INTERACTIONS BETWEEN SPECIES:
SOME COMPARISONS BETWEEN DETERMINISTIC AND STOCHASTIC MODELS[1]

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Introduction. Mathematical descriptions of the growth of inter-acting populations have been attempted since Lotka (1925) and Volterra (1926) first published their equations. The arguments for mathematical modeling of such processes are that such descriptive models provide a potential for successful prediction of future conditions and by manipulation of mathematical models one may obtain insight into the response of the interacting system due to changes in conditions. Furthermore mathematics provides a means of accurate communication between biologists. The earlier work in the mathematical theory of interacting species was generally formulated without reference to the randomness inherent in biological processes. A comprehensive treatment of the deterministic models of Lotka (1925), Volterra (1926), Thompson (1939), Nicholson and Bailey (1935), etc., may be found in the book by D'Ancona (1954).

The development of stochastic models to describe the growth of interacting populations has been hampered by the more difficult mathematics involved in solving the differential equations or difference equations. However, the presence of fast computers has encouraged some Monte Carlo studies of the stochastic models by Bartlett (1957), (1961), Leslie and Gower (1958), (1960), and Barnett (1962). Exact analytic solutions of the stochastic models are very scarce, except for greatly simplified models such as those considered by Weiss (1963), (1965), Dietz and Downton (1968) and Becker (1970a), (1970b). While these models are oversimplified they have the advantage of lending themselves to analytic solution and are hence ideally suited for a

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comparison of deterministic and stochastic models. It is the aim here to take some particular cases of these simplified models and use them to illustrate some significant discrepancies between the stochastic and the deterministic approaches. The models considered here are not the most general for which analytic solutions are possible. They are deliberately considered in an oversimplified form in the hope that this will clarify under which circumstances one might expect differences between the deterministic and stochastic formulations. Previous comparisons of deterministic with stochastic models have indicated agreement between the two under most conditions, provided the population sizes are not too small. For example, this is so for the model considered by Weiss (1963) for interaction between antagonistic species. The models for competition between species or predator-prey systems considered by Bartlett (1957), (1961), Leslie and Gower (1958), (1960) and Barnett (1962) are also found to be in general agreement with the deterministic Lotka-Volterra equations. The main discrepancy arises in the case of an unstable system. Given the initial conditions, the deterministic model will state which species is certain to become extinct, while in the stochastic model there is a probability that either species may become extinct. This probability is mostly determined by the *initial* fluctuations, after which the stochastic process usually follows the deterministic curves quite closely.

The comparisons made here are of stochastic population models with their deterministic analogues. One form of interaction considered is that where the birth rate for a population S_x increases with the size of another population S_y, e.g. S_x is a parasite population and S_y is the corresponding host population. We illustrate that for such an interaction a stochastic model can indicate that S_x 'explodes' in finite time whereas the deterministic model indicates that the size of S_x remains finite for all finite time. The other form of interaction considered is that where S_x is a prey population and S_y a predator population. For such a situation it is possible to conclude from the deterministic model that S_x becomes extinct whereas the stochastic model may indicate that the probability of extinction of S_x is less than 1/2 and in fact there is a good chance of no or very little predation occurring before S_y becomes extinct. When the deterministic model indicates that S_x becomes extinct it is also possible to have the mean size of S_x, as obtained from the stochastic model, become infinite. By allowing immigration into S_x and S_y we may cause the population size of S_x to fluctuate enormously for an indefinite period, while the deterministic model may indicate that the population size tends monotonically to a constant. Finally, the effect of differences in the pred-

ators' ability may be interpreted differently by the stochastic and deterministic models. In particular, differences between the predators may not affect the deterministic results. The stochastic model on the other hand may reveal that the expected size and the probability of extinction of S_x both increase as the difference between the predators increases. This reveals that stochastic models contain considerably more information than their deterministic analogues. The paper concludes with some reasons for the observed discrepancies and a brief summary of methods of solving or approximating stochastic models.

