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## A comparison of theoretical and empirical results for some stochastic population models\*

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### I. GENERAL REMARKS

In recent papers Bartlett (1957), Leslie (1958) and Leslie & Gower (1958) have illustrated by means of artificial series the properties of various idealized models of biological systems, including the single-species logistic stochastic process and two-species extensions. While these artificial series are always useful in an auxiliary qualitative sense, the theoretical intractability of many of these models has given the artificial series a somewhat more important role than they might otherwise have had. Nevertheless, what theoretical results there are should not be neglected, and indeed some of these were compared with empirical results from series in the last two of the papers mentioned above. It is the purpose of the present paper to indicate somewhat more systematically where theoretical results, even when only approximate, may be useful, and to make some further comparisons with the empirical results available.

### PART I. THEORETICAL RESULTS

#### 2. SINGLE-SPECIES MODELS (CONTINUOUS TIME)

Consider first a stochastic population model for a single species, with transition probabilities (in continuous time during the infinitesimal interval  $dt$ )  $\lambda_n dt$  of a 'birth', and  $\mu_n dt$  of a 'death', where  $n$  is the total population size. A 'death' may include emigration, but unless a 'birth' can include immigration,  $\lambda_0 = 0$ . If  $\lambda_0 = 0$ , an ultimate stationary distribution for  $n$  cannot strictly exist, but may effectively exist over all realizable time-intervals (see § 5; also Leslie (1958), Bartlett (1960)). Under conditions for which a stationary (or quasi-stationary) distribution does exist, the probability distribution for it must satisfy the recurrence relation

$$\mu_n P(n) = \lambda_{n-1} P(n-1) \quad (1)$$

(see, for example, Bartlett, 1960), from which relation the exact distribution  $P(n)$  may always be calculated numerically, as will be illustrated below (§ 6). Under some further conditions which include  $m, m/\sigma \gg 1$ , we have asymptotically

$$P(n) \sim C \exp \left\{ -\frac{1}{2}(n-m)^2/\sigma^2 \right\}, \quad (2)$$

where  $m$  is the relevant solution of  $\lambda_m = \mu_m$ , and

$$\sigma^2 = -1 \left/ \left[ \frac{d(\lambda_n/\mu_n)}{dn} \right]_{n=m} \right. . \quad (3)$$

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If alternatively the properties of small fluctuations about the mean of the stationary distribution are investigated directly, the results obtained to the first approximation will be equivalent to the normal approximation above. As the first mention of this approach (Bartlett, 1956) was rather brief, it seems worth while showing how it may be developed to include second-stage (or even higher order) corrections. The procedure is sufficiently illustrated by means of the logistic model

$$\lambda_n = a_1 n - b_1 n^2, \quad \mu_n = a_2 n + b_2 n^2, \quad (4)$$

where  $\lambda_n$  remains zero when  $n > a_1/b_1$ , ( $a_1, b_1, a_2, b_2 > 0$ ). The stochastic equation (cf. Bartlett, 1957) is

$$dN_t = (\lambda_N - \mu_N) dt + dZ_1 - dZ_2, \quad (5)$$

or

$$N_{t+dt} = N_t + (\lambda_N - \mu_N) dt + dZ_1 - dZ_2. \quad (6)$$

Averaging (6) on the assumption that a stationary distribution has been reached, we have (from the coefficient of  $dt$ )

$$(a_1 - a_2) m - (b_1 + b_2) (\sigma^2 + m^2) = 0, \quad (7)$$

where  $m \equiv E\{N\}$ ,  $\sigma^2 \equiv E\{(N - m)^2\}$ . Write further  $\delta N_t = N_t - m$ ; then

$$\delta N_{t+dt} = \delta N_t + (\lambda_N - \mu_N) dt + dZ_1 - dZ_2. \quad (8)$$

