly in the following sense. Let $G(t)$ be a distribution function (to be called the generation time distribution) which is such that $G(0-) = 0$. Suppose that at time 0 a single individual of age zero is present, and that its life length is L where $P\{L \leq t\} = G(t)$. At the end of its life it is replaced by two individuals of age zero and their life lengths L_1, L_2 are independently distributed according to the same law; that is, $P\{L_1 \leq t\} = P\{L_2 \leq t\} = G(t)$. At the end of their lives these two individuals are each replaced by two newly born ones in the same way. Note that at any instant of time the probability of fission for each individual depends on its own age, but not on the number of others present, nor on absolute time. This model is a special case of the process that is described in Harris ([1], chapter VI). We shall summarize certain results given there (which we shall use), which are particularly concerned with the behavior of the process for large values of the time.

Let $Z(t)$ be the population size at time t .

Let ρ , which we shall call the "Malthusian parameter," be the unique real positive root of the equation

$$(1) \quad \int_0^{\infty} e^{-\rho t} dG(t) = \frac{1}{2}.$$

Let

$$(2) \quad n_1 = \left[4\rho \int_0^{\infty} te^{-\rho t} dG(t) \right]^{-1}.$$

Then

$$(3) \quad Z(t)/(n_1 e^{\rho t}) \rightarrow W \quad \text{as } t \rightarrow \infty$$

where, under wide conditions given in [1], W is a random variable that has an absolutely continuous distribution. Writing \mathcal{E} for expectation, we can state the following properties of W . Let $\mathcal{E}e^{-sW} = \phi(s)$. Then a well known argument based on the regeneration point of the process gives the equation

$$(4) \quad \phi(s) = \int_0^\infty [\phi(se^{-\rho u})]^2 dG(u).$$

Differentiation of this equation with respect to s gives

$$(5) \quad \mathcal{E}W = 1, \text{ and } \text{Var } W = (4I_2 - 1)/(1 - 2I_2)$$

where we define

$$(6) \quad I_j = \int_0^\infty e^{-j\rho t} dG(t) \quad \text{for } j = 1, 2, \dots$$

From the point of view of applications, we may remark that if $\log Z(t)$ is plotted against t , then with increasing t it will approximate to a straight line of slope ρ whose intercept on the ordinate is $\log W + \log n_1$. The stochastic variations represented by W arise mainly from stochastic fluctuations in the life lengths of individuals in the early generations, which influence the whole later development of the population.

Let us define the coefficient of variation of the generation time distribution by

$$(7) \quad CV(L) = \sqrt{\text{Var } L}/\mathcal{E}L.$$

Then models in which $CV(L) \rightarrow 0$ can be taken to represent the situation of "approximate equivancy." D. G. Kendall [2] discussed the special age dependent binary fission process in which L has the distribution of $(1/2k\lambda)\chi_{2k}^2$, where λ is a fixed positive constant ($1/\lambda$ being $\mathcal{E}L$) so that $CV(L) \rightarrow 0$ as $k \rightarrow \infty$. He showed that

$$(8) \quad \frac{CV(W)}{CV(L)} \rightarrow \sqrt{2} \ln 2 \approx 0.98 \quad \text{as } k \rightarrow \infty,$$

and gave an heuristic argument suggesting that this limit would hold for more general forms of $G(t)$. He also pointed out that the ratio in (8) is never far from unity.

Let $Z(x, t)$ be the number of individuals alive at time t whose age does not exceed x . Then

$$(9) \quad \frac{Z(x, t)}{Z(t)} \rightarrow A(x) \quad \text{for each } x, \text{ with probability 1,}$$

as $t \rightarrow \infty$. This limit, known as the limiting age distribution, is related to the generation time distribution by

$$(10) \quad A(x) = 2\rho \int_0^x e^{-\rho t} [1 - G(t)] dt.$$

One of the problems which suggested the present investigation is biological.

Various hypothetical mechanisms of cellular growth and fission lead to corresponding hypotheses about the nature of $G(t)$, and it would be desirable to discriminate between them. Kendall [2] describes a process of duplication of subunits within the cell which might give rise to the χ^2 form of $G(t)$. In Kendall's process, duplication of subunits proceeded in sequence, and an alternative originating with Rahn [3] was to suppose that duplication took place in parallel or simultaneously. With certain assumptions about the system of probabilities involved, this leads to $G(t) = (1 - e^{-\lambda t})^k$ where λ is a positive constant and k is equal to the number of entities to be duplicated, and these two forms were compared by Powell [4] using goodness of fit methods on directly observed life lengths of individual bacterial cells. It is clearly difficult to obtain enough direct observations to discriminate sharply between the alternatives, even leaving aside the appearance of phenomena such as dependence between individuals, and day to day changes in growth rates. This leads us to enquire whether the age distribution or some other property of the process might be markedly different for alternative forms of $G(t)$.