Model 1. Consider two distinct populations S_x and S_y which consist, respectively, of $X(t)$ and $Y(t)$ members at time t. Assume the growth rate for S_x at time t to be proportional to $X(t)$ and to $Y(t)$, while the growth rate for S_y is proportional to $Y(t)$ only. More precisely we suppose that in the time increment $(t, t + \delta t)$ there are the following possible transitions and associated probabilities:

$$
\begin{aligned}
& (X, Y) \to (X + 1, Y) && \beta XY\delta t + o(\delta t) \\
(1.1) \quad & (X, Y) \to (X, Y + 1) && \lambda Y\delta t + o(\delta t) \\
& (X, Y) \to (X, Y) && 1 - \beta XY\delta t - \lambda Y\delta t + o(\delta t)
\end{aligned}
$$

with $X(0) = m$ and $Y(0) = n$, say. An example where the birth rate of one population is observed to increase with the size of another population is found in a host-parasite system. Since a parasite needs a host to lay its eggs in we see that the probability that a parasite finds a 'site' to lay its eggs in increases with the number of hosts.

The probabilities $p_{x,y}(t) = P[X(t) = x, Y(t) = y]$ then satisfy

$$
\begin{aligned}
p_{x,y}(t + \delta t) = {}& \beta(x - 1)yp_{x-1,y}(t)\delta t + \lambda(y - 1)p_{x,y-1}(t)\delta t \\
& + (1 - \beta xy\delta t - \lambda y\delta t)p_{x,y}(t) + o(\delta t).
\end{aligned}
$$

By rearranging this equation and letting $\delta t \to 0$ we obtain the differential-difference equation

$$
\frac{dp_{x,y}(t)}{dt} = \beta(x - 1)yp_{x-1,y}(t) + \lambda(y - 1)p_{x,y-1}(t)
$$
$$
(1.2) \qquad\qquad - (\beta x + \lambda)yp_{x,y}(t)
$$

with

$$
\begin{aligned}
p_{x,y}(0) &= 1 \quad \text{when } x = m, y = n, \\
&= 0 \quad \text{otherwise.}
\end{aligned}
$$

Let $x^{[r]} = x(x + 1) \cdots (x + r - 1)$. If we now multiply both sides of (1.2) by $x^{[r]}w^y$ and sum over all possible values of x and y we obtain the equation

$$(1.3) \qquad \partial G_r(t, w)/\partial t = (\lambda w - \lambda - r\beta)w \, \partial G_r(t, w)/\partial w$$

with $G_r(0, w) = m^{[r]}w^n$, for the generating function $G_r(t, w) = \sum_{x,y} x^{[r]}w^y p_{x,y}(t)$. Equation (1.3) may be solved to give

$$(1.4) \qquad G_r(t, w) = m^{[r]}(\lambda - r\beta)^n \left\{ \lambda + \frac{\lambda - r\beta - \lambda w}{w} e^{(\lambda - r\beta)t} \right\}^{-n}$$

provided $\lambda \neq r\beta$. Note that $G_0(t, w)$ gives the probability generating function for $Y(t)$, which corresponds to a pure simple birth process. Therefore, in particular,

$$(1.5) \qquad E(Y) = \frac{\partial G_0(t, w)}{\partial w} \bigg|_{w=1} = ne^{\lambda t}, \qquad t \geqq 0.$$

By substituting $w = 1$ in (1.4) we find the moments

$$E(X^{[r]}) = m(\lambda - r\beta)^n \{\lambda - r\beta e^{(\lambda - r\beta)t}\}^{-n}, \qquad t < \ln(\lambda/r\beta)/(\lambda - r\beta)$$

$$= \infty, \qquad t \geqq \ln(\lambda/r\beta)/(\lambda - r\beta).$$

Therefore the moments of X become infinite in finite time. The results when $\lambda = r\beta$ are similar. In particular when $\lambda = \beta$ we find

$$E(X) = m/(1 - \lambda t)^n, \qquad t < 1/\lambda,$$

$$= \infty, \qquad t \geqq 1/\lambda.$$

The deterministic analogue of this stochastic model is arrived at by considering the transition probabilities of (1.1) not as probabilities but as the exact increases in the population sizes. This approach requires us to approximate the sizes of the populations by continuous variables. Let $x(t)$ and $y(t)$ be the deterministic (continuous) analogues of the stochastic $X(t)$ and $Y(t)$, respectively. The deterministic growth model is therefore described by

$$dx/dt = \beta xy, \qquad dy/dt = \lambda y$$

with initial conditions $x(0) = m$ and $y(0) = n$. The solution of these equations is

$$x(t) = m \exp \left\{ \frac{n\beta}{\lambda} (e^{\lambda t} - 1) \right\}, \qquad y(t) = ne^{\lambda t}.$$

It is seen that $E(Y) = y(t)$; however, $E(X) > x(t)$ for all $t > 0$ and

although $x(t) \to \infty$ as $t \to \infty$, $x(t)$ remains finite for all finite t. Therefore $E(X) - x = \infty$ for $t > \ln(\lambda/\beta)/(\lambda - \beta)$.