Squaring and averaging this equation, we have exactly

$$2[(a_1 - a_2) \sigma^2 - (b_1 + b_2) \mu_3] + [(a_1 + a_2) m - (b_1 - b_2) (m^2 + \sigma^2)] = 0,$$

where  $\mu_3 \equiv E\{(\delta N)^3\}$ . Hence to the first order of approximation (noting that

$$m \sim (a_1 - a_2)/(b_1 + b_2), \quad \mu_3 \sim 0$$

to this order)

$$\sigma^2 \sim (a_1 - b_1 m)/(b_1 + b_2). \quad (9)$$

Similarly from the cube of (8) we obtain, noting that the averaged cube of  $dZ_1 - dZ_2$  is strictly zero at  $N = m$ ,

$$3E\{(\lambda_N - \mu_N) dt (\delta N)^2\} + 3E\{(dZ_1 - dZ_2)^2 \delta N\} = 0.$$

From the normality approximation, we can to the second order of approximation write in this equation  $\mu_4 \equiv E\{(\delta N)^4\} = 3\sigma^4$ . We thus obtain

$$(a_1 - a_2) (\mu_3 + m\sigma^2) - (b_1 + b_2) (m^2\sigma^2 + 2m\mu_3 + 3\sigma^4) = - (a_1 + a_2) \sigma^2 + (b_1 - b_2) (2m\sigma^2 + \mu_3),$$

whence to the same order, as  $m \gg 1$ ,

$$\mu_3 m (b_1 + b_2) \sim \sigma^2 m (b_2 - b_1),$$

that is

$$\mu_3 \sim \sigma^2 (b_2 - b_1)/(b_2 + b_1). \quad (10)$$

It will be seen that  $\mu_3$  is only zero to this order if  $b_1 = b_2$ ; and it changes sign as we move from a constant birth-rate ( $b_1 = 0$ ) to a constant death-rate ( $b_2 = 0$ ).

### 3. SINGLE-SPECIES MODELS (DISCRETE TIME)

Before, however, we consider comparing any of these results with empirical results obtained from Leslie's artificial series, we must recall that the latter were obtained on the basis of a discrete-time model (Leslie, 1958), which has its own theoretical distribution. Whilst its exact form would be complicated, the investigation of approximative moment

formulae proceeds very similarly, as was noted by Leslie & Gower (1958) in the case of a two-species model. We shall illustrate the procedure here for a single-species model, taking it to the next stage of approximation.

The transitions in Leslie's model are obtained from the recurrence formulae

$$\left. \begin{aligned} E\{N_{t+1}\} &= e^{b_t-d_t} N_t, \\ \sigma^2\{N_{t+1}\} &= \frac{b_t+d_t}{b_t-d_t} (e^{b_t-d_t} - 1) e^{b_t-d_t} N_t, \end{aligned} \right\} \quad (11)$$

treating  $b_t$  and  $d_t$  constant from  $t$  to  $t+1$ , and assuming also  $\Delta N_t$  normal (with the restriction  $N_{t+1} > 0$ ). Putting  $b_t - d_t = \log \lambda_t$ , we have in the recurrence relation

$$N_{t+1} = f(N_t) + Z_{t+1}, \quad (12)$$

$f(N_t) = \lambda_t N_t$  in this case, where  $\lambda_t$  for the logistic model is of the form  $\lambda/(1 + \alpha N_t)$ . Putting  $\delta N_t = N_t - m$ , where  $m = E\{N_t\}$  under stationary conditions, and writing

$$f(N_t) = f(m) + \delta N_t \frac{\partial f}{\partial m} + \frac{1}{2} (\delta N_t)^2 \frac{\partial^2 f}{\partial m^2} + \dots,$$

where  $\partial f/\partial m$  denotes  $\partial f/\partial N_t$  at the value  $N_t = m$ , etc., we have in the first approximation

$$m = f(m) = (\lambda - 1)/\alpha, \quad (13)$$

$$\left. \begin{aligned} \sigma^2 &= \frac{\sigma_Z^2}{1 - (\partial f/\partial m)^2} = \frac{\sigma_Z^2}{1 - (1/\lambda)^2}, \\ \mu_3 &= 0. \end{aligned} \right\} \quad (14)$$