The other problem we had in mind was a theoretical one. Consider non-negative, negative exponential random variables $\tau_1, \tau_2, \dots, \tau_k$. Suppose τ_i has the probability density $\theta_i^{-1} \exp(-t/\theta_i)$ where $\theta_i (= \mathcal{E}\tau_i)$ is a fixed positive constant. Then, in well known terminology, if the life length L has the distribution of the sum $\tau_1 + \tau_2 + \dots + \tau_k$, we shall say that the generation time is "Erlangian." Note that the symbol E_k is used to indicate the appearance of the same sort of distribution in the standard notation specifying inter arrival time and service time in a queueing system. The parameter k is called the "number of phases."

Both in population and in queueing problems, waiting times of the E_k type have often been introduced. One reason has been that it seems plausible that they will give results that are approximately true for systems involving more general distributions of waiting times. In [5], D. G. Kendall made several remarks about this practice in queueing theory. We may quote: "Suppose, for example, that we are concerned with $M/G/s$ and that we decide to replace this by $M/E_k/s$; how should k be chosen? . . . If, for instance, we are mainly interested in the mean waiting time, then we may recall that for $M/G/1$ this depends only on the first two moments of the service-time distribution, and so we should feel tempted to choose k so that E_k and G have the same coefficient of variation, even for $s > 1$. Is this correct, and how large can the error be?" These remarks suggest a similar problem for population growth processes. We can set up processes based on different Erlangian generation times E_k and $E_{k'}$ where the means and variances are equal, but the parameter sets $\theta_1, \dots, \theta_k$ and $\theta'_1, \dots, \theta'_{k'}$ are not the same, and compare properties of the processes. We can also select specific forms of $G(t)$ other than Erlangian and compare processes based on these with the Erlangian ones.

In the ensuing sections of this paper we first show that in the situation described as the "approach to equivancy," the limit (8) holds for all Erlangian

processes. We then select a number of specific forms of $G(t)$ and carry out some computer studies of the limit (8), with particular reference to the rate of convergence, and of the limiting age density $A'(x)$ defined by (10). Within the family of Erlangian processes, our theoretical study of the limit (8) suggests that the χ^2 form represents an extreme of behavior and also suggests an opposite extreme. We therefore numerically study these two extremes and a related limiting distribution. We also select for study some non-Erlangian forms of $G(t)$, either on the basis of suggestions appearing in biological work, or in an attempt to find examples that deviate from the general pattern.

2. The “approach to equivancy” for Erlangian processes

Let $\theta_1, \dots, \theta_k$ be the set of parameters of a k -phase Erlangian generation time distribution. We shall suppose that the mean generation time εL is fixed. Let

$$(11) \quad \sum_{r=1}^k \theta_r^j = s_j \quad \text{for } j = 1, 2, 3.$$

Without loss of generality, we can suppose that

$$(12) \quad s_1 = \varepsilon L = 1,$$

and note that $s_2 = \text{Var } L$, and s_3 is proportional to the third central moment of L . We shall show that as $\text{Var } L \rightarrow 0$ (when, necessarily, $k \rightarrow \infty$) the limit (8) holds in the equivalent form

$$(13) \quad \frac{\text{Var } W}{\text{Var } L} \rightarrow 2(\log 2)^2.$$

We shall first express ρ , and then $\text{Var } W$, in terms of the sums s_1, s_2, s_3 . For $G(t)$ of Erlangian form we have

$$(14) \quad I_j = \prod_{r=1}^k (1 + j\rho\theta_r)^{-1}.$$

Taylor’s theorem, with the remainder at the second term, gives

$$(15) \quad \log (1 + \rho\theta_r) = \rho\theta_r - \frac{1}{2} (\rho\theta_r)^2 / (1 + \Theta\rho\theta_r)^2.$$

Here, and later, we shall use Θ as a general symbol for a quantity such that $0 < \Theta < 1$, and it may represent a different quantity of this type at different times. Now by (14), $I_1^{-1} > 1 + \rho \sum_{r=1}^k \theta_r$, whereby using (1) we get $1 + \rho < 2$. Thus $\rho < 1$, from which we obtain *a fortiori* $\rho\theta_r < 1$; and so

$$(16) \quad \frac{1}{4} < (1 + \Theta\rho\theta_r)^{-2} < 1,$$

which, with a different Θ , gives in (15)

$$(17) \quad \log (1 + \rho\theta_r) = \rho\theta_r - \frac{1}{2} \theta_r^2 \Theta.$$

Summing for $r = 1, \dots, k$, we obtain on the left $\ln I_1^{-1}$, which by (1) is equal to $\ln 2$. Therefore,

$$(18) \quad \rho = \log 2 + \frac{1}{2} \Theta s_2.$$

We now obtain an estimate for $4I_2$. Let $\rho\theta_r = \epsilon_r$. Then $4 = \prod_{r=1}^k (1 + \epsilon_r)^2$; hence, again using Taylor's theorem and expressing the remainder by means of a Θ symbol, we have

$$(19) \quad \begin{aligned} \log 4I_2 &= \sum_{r=1}^k \log \frac{(1 + \epsilon_r)^2}{1 + 2\epsilon_r} \\ &= \sum_{r=1}^k \log \left(1 + \frac{\epsilon_r^2}{1 + 2\epsilon_r} \right) \\ &= \sum_{r=1}^k \frac{\epsilon_r^2}{1 + 2\epsilon_r} - \frac{\Theta}{2} \sum_{r=1}^k \frac{\epsilon_r^4}{(1 + 2\epsilon_r)^2} \\ &= \sum_{r=1}^k \epsilon_r^2 - \sum_{r=1}^k \epsilon_r^3 \frac{2(1 + 2\epsilon_r) + \frac{1}{2}\Theta\epsilon_r}{(1 + 2\epsilon_r)^2}. \end{aligned}$$