Model 2. Suppose now that S_x does not benefit from the presence of individuals from S_y, but instead that individuals from S_x are subject to predation by individuals from S_y. Members from S_y are also assumed to be subject to natural death at a rate μ. In the time increment $(t, t + \delta t)$ there are then the following possible transitions and associated probabilities:

(2.1)
$$
\begin{aligned}
(X, Y) &\to (X - 1, Y) & \alpha XY\delta t + o(\delta t) \\
(X, Y) &\to (X, Y + 1) & \lambda Y\delta t + o(\delta t) \\
(X, Y) &\to (X, Y - 1) & \mu Y\delta t + o(\delta t) \\
(X, Y) &\to (X, Y) & 1 - \alpha XY\delta t - \lambda Y\delta t - \mu Y\delta t + o(\delta t).
\end{aligned}
$$

We proceed as in the previous example and find

(2.2)
$$
\begin{aligned}
dp_{x,y}(t)/dt = {}& \alpha(x + 1)yp_{x+1,y} + \lambda(y - 1)p_{x,y-1} \\
& + \mu(y + 1)p_{x,y+1} - (\alpha x + \lambda + \mu)yp_{x,y}.
\end{aligned}
$$

Let $x^{(r)} = x(x - 1) \cdots (x - r + 1)$. From (2.2) we then find that the generating function

$$
H_r(t, w) = \sum_{x,y} x^{(r)}w^y p_{x,y}(t)
$$

satisfies the equation

(2.3) $\qquad \partial H_r/\partial t = \{\lambda w^2 - (\lambda + \mu + r\alpha)w + \mu\}\partial H_r/\partial w$

with initial condition $H_r(0, w) = m^{(r)}w^n$. We see that $H_0(t, w)$ gives the probability generating function for $Y(t)$, which is

(2.4)
$$
\begin{aligned}
H_0(t, w) &= \left[\frac{\mu\{e^{(\lambda-\mu)t} - 1\} - \{\mu e^{(\lambda-\mu)t} - \lambda\}w}{\{\lambda e^{(\lambda-\mu)t} - \mu\} - \lambda\{e^{(\lambda-\mu)t} - 1\}w} \right]^n, \qquad \lambda \neq \mu, \\
&= \left[\frac{w + (1 - w)\lambda t}{1 + (1 - w)\lambda t} \right]^n, \qquad \lambda = \mu.
\end{aligned}
$$

This is, as expected, the probability generating function of a simple birth-death process. For $r \geqq 1$ we find from (2.3) that

(2.5) $\qquad H_r(t, w) = m^{(r)} \left\{ \dfrac{w + (\rho_r + \epsilon_r)(w - \rho_r)(e^{-\epsilon_r\lambda t} - 1)/\epsilon_r}{1 + (w - \rho_r)(e^{-\epsilon_r\lambda t} - 1)/\epsilon_r} \right\}^n$

where the ρ_r and ϵ_r are defined by

$$\lambda(w - \rho_r)(w - \rho_r - \epsilon_r) = \lambda w^2 - (\lambda + \mu + r\alpha)w$$

(2.6)
$$+ \mu, \quad \epsilon_r > 0.$$

The factorial moments are given by $E(X^{(r)}) = H_r(t, 1)$.