To the next approximation  $f(m) - m + \frac{1}{2} \frac{\partial^2 f}{\partial m^2} \sigma^2 = 0$ ,

where  $\partial f/\partial m = 1/\lambda$ ,  $\partial^2 f/\partial m^2 = -2\alpha/\lambda^2$ ; and

$$\begin{aligned} \mu_3 &= E \left\{ \left( \delta N_t \frac{\partial f}{\partial m} + \frac{1}{2} [(\delta N_t)^2 - \sigma^2] \frac{\partial^2 f}{\partial m^2} + Z_{t+1} \right)^3 \right\} \sim \mu_3(Z) + \left( \frac{\partial f}{\partial m} \right)^3 \mu_3 \\ &\quad + \frac{3}{2} \left( \frac{\partial f}{\partial m} \right)^2 \frac{\partial^2 f}{\partial m^2} (\mu_4 - \sigma^4) + 3E \left\{ \sigma^2(Z_{t+1} | N_t) \left( \delta N_t \frac{\partial f}{\partial m} + \frac{1}{2} [(\delta N_t)^2 - \sigma^2] \frac{\partial^2 f}{\partial m^2} \right) \right\}. \end{aligned}$$

Now  $\mu_3(Z) = 0$ ,  $\mu_4 \sim 3\sigma^4$ , and it only remains to evaluate such terms as  $E\{\sigma^2(Z_{t+1} | N_t) \delta N_t\}$ . It should be noted that the value of this expression may depend on the precise numerical procedure adopted in obtaining the artificial series. Thus if  $\sigma^2(Z_{t+1} | N_t)$  were taken constant, say at the value  $\sigma^2(Z_{t+1} | m)$ , the whole of the last term in the expression above for  $\mu_3$  would be zero. However, if, more accurately, we expand  $\sigma^2(Z_{t+1} | N_t)$  in (11) in the neighbourhood of  $N_t = m$  (where  $b_t \sim d_t$ ), we find

$$\sigma^2(Z_{t+1} | N_t) \sim (2b - (3b - 1)\alpha\delta N_t/\lambda) N_t \quad (15)$$

when the birth-rate is constant ( $b$ ), and

$$\sigma^2(Z_{t+1} | N_t) \sim (2d - (3d + 1)\alpha\delta N_t/\lambda) N_t \quad (16)$$

when the death-rate is constant ( $d$ ). These results, incidentally, may be useful as approximations for  $\sigma^2(Z_{t+1})$  when artificial series are being constructed. Thus, retaining terms of the appropriate order, we find for  $b_t \equiv b$ ,

$$\mu_3(1 - (1/\lambda)^2) \sim \frac{3\sigma^2(\lambda - 1)}{\lambda^2} \left\{ \frac{(2b)(\lambda + 2)}{\lambda + 1} - (3b - 1) \right\}. \quad (17)$$

Similarly in the case of constant death-rate ( $d$ ),

$$\mu_3(1 - (1/\lambda)^3) \sim \frac{3\sigma^2(\lambda - 1)}{\lambda^3} \left\{ \frac{(2d)(\lambda + 2)}{\lambda + 1} - (3d + 1) \right\}. \quad (18)$$

It may be useful to summarize the formulae derived in §§ 2 and 3.

*Logistic model; continuous time*

$$\lambda_n = a_1 n - b_1 n^2; \mu_n = a_2 n + b_2 n^2.$$

$$\text{Variance (1st approx.) } \sigma^2 \sim (a_1 - b_1 m)/(b_1 + b_2).$$

$$\text{Mean (2nd approx.) } m' \sim m - \sigma^2/m, \text{ where } m = (a_1 - a_2)/(b_1 + b_2).$$

$$\text{Skewness (2nd approx.) } \mu_3 \sim \sigma^2(b_2 - b_1)/(b_2 + b_1).$$

*Discrete time*

$$\lambda_t = \lambda/(1 + \alpha N_t), \text{ (i) birth-rate constant, } b; \text{ (ii) death-rate constant, } d.$$

$$\text{(i) Variance (1st approx.) } \sigma^2 \sim 2bm/\{1 - (1/\lambda)^2\}, \text{ where } m = (\lambda - 1)/\alpha.$$