Consideration of possible values in and on the boundary of the square $0 \leq \theta \leq 1, 0 \leq \epsilon_r \leq 1$ shows that

$$(20) \quad \frac{2}{3} < \frac{2(1 + 2\epsilon_r) + \frac{1}{2}\Theta\epsilon_r}{(1 + 2\epsilon_r)^2} < 2.$$

From (19), (20), and (18), by using two symbols Θ and Θ' , we obtain

$$(21) \quad \begin{aligned} \log 4I_2 &= \rho^2 s_2 - \rho^3 s_3 \frac{2}{3} (1 + 3\Theta') \\ &= (\log 2)^2 s_2 + \Theta (\log 2) s_2^2 + \frac{1}{4} \Theta^2 s_2^3 \\ &\quad - \frac{2}{3} (1 + 3\Theta') \{ (\log 2)^3 s_3 + \frac{3}{2} \Theta (\log 2)^2 s_2 s_3 \\ &\quad + \frac{3}{4} \Theta^2 s_2^2 s_3 + \frac{1}{8} \Theta^3 s_2^3 s_3 \} \\ &= (\log 2)^2 s_2 + B(s_2, s_3). \end{aligned}$$

Note that if $s_3/s_2 \rightarrow 0$ as $s_2 \rightarrow 0$, then $B(s_2, s_3)/s_2 \rightarrow 0$. Using $e^x - 1 = x + 1/2x^2e^{\theta x}$, we have from (21)

$$(22) \quad 4I_2 - 1 = (\log 2)^2 s_2 + B(s_2, s_3) + \frac{1}{2} \{ (\log 2)^2 s_2 + B(s_2, s_3) \}^2 \exp \{ \Theta \log 4I_2 \}$$

where the term $\exp \{ \Theta \log 4I_2 \}$ is bounded, say by M . Thus

$$(23) \quad \begin{aligned} \frac{\text{Var } W}{\text{Var } L} &= \frac{4I_2 - 1}{s_2(1 - 2I_2)} \\ &= [1 - 2I_2]^{-1} \left[(\log 2)^2 + \frac{B(s_2, s_3)}{s_2} + \frac{1}{2} \left\{ (\log 2)^2 \sqrt{s_2} + \frac{B(s_2, s_3)}{\sqrt{s_2}} \right\}^2 M \right] \end{aligned}$$

$\rightarrow 2(\log 2)^2$, which is (13).

To prove that (13) holds for all Erlangian processes as $\text{Var } L \rightarrow 0$ with $\epsilon L = 1$,

we need only note that the restricted maximum of s_3 under the conditions $s_1 = 1$ and $s_2 = \delta$ can be obtained by means of Lagrange's multipliers and is

$$(24) \quad s_3(\max) = \frac{\delta}{k^2} \left\{ 3k - \frac{2}{\delta} + \left(k - \frac{1}{\delta} \right) (k - 2) \left[\frac{\delta \left(k - \frac{1}{\delta} \right)}{k - 1} \right]^{1/2} \right\}$$

where necessarily $k \geq 1/\delta$. It follows that $s_3(\max)/\delta \rightarrow 0$ whence $s_3/s_2 \rightarrow 0$ as required to ensure the limit in (23). We may remark that if fission is to form a fixed number b of offspring where $b \geq 2$, the preceding work can be generalized to show that $\text{Var } W/\text{Var } L \rightarrow (b/b - 1)(\log b)^2$, but since binary fission is the case of biological interest, we omit the proof.

3. Basis of numerical investigation

For the numerical investigation, values of ρ , n_1 , $\text{Var } W/\text{Var } L$, and $A'(x)$ were computed for various generation time distributions $G(t)$. The following distributions were investigated.

(a) *Erlangian E_k of χ^2 form.* Results for this model are well known (see [2]). We tabulate numerical values for comparison with other models and particularly with those to be described under (b) and (c).