From the H_r we may deduce the probability distributions for x. It follows from

$$\sum_{x,y} u^x w^y p_{x,y}(t) = \sum_{r,y} \frac{(u-1)^r}{r!} H_r(t, w)$$

that $p_x(t) = P\{X(t) = x\}$ satisfies

(2.7)
$$p_x(t) = \sum_{r=x}^{m} \frac{(-1)^{r-x}}{x!(r-x)!} H_r(t, 1).$$

The ultimate distribution for X is thus

(2.8)
$$p_x(\infty) = \binom{m}{x} \sum_{r=x}^{m} (-1)^{r-x} \binom{m-x}{r-x} \rho_r^x$$

where we now define ρ_0 to be unity, instead of $\min(1, \mu/\lambda)$ as it is defined by (2.6). The limiting distribution (2.8) is shown in Table 1 for $m = 10$, $n = 1$, $\mu = 0.75$, $\alpha = 0.25$ and various values of λ. Table 1 also gives the limiting means computed from $E\{X(\infty)\} = m\rho_1^n$.

The deterministic analogue of this stochastic model is described by the equations

$$dx/dt = -\alpha xy, \quad dy/dt = (\lambda - \mu)y.$$

The solutions to these equations are

$$x(t) = m \exp(-n\alpha t), \quad \lambda = \mu,$$

$$= m \exp\left\{-\frac{n\alpha}{\lambda - \mu}(e^{(\lambda-\mu)t} - 1)\right\}, \quad \lambda \neq \mu,$$

$$y(t) = ne^{(\lambda-\mu)t}.$$

In the limit we find

$$x(\infty) = 0, \quad \lambda \gtreqless \mu,$$

$$= me^{-n\alpha/(\mu-\lambda)}, \quad \lambda < \mu,$$

which is given for $m = 10$, $n = 1$, $\mu = 0.75$, $\alpha = 0.25$ and various values of λ in Table 1. A comparison of $x(\infty)$ with $p_x(\infty)$ in Table 1 reveals that $x(\infty)$ gives an inadequate description of the process. In

particular if $\lambda \geqq \mu$, then $x(\infty) = 0$ although $P\{X(\infty) > 0\}$ may be greater than 1/2. In fact the stochastic model does not only suggest that there is a good chance of S_x not becoming extinct but indeed a good chance of no or very little predation occurring before S_y becomes extinct. This follows from the fact that the distribution of $X(\infty)$ is U-shaped.

TABLE 1. Limiting probabilities $p_x(\infty)$, means $E\{X(\infty)\}$ and corresponding deterministic values $x(\infty)$ when $m = 10$, $n = 1$, $\mu = 0.75$, $\alpha = 0.25$.

x \ λ	.10	.25	.50	.75	1.00	1.50	2.00
0	.010	.029	.095	.201	.318	.5082	.6261
1	.018	.032	.047	.043	.030	.0090	.0023
2	.029	.038	.044	.038	.028	.0110	.0037
3	.041	.046	.047	.039	.030	.0138	.0057
4	.056	.057	.053	.044	.034	.0177	.0086
5	.073	.071	.062	.051	.041	.0234	.0130
6	.094	.088	.076	.063	.051	.0321	.0199
7	.120	.110	.094	.080	.067	.0458	.0314
8	.150	.138	.121	.105	.091	.0679	.0512
9	.185	.173	.156	.141	.127	.1046	.0866
10	.225	.218	.206	.195	.184	.1667	.1516
$E\{X(\infty)\}$	7.30	6.97	6.34	5.66	5.00	3.92	3.17
$x(\infty)$	6.81	6.07	3.68	0	0	0	0

Model 3. Let us now change the predator-prey model by allowing births of prey and taking $Y(t)$ to be a Poisson process. More specifically we consider the following possible transitions and associated probabilities in the time increment $(t, t + \delta t)$:

$$(X, Y) \to (X + 1, Y) \qquad \lambda X \delta t + o(\delta t)$$

$$(X, Y) \to (X - 1, Y) \qquad \alpha X Y \delta t + o(\delta t)$$

$$(X, Y) \to (X, Y + 1) \qquad \nu t + o(\delta t)$$

$$(X, Y) \to (X, Y) \qquad 1 - (\lambda X + \alpha X Y + \nu)\delta t + o(\delta t)$$

with $X(0) = m$ and $Y(0) = 0$.