$$\text{Mean (2nd approx.) } m' \sim m - \sigma^2/(\lambda m).$$

$$\text{Skewness (2nd approx.)}$$

$$\mu_3 \sim \frac{3\sigma^2\lambda(\lambda - 1)}{\lambda^3 - 1} \left\{ \frac{2b(\lambda + 2)}{\lambda + 1} - (3b - 1) \right\}.$$

$$\text{(ii) Variance (1st approx.) } \sigma^2 \sim 2dm/\{1 - (1/\lambda)^2\}.$$

$$\text{Mean (2nd approx.) } m' \sim m - \sigma^2/(\lambda m).$$

$$\text{Skewness (2nd approx.)}$$

$$\mu_3 \sim \frac{3\sigma^2\lambda(\lambda - 1)}{\lambda^3 - 1} \left\{ \frac{2d(\lambda + 2)}{\lambda + 1} - (3d + 1) \right\}.$$

#### 4. MODELS WITH TWO SPECIES

Whilst the above methods are available for models with two (or more) species, the formulae get rather complicated; as the first approximation results in the case of a quasi-stationary distribution for two species have already been indicated by Leslie & Gower (1958), they will not be listed here. With regard to the exact recurrence relation (1) for the distribution  $P(n)$ , the corresponding relation for two species is easy to write down, but has no simple method of solution. However, under conditions for which a well-defined stationary (or quasi-stationary) distribution exists with  $m_i, m_i/\sigma_i \gg 1$ , the distribution will be approximately bivariate normal, with its moments given by the approximate formulae already referred to.

In the case of models for which one species will become extinct, it is also easy to write down the equation satisfied by the extinction probability, say,  $p(n, n')$  for the first species, if  $n$  and  $n'$  are the initial numbers of the two species. Thus consider a continuous time model with birth- and death-rates:

1st species	2nd species
$\lambda(n, n') = a_1 - b_1 n - c_1 n'$	$\lambda'(n, n') = a'_1 - b'_1 n' - c'_1 n$
$\mu(n, n') = a_2 + b_2 n + c_2 n'$	$\mu'(n, n') = a'_2 + b'_2 n' + c'_2 n$

The equation for  $p(n, n')$  is obtained from the differential equation for the chance of extinction  $p_t(n, n')$  by time  $t$ , and letting  $t \rightarrow \infty$ ; this equation for  $p_t(n, n')$  is readily derived from the possible transitions in the first infinitesimal interval  $dt$ . We obtain

$$n\lambda(n, n') [p(n + 1, n') - p(n, n')] + n\mu(n, n') [p(n - 1, n') - p(n, n')] + n'\lambda'(n, n') [p(n, n' + 1) - p(n, n')] + n'\mu'(n, n') [p(n, n' - 1) - p(n, n')] = 0, \quad (19)$$

with boundary conditions  $p(n, 0) = 0, p(0, n') = 1$ . While it is possible to solve this equation, for example, by iteration, in any actual example, it seems quicker to obtain approximate answers by Monte Carlo methods, as shown by Leslie & Gower (1958).

### 5. RECURRENCE TIMES

If it is desired to check recurrence times to any state  $S$  in a stationary process with a finite number of states, the relevant formulae have been given by Bartlett (1955, § 6.41). Thus in the case of discrete time, the mean recurrence time is

$$\Theta_1 = \frac{1 - P(S)}{P(S)[1 - P(S|S)]}, \quad (20)$$

where  $P(S|S)$  denotes the conditional probability of  $S$  at one instant, given  $S$  at the previous instant. In the case of continuous time, if  $P(S|S)$  for times separated by an interval  $\delta t$  is  $1 - \epsilon \delta t + o(\delta t)$ , then

$$\Theta_1 = \frac{1 - P(S)}{\epsilon P(S)}. \quad (21)$$

This formulae is relevant in assessing the passage-time to the zero state  $S$  for population processes with an 'absorbing barrier' at this state, for if we insert a fictitious escape probability  $\epsilon \delta t$  in  $\delta t$ , we have from the equilibrium for the state  $N = 1$ ,

$$\mu_1 P(1) = \epsilon P(0), \quad (22)$$

whence 
$$\Theta_1 = \frac{1 - P(0)}{\mu_1 P(1)}. \quad (23)$$

Under conditions for which  $P(0)$  is small, the quasi-stationary distribution  $P(n), (n > 0)$ , exists approximately independently of  $\epsilon$ , and under such conditions the mean recurrence time  $\Theta_1 \sim 1/[\mu_1 P(1)]$  gives the order of magnitude of the passage-time to zero. For processes of the type discussed in § 2 such passage-times may be so large as to be considered infinite (cf. Leslie, 1958).