(b) *Erlangian E_k of maximum skewness.* Let $\mu_3(L)$ denote the third central moment of the generation time. The condition following (21) in section 2 is equivalent to

$$(25) \quad \mu_3(L)/\text{Var } L \rightarrow 0 \quad \text{as} \quad \text{Var } L \rightarrow 0.$$

For comparison with (a) we take $\text{Var } L = 1/j$. Then we can consider two Erlangian distributions which we indicate by $E_j(\chi^2)$ and E_k (skew). For given j the parameters for the $E_j(\chi^2)$, which is as described in (a), are necessarily $\theta_1 = \theta_2 = \dots = \theta_j = 1/j$. For $k > j$ one can obtain an infinity of parameter sets $\theta_1, \dots, \theta_k$ such that

$$(26) \quad \sum_{r=1}^k \theta_r = 1, \quad \sum_{r=1}^k \theta_r^2 = 1/j.$$

Among these there is the set

$$(27) \quad \theta_1 = \dots = \theta_{k-1} = \frac{1}{k} \left\{ 1 - \left(\frac{k-j}{j(k-1)} \right)^{1/2} \right\},$$

$$\theta_k = \frac{1}{k} \left\{ 1 + \left(\frac{(k-j)(k-1)}{j} \right)^{1/2} \right\},$$

which gives the maximum value of $\sum_{r=1}^k \theta_r^3$. We call the corresponding Erlangian distribution E_k (skew). Note also that the set

$$(28) \quad \theta_1 = \dots = \theta_j = \frac{1}{j},$$

$$\theta_{j+1} = \dots = \theta_k = 0,$$

gives the minimum value to $\sum_{r=1}^k \theta_r^2$ under the conditions (28). Now (25) holds for all Erlangians under (26), but the role $\mu_3(L)/\text{Var } L$ plays in (21) suggests

that skewness of $G(t)$ may influence the rate of convergence in (13). The $E_k(\chi^2)$ are those with minimum skewness, and for comparison we take E_k (skew), which has maximum skewness.

(c) *Limit of Erlangian distribution of maximum skewness.* Still under conditions (26) we now consider j as temporarily fixed and let $k \rightarrow \infty$. The distribution E_k (skew) has as its limit a distribution which we shall denote by E_∞ (skew). This limiting distribution can be specified by defining L as the sum of a negative exponential random variable having mean $1/\sqrt{j}$, plus a fixed waiting time $1 - 1/\sqrt{j}$. Since for fixed j and $k > j$ the skewness of E_k (skew) increases with k , we take E_∞ (skew) for further comparison with $E_j(\chi^2)$.

(d) *Reciprocals of Erlangian and normal variates.* A suggestion has recently been made that the generation rate is approximately normal (see Kubitschek [6]). Since in deterministic growth the generation time is the reciprocal of the generation rate, we take L^{-1} to have a truncated normal distribution, since L must be nonnegative. Because of the requirement of nonnegativeness, and for comparison with (a), we also take L^{-1} to have a distribution of χ^2 type, but we change the scale to give $\epsilon L = 1$. The distribution of L that results will be denoted by $E_k^{-1}(\chi^2)$.

The $E_k^{-1}(\chi^2)$ distribution has the density function $g(t)$ given by

$$(29) \quad g(t) = \begin{cases} \frac{(k-1)^k}{(k-1)!} t^{k-1} e^{-(k-1)/t} & \text{for } t \geq 0 \\ 0 & \text{for } t < 0 \end{cases}$$

when $k \geq 2$. Note that L has only $k - 1$ moments. We also consider the case where L^{-1} is a negative exponential variable with mean $\epsilon L^{-1} = 1$, and denote this by $E_1^{-1}(\chi^2)$.

In general we have

$$(30) \quad \epsilon L = 1 \text{ (for } k \geq 2) \text{ and } \text{Var } L = (k - 2)^{-1} \text{ (for } k \geq 3).$$

We have pointed out (following (6)) that stochastic fluctuations in the life lengths in the early generations strongly affect W . In particular, extreme values of $L, L_1, L_2,$ and so on, should be important. Distributions with no moments such as $E_1^{-1}(\chi^2)$ can therefore be expected to produce marked differences of behavior from the norm displayed by the $E_k(\chi^2)$ model, for example, and this appears in our numerical results. In (29), for $k \geq 2$, the variable is obtained by taking the reciprocal of a variable distributed as $(1/2k)\chi_{2k}^2$ and then rescaling to give mean 1. Since $E_1^{-1}(\chi^2)$ has no mean, we also, for comparison, scale the reciprocals of χ^2 type variables to have median 1, and the different behavior for small values of k will be noted in sections 4 and 5.

(e) *Logarithmic variable.* The variables $E_k^{-1}(\chi^2)$ for small k , and also the truncated normal, have no moments, and in this sense, large "tails" as $t \rightarrow \infty$. In view of the possible effect of extreme values, it seemed desirable to compare the behavior of a model where the generation time density has a singularity at $t = 0$, and for this purpose we took the density $g(t)$ given by

$$(31) \quad g(t) = \begin{cases} \frac{1}{4}(\log 4 - \log t) & \text{for } 0 \leq t \leq 4 \\ 0 & \text{for } t < 0 \text{ and for } t > 4. \end{cases}$$

4. Remarks on numerical results for Variance ratio

In tables I through VI we give values of ρ , n_1 , $\text{Var } W$, and the ratio $\text{Var } W/\text{Var } L$ for the models described in section 3. Tables I, II, and III provide a direct