Proceeding as before, this leads to

$$\frac{dp_{x,y}(t)}{dt} = \lambda(x - 1)p_{x-1,y} + \alpha(x + 1)yp_{x+1,y} + \nu p_{x,y-1}$$

(3.1)

$$- (\lambda x + \alpha xy + \nu)p_{x,y}.$$

Then, for $H_1(t, w) = \sum_{x,y} x w^y p_{x,y}(t)$, we find

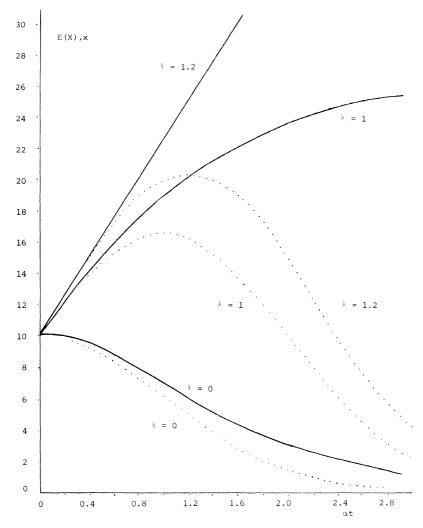(3.2) $\qquad \partial H_1/\partial t = -\alpha w \, \partial H_1/\partial w + (\lambda + \nu w - \nu)H_1$

FIGURE 1 — Deterministic values and stochastic means for the size of population S_x when $m = 10$, $\nu = 1$. . . . . . . deterministic, ———— stochastic.

with initial condition $H_1(0, w) = m$. Solving this equation for H_1 and setting $w = 1$ leads to

(3.3) $$E(X) = m \exp \{(\lambda - \nu)t + \nu(1 - e^{-\alpha t})/\alpha\}.$$

In the limit therefore

(3.4)
$$\begin{aligned} E\{X(\infty)\} &= 0, & \lambda < \nu, \\ &= me^{\nu/\alpha}, & \lambda = \nu, \\ &= \infty, & \lambda > \nu. \end{aligned}$$

The deterministic analogue of this stochastic model is described by

(3.5) $$dx/dt = \lambda x - \alpha xy, \qquad dy/dt = \nu$$

with $x(0) = m$ and $y(0) = 0$. Therefore

$$x(t) = me^{\lambda t - \alpha \nu t^2/2}, \qquad y(t) = \nu t$$

from which we see that $x(\infty) = 0$. To enable a more detailed comparison of $E(X)$ with $x(t)$ we show the curves of $E(X)$ and $x(t)$ in Fig. 1 for the parameter values: $m = 10$, $\nu = 1$ and $\lambda = 0, 1, 1.2$ on a time scale such that $\alpha = 1$.

Model 4. Let us now consider still another variation of the predator-prey model. Imagine a population of fish S_x in a riverpool. S_x increases in size due to random immigration at a rate ϵ and decreases in size due to 'predation' by anglers who arrive at the pool at random times to catch fish for a random length of time. Let $Y(t)$ denote the number of anglers at the pool at time t. We may argue that the stochastic process involving the fish and angler populations may be approximately described by the following possible transitions and associated probabilities corresponding to the time increment $(t, t + \delta t)$:

$$\begin{aligned} (X, Y) &\to (X + 1, Y) & \epsilon \delta t + o(\delta t) \\ (X, Y) &\to (X - 1, Y) & \alpha XY \delta t + o(\delta t) \\ (X, Y) &\to (X, Y + 1) & \nu \delta t + o(\delta t) \\ (X, Y) &\to (X, Y - 1) & \mu Y \delta t + o(\delta t) \\ (X, Y) &\to (X, Y) & 1 - (\epsilon + \nu + \mu Y + \alpha XY)\delta t + o(\delta t) \end{aligned}$$

with $X(0) = Y(0) = 0$, say.

Analytic treatment of this process for $\epsilon > 0$ is awkward. Dietz and Downton (1968) have found $E(X)$ expressed as an integral; however,

the mean $E(X)$ contains very limited information about the behaviour of $X(t)$. Due to the difficulties in obtaining analytic solutions for this process we have conducted simulations of the realizations of $X(t)$. An illustration of such a simulation is given in Fig. 2 for $\epsilon = 0.1$, $\alpha = 0.1$, $\nu = 0.005$ and $\mu = 0.1$. The simulations reveal that $X(t)$ tends to proceed according to 'random oscillations.'