## PART II. NUMERICAL RESULTS

### 6. EXAMPLE OF DISTRIBUTION $P(n)$

It was noted in § 2 that the recurrence relation for  $P(n)$  enabled  $P(n)$  to be calculated exactly. This is strictly true only if the zero state is not absorbing, but from the last section  $P(n)$  is effectively defined in quasi-stationary cases also. Whilst it is still a purely theoretical result, we give a numerical example of  $P(n)$  in this last case, for the logistic model

$$a_1 = 0.8077, \quad b_1 = 0.006932, \\ a_2 = 0.1145, \quad b_2 = 0.$$

$P(n)$ , standardized to a total of 4975, was found to have the values given in Table 1.

Table 1 (giving  $f = 4975 P(n)$ )

$n = 81$	$f = 0.1$	$n = 93$	$f = 118.3$	$n = 105$	$f = 236.7$
82	0.2	94	166.7	106	163.4
83	0.5	95	224.7	107	103.1
84	1.0	96	289.7	108	58.8
85	1.9	97	356.0	109	30.1
86	3.7	98	416.3	110	13.5
87	6.7	99	461.8	111	5.3
88	11.8	100	484.8	112	1.7
89	20.2	101	480.1	113	0.5
90	33.2	102	446.8	114	0.1
91	52.7	103	388.9		
92	80.6	104	315.1		
				Total	4975.0

The constants of this distribution as calculated by the approximate formulae of § 2 agree very well with the exact results:

	Exact	Approximation
$m$ :	99.83	99.83 (2nd approx.)
$\sigma^2$ :	16.71	16.52 (1st approx.)
$\mu_3$ :	-16.61	-16.52 (2nd approx.)

7. COMPARISON OF APPROXIMATE MOMENTS FOR DISCRETE-TIME MODEL WITH EMPIRICAL RESULTS

Four empirical distributions for a logistic process in the region of the stationary state were built up on the Elliott—N.R.D.C. 401 computer at Rothamsted Experimental Station, taking the values of the parameters in the discrete-time model

$$E\{N_{t+1} | N_t\} = \frac{\lambda}{1 + \alpha N_t} N_t = \lambda_t N_t \quad (\lambda = e^{b-d}),$$

given in Table 2. In each case  $m = (\lambda - 1)/\alpha = 100$ , and it will be noted that the unit of time in *Ib* is  $\frac{1}{5}$ th of that adopted in the remaining three models.

Model	$\lambda$	$\alpha$	Constant birth-rate ( $b$ )	Constant death-rate ( $d$ )
Ia	2.0	0.01	1.0083	—
Ib	1.1487	0.001487	0.2017	—
IIa	2.0	0.01	—	0.1145
IIb	2.0	0.01	—	0.3151

The programmes used for computing *Ia*, *IIa* and *IIb* were originally written for a system of two competing species (Leslie & Gower, 1958), but by putting two of the parameters equal to zero (cf. the equations given later in § 8), these could be used for computing simultaneously a pair of logistic processes. In order to simplify these programmes, however, certain approximations had been made to  $\text{var}(N_{t+1} | N_t)$ . Thus, if the expression for the variance in (11) is written as

$$\sigma^2\{N_{t+1}\} = \phi E\{N_{t+1}\},$$

where, when the birth-rate ( $b$ ) remains constant (BRC model),

$$\phi = \left( \frac{2b}{r_t} - 1 \right) (\lambda_t - 1), \tag{24}$$

and when the death-rate ( $d$ ) remains constant (DRC model),

$$\phi = \left(\frac{2d}{r_t} + 1\right) (\lambda_t - 1), \tag{25}$$

then it may be shown empirically (Leslie, 1958), by tabulating  $\phi$  over a relatively wide range of possible values of  $\lambda_t$  (or  $\log_e \lambda_t = r_t$ ), that in the BRC model we have, when  $\lambda = 2.0$  and constant ( $b$ ) = 1.0083,