TABLE I

 $E_k(\chi^2)$

k	ρ	n_1	$\text{Var } W$	$\text{Var } W/\text{Var } L$
1	1.0000	1.0000	1.0000	1.0000
2	.8284	.8536	.4890	.9781
3	.7798	.8079	.3239	.9716
4	.7568	.7857	.2422	.9686
6	.7348	.7638	.1610	.9658
8	.7241	.7530	.1206	.9645
10	.7177	.7466	.0964	.9637
12	.7136	.7424	.0803	.9632
15	.7094	.7381	.0642	.9628
20	.7053	.7339	.0481	.9623
25	.7028	.7314	.0385	.9620
30	.7012	.7297	.0321	.9618
35	.7001	.7285	.0275	.9617
40	.6992	.7276	.0240	.9616
60	.6972	.7255	.0160	.9614
80	.6962	.7245	.0120	.9611
100	.6956	.7239	.0096	.9611

TABLE II

 $E_k^{-1}(\chi^2)$

k	ρ	n_1	$\text{Var } W$	$\text{Var } W/\text{Var } L$
2	1.0272	.8894	.5223	—
3	.8462	.8285	.3487	.3487
4	.7899	.7989	.2603	.5206
6	.7478	.7704	.1714	.6857
8	.7310	.7569	.1272	.7635
10	.7220	.7492	.1010	.8078
12	.7165	.7442	.0836	.8362
15	.7112	.7393	.0664	.8635
20	.7063	.7346	.0494	.8897
25	.7035	.7318	.0393	.9049
30	.7016	.7300	.0327	.9147
35	.7004	.7287	.0279	.9217
40	.6994	.7278	.0244	.9268
60	.6973	.7256	.0162	.9384
80	.6962	.7245	.0121	.9442
100	.6956	.7239	.0097	.9474

TABLE III
 E_∞ (skew)

j	ρ	n_1	Var W	Var W /Var L
2	.8141	.8281	.3642	.7284
3	.7699	.7898	.2336	.7009
4	.7496	.7723	.1746	.6985
6	.7304	.7554	.1180	.7077
8	.7210	.7471	.0899	.7196
10	.7154	.7422	.0731	.7305
12	.7117	.7389	.0617	.7402
15	.7081	.7355	.0502	.7527
20	.7044	.7321	.0385	.7691
25	.7022	.7301	.0313	.7819
30	.7007	.7287	.0264	.7922
35	.6996	.7277	.0229	.8008
40	.6988	.7269	.0202	.8080
60	.6970	.7251	.0138	.8290
80	.6960	.7242	.0105	.8428
100	.6955	.7237	.0085	.8528
200	.6943	.7225	.0044	.8799
300	.6939	.7221	.0030	.8930
400	.6937	.7219	.0023	.9011
500	.6936	.7218	.0018	.9068
750	.6935	.7217	.0012	.9160
1000	.6934	.7216	.0009	.9216

comparison between the models $E_k(\chi^2)$, $E_k^{-1}(\chi^2)$, and E_∞ (skew). For all these models $\rho \rightarrow \log 2 = 0.69315$. Note also that $2(\log 2)^2 = 0.96091$ and that $\text{Var } L = 1/k$. Values of k have been chosen for the following purposes: (i) to illustrate the behavior of the process for fairly small values of k (1) through (15)). Some differences appear here; (ii) to look for differences in the range of $\text{Var } L$ that is of biological interest, corresponding to values of k from 20 through 60; and (iii) to take $\text{Var } L$ sufficiently small to get close to the limits in each case.

Note that in the range of k that is of biological interest, the differences in $\text{Var } W/\text{Var } L$ among the models is not large. Compared with $E_k(\chi^2)$, E_∞ (skew) differs more greatly and approaches its limit more slowly than $E_k^{-1}(\chi^2)$.

Table IV provides two special models. One is based on making L^{-1} a normal $N(1, 30^{-1/2})$ variable, conditional on being nonnegative, following the suggestion of Kubitschek [6]. The probability of negative values is, in fact, negligible,

TABLE IV
OTHER DISTRIBUTIONS

	ρ	n_1	Var W	Var W /Var L
Reciprocal of a truncated normal [L^{-1} is $N(1, 30^{-1/2})$]	.6777	.7311	.0358	—
Logarithmic	.9674	1.0123	1.1056	1.4215

but the nonexistence of moments prevents consideration of $\text{Var } W/\text{Var } L$. In order to obtain a dispersion of approximately the order of magnitude involved in biological problems, we have taken $\text{Var } L^{-1} = 30$. The other model, which we call "logarithmic" (see section 3(e)), was deliberately chosen in a search for a model that would differ appreciably from the others, and we note that $\text{Var } W/\text{Var } L$ does appear somewhat larger.