The deterministic analogue of this stochastic model is described by

$$dx/dt = \epsilon - \alpha xy, \qquad dy/dt = \nu - \mu y.$$

Subject to $x(0) = y(0) = 0$ we find the solutions to be

(4.1)

$$x(t) = \frac{\epsilon}{\mu} T^a e^{-aT} \int_T^1 u^{-a-1} e^{au} \, du,$$

$$y(t) = \frac{\nu}{\mu}(1 - T),$$

where $T = e^{-\mu t}$ and $a = \alpha \nu / \mu^2$. It follows that $x(\infty) = \epsilon \mu / \alpha \nu$. For $\epsilon = \alpha = \mu = 0.1$ and $\nu = 0.005$, the deterministic curve (4.1) is monotonically increasing, as is shown in Fig. 2.

Model 5. Consider now a predator-prey model with two kinds of predators. The two kinds of predators may be different species or members of the same species with different abilities as predators. Let $Y_i(t)$ denote the number of predators of kind i, $i = 1, 2$. Then we assume that in the time increment $(t, t + \delta t)$ there are the following possible transitions and associated probabilities:
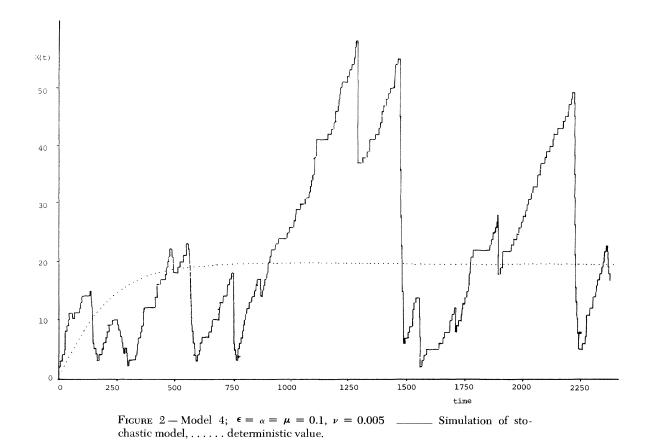
$(X, Y_1, Y_2) \to (X - 1, Y_1, Y_2) \qquad (\alpha_1 XY_1 + \alpha_2 XY_2)\delta t + o(\delta t)$

$(X, Y_1, Y_2) \to (X, Y_1 - 1, Y_2) \qquad \mu Y_1 \delta t + o(\delta t)$

$(X, Y_1, Y_2) \to (X, Y_1, Y_2 - 1) \qquad \mu Y_2 \delta t + o(\delta t)$

$(X, Y_1, Y_2) \to (X, Y_1, Y_2) \qquad 1 - (\alpha_1 XY_1 + \alpha_2 XY_2 + \mu Y_1 + \mu Y_2)\delta t$
$$+ o(\delta t)$$

with $X(0) = m$ and $Y_i(0) = n_i$, $i = 1, 2$. For

$$p_{x,y_1,y_2}(t) = P\{X(t) = x, Y_1(t) = y_1, Y_2(t) = y_2\}$$

it then follows that

$$\frac{dp_{x,y_1,y_2}(t)}{dt} = (x + 1)(\alpha_1 y_1 + \alpha_2 y_2)p_{x+1,y_1,y_2}$$

$$+ \mu(y_1 + 1)p_{x,y_1+1,y_2} + \mu(y_2 + 1)p_{x,y_1,y_2+1}$$

$$- (\alpha_1 xy_1 + \alpha_2 xy_2 + \mu y_1 + \mu y_2)p_{x,y_1,y_2} \quad .$$

FIGURE 2 — Model 4; $\epsilon = \alpha = \mu = 0.1$, $\nu = 0.005$ _____ Simulation of stochastic model, ... deterministic value.

For the generating function

$$H_r(t, w_1, w_2) = \sum_{x, y_1, y_2} x^{(r)} w_1{}^{y_1} w_2{}^{y_2} p_{x, y_1, y_2}(t)$$

we find the equation

$$\frac{\partial H_r}{\partial t} = (\mu - \mu w_1 - r\alpha_1 w_1) \frac{\partial H_r}{\partial w_1} + (\mu - \mu w_2 - r\alpha_2 w_2) \frac{\partial H_r}{\partial w_2}$$

with initial condition $H_r(0, w_1, w_2) = m^{(r)} w_1{}^{n_1} w_2{}^{n_2}$. The solution is found to be

$$H_r(t, w_1, w_2) = m^{(r)} \prod_{i=1}^{2} \left\{ w_i e^{-(\mu + r\alpha_i)t} + \frac{\mu}{\mu + r\alpha_i}(1 - e^{-(\mu + r\alpha_i)t}) \right\}^{n_i}.$$