$$\sigma^2\{N_{t+1}\} \sim 2E\{N_{t+1}\} \tag{26}$$

and in the DRC model for

$$\begin{aligned} \text{constant } (d) = 0.1145: & \sigma^2\{N_{t+1}\} \sim (-0.87 + 1.10\lambda_t) E\{N_{t+1}\}, \\ \text{constant } (d) = 0.3151: & \sigma^2\{N_{t+1}\} \sim (-0.66 + 1.29\lambda_t) E\{N_{t+1}\}. \end{aligned} \tag{27}$$

These empirical approximations, which should hold over the entire development of any process with the given parameters, are closely related to (15) and (16) for systems in the neighbourhood of the stationary mean. For, expressing the latter in terms of  $E\{N_{t+1} | N_t\}$ , we have in the region of  $N_t \sim m$ ,

$$N_t \sim \left(1 + \frac{\alpha}{\lambda} \delta N_t\right) E\{N_{t+1}\}, \quad \lambda_t \sim 1 - \frac{\alpha}{\lambda} \delta N_t,$$

and (15) and (16) can be written, respectively, as

$$\sigma^2\{Z_{t+1} | N_t\} \sim [(b + 1) + (b - 1) \lambda_t] E\{N_{t+1}\}, \tag{28}$$

$$\sigma^2\{Z_{t+1} | N_t\} \sim [(d - 1) + (d + 1) \lambda_t] E\{N_{t+1}\}. \tag{29}$$

Thus, in the BRC model, when  $b \sim 1$ ,

$$\sigma^2\{Z_{t+1} | N_t\} \sim 2E\{N_{t+1}\},$$

while in the DRC model, for  $d = 0.1145$ ,

$$\sigma^2\{Z_{t+1} | N_t\} \sim [-0.8855 + 1.1145\lambda_t] E\{N_{t+1}\},$$

and for  $d = 0.3151$   $\sigma^2\{Z_{t+1} | N_t\} \sim [-0.6849 + 1.3151\lambda_t] E\{N_{t+1}\},$

which correspond very closely to (27).

In the remaining model (Ib), a programme was used in which the ‘exact’ expression (24) for  $\phi$  was incorporated. This has the advantage that the choice of the constant birth-rate ( $b$ ) is not restricted to only a very limited range of values, as in the case of the approximation (26).

The observed moments of these computed distributions, together with those expected from the theoretical approximations for the discrete-time (D-T) and equivalent continuous-time (C-T) models, are shown in Table 3.

The agreement between the observed moments and the theoretical approximations for the discrete-time model seems very satisfactory, considering the errors involved in estimating the former, even in samples of this size. The standard errors quoted are in general classical values, ignoring the serial correlations between the successive observations, and representing lower limits to the correct values. The correlation  $\rho_1$  between successive observations is to the first approximation  $1/\lambda$ , and the correcting factors to the standard errors of the mean and standard deviation are respectively  $\sqrt{\{(1 + \rho_1)/(1 - \rho_1)\}}$  and  $\sqrt{\{(1 + \rho_1^2)/(1 - \rho_1^2)\}}$ . Where the differences between the observed and theoretical means or standard deviations

exceed twice the classical standard error, the corrected standard error is shown in brackets, and it will be seen that the one such difference no longer appears anomalous. The corrections to the standard errors of moments to allow for dependence become more complicated for the higher moments, but are not needed for the  $\gamma_1$  values in Table 3 (formulae for them may be ascertained if required from Chanda (1958)).