In table V we take L^{-1} to have a distribution of χ^2 type, but we center L^{-1}

TABLE V
 $E_k^{-1}(\chi^2)$ WITH L CENTERED AT MEDIAN $m(L)$

k	$m(L)^\rho = 1$	$\varepsilon L^\rho = 1$
1	.5700	—
2	.6120	1.0272
3	.6329	.8462
4	.6453	.7899
40	.6877	.6994

Note: for $k = 1$, εL does not exist. Measuring in units of $\varepsilon L^{-1} = 1$ in this case we have $\rho = 0.3951$.

at its median. This gives a basis for comparing the reciprocal of a negative exponential variable with the others.

In table VI we give some results for an approximation by an Erlangian model

TABLE VI
 E_k (skew) FOR FIXED VARIANCE OF GENERATION TIME $\text{Var } L = 1/2$

k	ρ	n_1	$\text{Var } W/\text{Var } L = 2 \text{Var } W$
2	.8284	.8356	.9781
3	.8217	.8409	.8598
4	.8188	.8367	.8178
6	.8169	.8333	.7830
8	.8161	.8318	.7677
10	.8157	.8310	.7591
12	.8154	.8305	.7536
15	.8151	.8300	.7482
20	.8148	.8295	.7430
25	.8147	.8292	.7400
30	.8146	.8290	.7380
35	.8146	.8289	.7366
∞	.8144	—	.7284

where the situation is *not* one of "approach to equivivancy." We take $\text{Var } L = 1/2$ and tabulate results for E_k (skew) having this fixed variance. Thus the table

shows a comparison between the E_k (skew) models and $E_2(\chi^2)$, which appears again at the top of table VI.

5. Remarks on numerical results for age distribution

As with the ratio $\text{Var } W/\text{Var } L$, some differences appear among the models with $\text{Var } L = 1/k$ when k is not large. These can be seen in the early entries in table VII. Note also that in the "logarithmic" model for which $\varepsilon L = 1$ and

TABLE VII
MEANS AND VARIANCES OF AGES

k	$E_k(\chi^2)$		$E_k^{-1}(\chi^2)$	
	Mean	Variance	Mean	Variance
2	.5000	.2071	.4263	.2075
3	.4887	.1747	.4686	.2101
4	.4804	.1549	.4736	.1863
6	.4701	.1325	.4693	.1512
8	.4641	.1205	.4643	.1320
10	.4602	.1131	.4607	.1207
12	.4576	.1080	.4579	.1134
15	.4548	.1028	.4551	.1063
20	.4519	.0976	.4521	.0995
25	.4501	.0944	.4503	.0956
30	.4489	.0922	.4491	.0931
35	.4481	.0907	.4482	.0913

Note: for the "logarithmic" model the age has mean 0.5321 and variance 0.2484.

$\text{Var } L = 7/9$ the mean age is somewhat larger than in the other models. However, when $k = 35$, once more in the range suggested by the biological applications, the difference between $E_k(\chi^2)$ and $E_k^{-1}(\chi^2)$ is very slight. The densities (figures 1, 2, and 3 are all of very similar appearance, clearly due to the strong effect on the age distribution of the exponential term in (10).

6. Conclusions

The features of the binary branching process that we have examined are the growth rate, the variance of the population size for large values of the time, and the limiting age distribution. These depend on the generation time distribution $G(t)$, and numerical investigations show some differences, especially between models in which $G(t)$ takes markedly different forms. The differences are less, and would perhaps be difficult to detect experimentally, in the biologically interesting situation where $\text{Var } L$ is fairly small. A similar situation occurs in Slater's stochastic dissociation rate theory ([6], chapter 9) in which