The probability distribution for $X(t)$ is given by

$$p_x(t) = \sum_{r=x}^{m} \frac{(-1)^{r-x}}{x!(r-x)!} H_r(t, 1, 1)$$

(cf. equation (2.7)). This leads to the limiting distribution

$$p_x(\infty) = \binom{m}{x} \sum_{r=x}^{m} (-1)^{r-x} \binom{m-x}{r-x} \left(\frac{\mu}{\mu + r\alpha_1}\right)^{n_1} \left(\frac{\mu}{\mu + r\alpha_2}\right)^{n_2}.$$

These probabilities are given in Table 2 for $m = 6$, $n_1 = n_2 = 1$, $\mu = 0.75$ and various values of α_1/α_2 such that $\alpha_1 + \alpha_2 = 0.5$. By taking $\alpha_1 + \alpha_2 = 0.5$ in each case we have standardized them in the sense that the risk of predation is initially the same. Subject to this type of

TABLE 2. Limiting probabilities $p_x(\infty)$ and mean $E\{X(\infty)\}$ for the ultimate number of prey when initially there are two predators with different abilities; $m = 6$, $n_1 = n_2 = 1$, $\mu = 0.75$.

α_1/α_2 \ x	1	2	3	4	5	∞
0	.047	.050	.053	.055	.057	.068
1	.107	.105	.104	.103	.103	.102
2	.160	.155	.149	.145	.142	.128
3	.195	.190	.184	.179	.175	.149
4	.203	.202	.200	.197	.195	.168
5	.177	.181	.185	.188	.190	.185
6	.111	.117	.125	.132	.138	.200
$E\{X(\infty)\}$	3.375	3.399	3.429	3.453	3.471	3.600
$x(\infty)$	3.08	3.08	3.08	3.08	3.08	3.08

standardization we are varying the rates of predation. The probability distributions in Table 2 indicate that the expected size of the prey population increases as the difference between α_1 and α_2 increases, while the probability of extinction of the prey population increases. Clearly a deterministic model cannot lead to this conclusion.

The deterministic analogue of this stochastic model is described by

$$dx/dt = -\alpha_1 xy_1 - \alpha_2 xy_2,$$

$$dy_i/dt = -\mu y_i, \qquad i = 1, 2.$$

It follows that

$$x(t) = m \exp \left\{ - \frac{n_1\alpha_1 + n_2\alpha_2}{\mu} (1 - e^{-\mu t}) \right\},$$

$$y_i(t) = n_i e^{-\mu t}, \qquad i = 1, 2.$$

Therefore, if $n_1 = n_2$ and $\alpha_1 + \alpha_2$ is kept fixed while α_1/α_2 is changed, we find that $x(t)$ remains unchanged. For $m = 6$, $n_1 = n_2 = 1$, $\mu = 0.75$ and $\alpha_1 + \alpha_2 = 0.5$, we find that $x(\infty) = 6e^{-2/3} = 3.08$ irrespective of the value of α_1/α_2.

Discussion. For Models 1 and 3 it was observed that the difference between $E(X)$ and the corresponding deterministic value x may be infinite, thus verifying that these concepts are quite different. The reason for the discrepancy becomes clearer when we compare the differential equation for $E(X)$ with that for x. For Model 3, for example, we may find the differential equation for $E(X)$ by multiplying both sides of equation (3.1) by x and then summing over x and y. This leads to

$$dE(X)/dt = \lambda E(X) - \alpha E(XY)$$

with $E\{X(0)\} = m$. The equation has the same form as its deterministic analogue (3.5) if we assume $E(XY) = E(X) \cdot E(Y)$ i.e., if we assume the covariance of $X(t)$ and $Y(t)$ to be zero. However, this is not a valid assumption for this model, since in fact this covariance becomes infinite as $t \to \infty$ [see Becker (1970a)]. A similar argument applies to the discrepancy in Model 1. This discrepancy between $E(X)$ and $x(t)$ does not imply that the deterministic value is useless; in fact, it may be a closer representation of the process than $E(X)$ by itself. For example, for Model 3 it may be shown that the probability of ultimate extinction is unity (see Becker (1970a)). The limit $x(\infty) = 0$ suggests just that, while $E(X) \to \infty$ $(\lambda > \nu)$ is misleading.