Table 3

Model	No. of observations	Moment	Approximations		Observed (D-T) model
			(C-T) model	(D-T) model	
Ia	9950	Mean	98.54	98.66	98.60 ± 0.16
		$\sigma$	12.06	16.40	16.47 ± 0.12
		$\gamma_1$	0.083	0.035	0.072 ± 0.025
Ib	5240	Mean	98.54	98.55	98.63 ± 0.17
		$\sigma$	12.06	12.90	12.53 ± 0.12 (0.33)
		$\gamma_1$	0.083	0.076	0.053 ± 0.034
IIa	4975	Mean	99.83	99.85	99.97 ± 0.08
		$\sigma$	4.06	5.53	5.51 ± 0.06
		$\gamma_1$	-0.246	-0.161	-0.182 ± 0.035
IIb	4975	Mean	99.55	99.58	99.44 ± 0.13
		$\sigma$	6.74	9.17	9.16 ± 0.09
		$\gamma_1$	-0.148	-0.103	-0.103 ± 0.035

Table 4

<i>N</i>	<i>f(N)</i>	<i>N</i>	<i>f(N)</i>	<i>N</i>	<i>f(N)</i>
77	1	92	138	107	188
78	0	93	166	108	120
79	0	94	194	109	90
80	1	95	213	110	64
81	2	96	270	111	54
82	5	97	285	112	25
83	3	98	310	113	17
84	4	99	329	114	14
85	9	100	350	115	6
86	20	101	361	116	0
87	33	102	357	117	0
88	35	103	339	118	1
89	51	104	318		
90	67	105	261		
91	97	106	177		
				Total	4975

As an illustration, we give in Table 4 the observed frequency distribution for model IIa, corresponding to the continuous-time model for which the exact distribution is given in § 6.

The main difference between this observed distribution and the exact form for the equivalent continuous-time model is in the scale of the variance  $\sigma^2$  (one notes in passing that in both cases  $\mu_3 \sim -\sigma^2$ ). It is, however, always possible to make the variances of the two types of model more in agreement by adopting a smaller unit of time in the discrete-time model, as is illustrated in the cases of Ia and Ib in the above table.

It may also be of interest to consider the recurrence times which were observed in this set of realizations for model IIa. Regarding the occurrence of a particular integer as a specified state *S* being occupied, the mean life-time spent in the state *S*,  $T_1 = 1/\{1 - P(S | S)\}$ ,

could be determined from the typed lists of results, and hence the mean recurrence time for the state  $S$ ,

$$\Theta_1 = T_1 \frac{1 - P(S)}{P(S)}.$$

The observed values of  $T_1$  and  $\Theta_1$ , neglecting the tails of the distribution where the observed frequencies became small, are given in Table 5.

Table 5

State $S$	Observed		Normal approximation $\Theta_1$	State $S$	Observed		Normal approximation $\Theta_1$
	$T_1$	$\Theta_1$			$T_1$	$\Theta_1$	
85	1.1250	623.0	551.7	100	1.0870	14.3	13.8
86	1.0000	247.7	343.2	101	1.0841	13.9	14.1
87	1.0312	154.5	220.5	102	1.0593	13.7	14.8
88	1.0294	145.2	146.4	103	1.1042	15.1	16.1
89	1.0851	104.7	100.5	104	1.1042	16.1	18.0
90	1.0635	78.0	71.2	105	1.0830	19.6	20.9
91	1.0211	51.4	52.2	106	1.0727	29.1	25.0
92	1.0455	36.7	39.5	107	1.1124	28.4	30.9
93	1.0573	30.7	30.9	108	1.0526	42.6	39.5
94	1.0838	26.7	25.0	109	1.0465	56.8	52.2
95	1.1036	24.7	20.9	110	1.0159	77.9	71.2
96	1.0887	18.9	18.0	111	1.0000	91.1	100.5
97	1.0634	17.5	16.1	112	1.0870	215.2	146.4
98	1.0954	16.4	14.8	113	1.0625	309.8	220.5
99	1.0717	15.1	14.1	114	1.0000	354.8	343.2

If the conditional probability of  $S$ , given  $S$  at the preceding instant,  $P(S | S) \sim P(S)$ , as appears very roughly to be the case in this example (e.g. for the ten states disposed symmetrically about the mean, the average  $P(S | S) = 0.0785$  and the average  $P(S) = 0.0630$ ), then

$$\Theta_1 \sim 1/P(S).$$

Taking the first approximations to the moments of the discrete-time distribution, when the death-rate remains constant, viz.