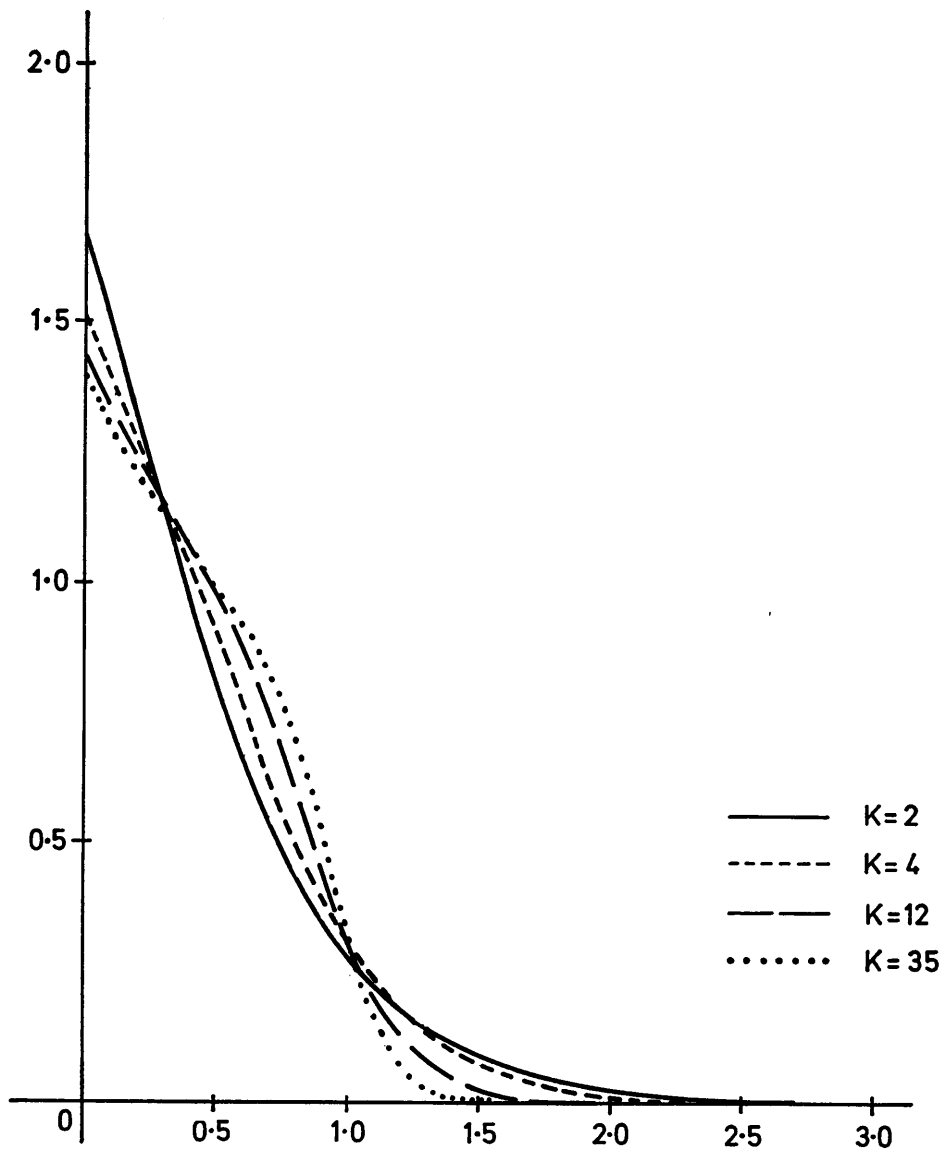


FIGURE 1
Age density $A'(t)$ for $E_k(\chi^2)$ model.

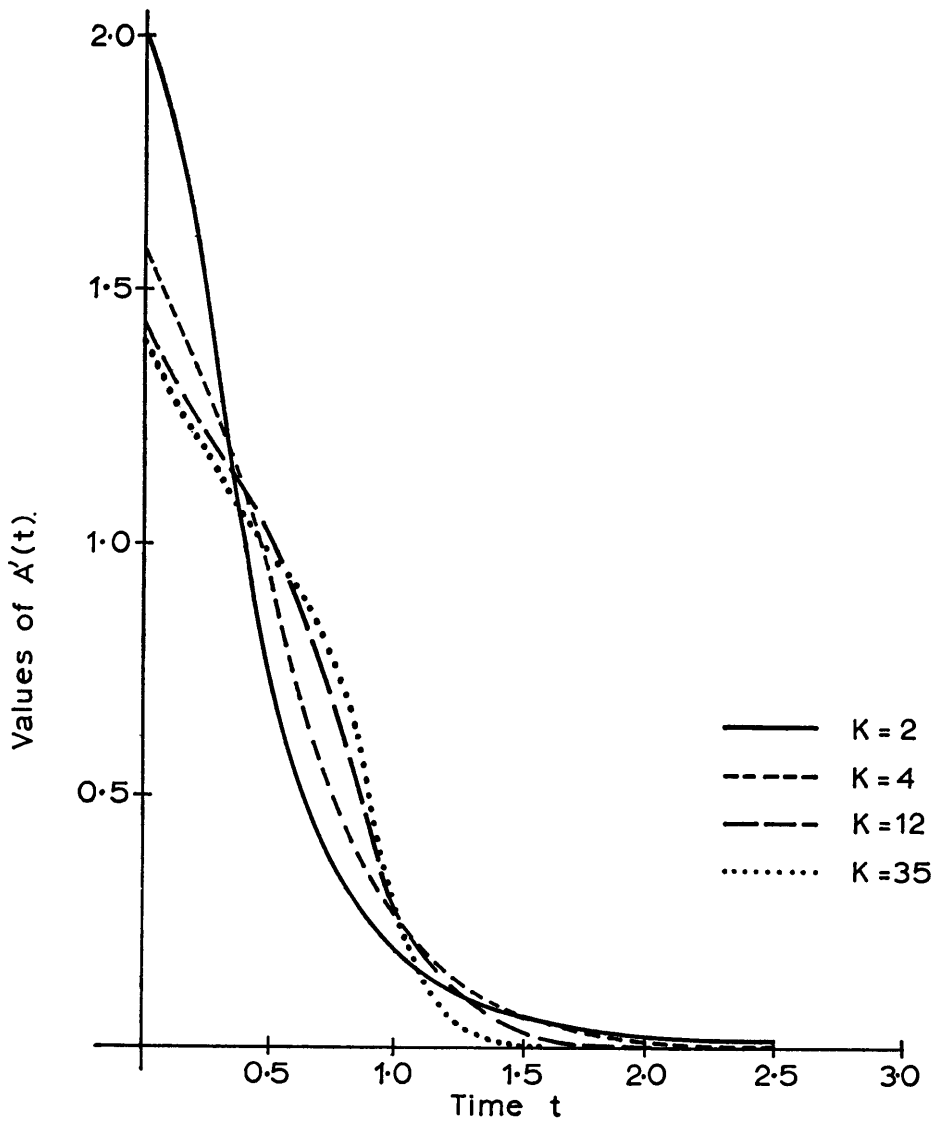


FIGURE 2
Age density $A'(t)$ for $E_k^{-1}(\chi^2)$ model.