The discrepancy found between $E(X)$ and x helps to emphasize that

care needs to be exercised, when a stochastic process for interacting populations is approximated by replacing one or more random variables by a corresponding deterministic or mean value. This method of approximation is used, for example, by Bartlett (1955), Gani (1965a) and Kendall (1956). If this method is applied in Model 1 or 3 by, say, replacing $Y(t)$ by $y(t) = E(Y)$, then the approximation obtained for $E(X)$ is equivalent to $x(t)$, which indicates that it results in a significantly different process for $X(t)$.

For Model 2 it was observed that the deterministic approximation x to the size of S_x may be zero when the stochastic model indicates that the probability of S_x becoming extinct is relatively small (e.g. about .2 when $\lambda = \mu$ in the above example). This discrepancy is mainly the result of the small initial size of population S_y. This also explains why the number of survivors from S_x, given S_x, does not become extinct, tends to be large. The reason is that if S_y becomes extinct it is likely to do so early while $Y(t)$ is small, in which case little time has elapsed for predation to occur. That only one population size needs to be small in order to observe large discrepancies is even more clearly reflected by the simulations of Model 4, where the random oscillations are the result of the occasional presence of efficient predators.

The discrepancy between the stochastic and deterministic versions of Model 5 is of another kind. A fundamental question asked by ecologists is: If a species evolves in a certain way so that its relationship to other species and its environment alters, how does this affect the species' chance of survival? In the very limited sense that the effect of variations in the α_i in Model 5 addresses this problem, we find different answers from our stochastic and deterministic formulations as is indicated in Table 2.

It is hoped that the discrepancies between the stochastic and deterministic formulations outlined here reveal the need for further study of stochastic models for the description of the growth of interacting populations despite the mathematical difficulties involved. Let us now briefly outline different methods by which the more difficult mathematics inherent in stochastic models may be attacked.

For the simpler nonlinear stochastic models it may be possible to obtain exact analytic solutions, for example by introducing different types of generating functions such as the $G_r(t, w)$ and $H_r(t, w)$ used here. Generating functions of this type have been very successful in obtaining explicit analytic solutions for nonlinear stochastic models [see Downton (1967), Dietz and Downton (1968), Becker (1970a), (1970b)]. The more commonly used probability generating function

$$\prod (u, w, t) = \sum_{x,y} u^x w^y p_{x,y}(t)$$

has also proven useful for nonlinear processes. The second order differential equations for $\prod (u, w, t)$ may be sidestepped by writing

$$\prod (u, w, t) = \sum_{x} u^x f_x(w, t)$$

and then attempting to solve the differential-difference equation for the $f_x(w, t)$, which contain only first order derivatives. This method of solution has been successfully used on nonlinear processes by Gani (1965b), (1967), Siskind (1965) and Dietz (1966).

When an exact analytic solution seems unlikely it may be useful to consider an approximation to the process. Several methods of approximation have proved to be useful. One method is to replace one or more random variables by a deterministic function. As mentioned above, care needs to be exercised in the use of this method. Another method is to use approximating birth-death processes. Thus Whittle (1955) was able to give a precise formulation of the stochastic version of the epidemic threshold theorem by 'sandwiching' the stochastic general epidemic model between two birth-death processes. Daley and Kendall (1965) combine the deterministic and stochastic approaches for a method they call the 'Principle of the Diffusion of Arbitrary Constants.' In applying this method to a stochastic model (with nonlinear transition rates) for the spread of rumours, they find results in excellent agreement with those obtained from simulations of the exact embedded random walk. Several other methods of obtaining approximations to stochastic processes may be found in the books by Bailey (1964, Chapter 15) and Bartlett (1960).

Monte Carlo studies always improve one's insight into stochastic processes, however the analytic intractability of many of the stochastic models for interacting populations has given the simulation methods an even more significant role in the study of these stochastic processes. The studies of Bartlett (1957), (1961), Leslie and Gower (1958), (1960) and Barnett (1962) clearly show this.

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