$$\begin{aligned} \text{mean} &= (\lambda - 1)/\alpha = m, \\ \sigma^2 &= 2dm/\{1 - (1/\lambda)^2\}, \\ \mu_3 &= 0, \end{aligned}$$

then the normal approximation is

$$\Theta_1 \sim \sqrt{(2\pi)\sigma} \exp\left[-\frac{(N - m)^2}{2\sigma^2}\right].$$

These figures are given in the third column of the above table, and it will be seen that although the departures from normality of the actual distribution are appreciable, yet on the whole the approximation indicates the order of magnitude of the observed recurrence times, more particularly for the states which are less than the mean value. By extrapolation

$$1/P(1) \sim 7.0 \times 10^{70},$$

and it is evident, without proceeding any further, and without taking the approximate value too literally, that the probability of random extinction for this system is negligible, even in the case of the discrete-time model with its larger variance.

## 8. COMPARISON OF APPROXIMATE MOMENTS WITH EMPIRICAL RESULTS FOR A TWO-SPECIES SYSTEM

Two bivariate distributions were computed for a system of two competing species fluctuating in the region of the stable stationary state. It was assumed in both cases that the death-rate ( $d$ ) of each species remained constant, and in the set of deterministic equations defining the expectations for this type of system (Leslie & Gower, 1958),

$$E\{N_1(t+1) | N_1(t), N_2(t)\} = \frac{\lambda_1 N_1(t)}{1 + \alpha_1 N_1(t) + \beta_1 N_2(t)}, \quad (30)$$

$$E\{N_2(t+1) | N_1(t), N_2(t)\} = \frac{\lambda_2 N_2(t)}{1 + \alpha_2 N_2(t) + \beta_2 N_1(t)}, \quad (31)$$

the following parameters were adopted in System A,

$$\begin{aligned} \lambda_1 &= 2.5, & d_1 &= 0.1145, & \alpha_1 &= 0.008, & \beta_1 &= 0.003, \\ \lambda_2 &= 2.0, & d_2 &= 0.3151, & \alpha_2 &= 0.00625, & \beta_2 &= 0.0025. \end{aligned}$$

In the second case, System B, the same set of parameters was used, except that the value of  $\alpha_1$ , was changed to  $\alpha_1 = 0.005$ . The computed distributions were based on 1000 observations for A, and on 995 for B.

The first approximations to the moments are (assuming that both  $N_1$  and  $N_2$  are distributed normally about the stationary state)

$$\text{mean}(N_1) = \frac{\alpha_2(\lambda_1 - 1) - \beta_1(\lambda_2 - 1)}{\alpha_1\alpha_2 - \beta_1\beta_2}, \quad (32)$$

$$\text{mean}(N_2) = \frac{\alpha_1(\lambda_2 - 1) - \beta_2(\lambda_1 - 1)}{\alpha_1\alpha_2 - \beta_1\beta_2}, \quad (33)$$

and for the marginal distributions,

$$\mu_3(N_1) = \mu_3(N_2) = 0; \quad (34)$$

while the variances and covariances may be obtained from the solution of the equations which have already been given for the discrete-time model (Leslie & Gower, 1958, § 5). The results are shown in Table 6.

Table 6

	System A		System B	
	Approximation	Observed	Approximation	Observed
Mean ( $N_1$ )	150.0	150.82	268.4	270.16
Mean ( $N_2$ )	100.0	99.19	52.6	50.75
$\sigma(N_1)$	7.84	7.85	11.06	11.37
$\sigma(N_2)$	11.49	12.03	11.63	12.42
$\rho(N_1, N_2)$	-0.364	-0.446	-0.529	-0.602
$\gamma_1(N_1)$	0	+0.001	0	-0.005
$\gamma_1(N_2)$	0	+0.074	0	-0.022

The agreement between the approximations and the observed means, standard deviations and correlation coefficients seems very satisfactory in both cases; while the magnitude of the skewness coefficients suggest that both distributions could be regarded as approximately bivariate normal in form.

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