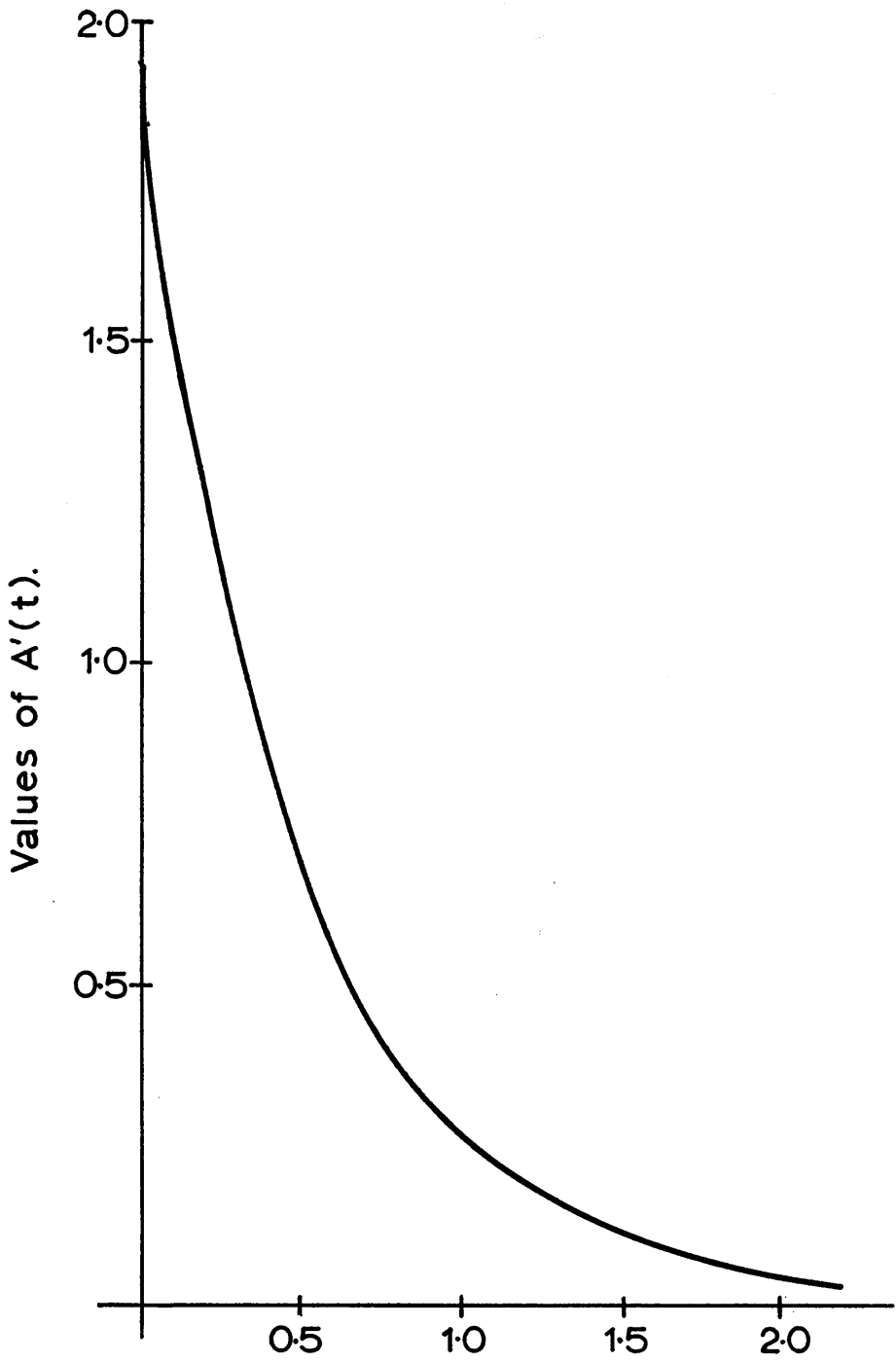


FIGURE 3

Age density $A'(t)$ for "logarithmic" model.

dissociation of a molecule depends on the random time gap τ between occurrences of a critical value of a normal mode coordinate, and thus is affected by the gap distribution. After introducing a gamma type gap distribution as an intermediate between a negative exponential distribution for τ , and the model in which τ is fixed, Slater concludes from numerical values of the rate constant that "gap distribution effects are likely to be of secondary importance among factors determining the rate, but they deserve inclusion in a refined theory."

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