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The properties of a stochastic model for the predator–prey type of interaction between two species

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1. INTRODUCTION

The two main types of interaction between any pair of biological species, which are of most interest to the ecologist, are either when they are competing together for some common source of food supply, or when one of the species preys upon the other. The properties of a stochastic model for a system of two competing species have been illustrated by a set of artificial realizations in an earlier paper (Leslie & Gower, 1958). We now consider some of the properties of a model for the interaction between a predatory species and its prey, more particularly in regard to the behaviour of such systems in the region of the stationary state, and the chances of random extinction for one or other of the two species. The interaction is imagined to take place in some limited environment where there is an ample supply of food for the prey, and in the first place it is assumed that all the members of the prey population are exposed to the risk of capture or attack by the predator. Later, this last condition is relaxed, and it is supposed that because of some heterogeneity in the environment, only a fraction of the prey population is exposed to risk, and some of the consequences of this partial interaction are illustrated in the last section. The basic model has already been described (Leslie, 1948, 1958), but it will be useful if the formulae are summarized here.

If S_1 is a species of prey and S_2 a predator, then working in discrete-time intervals and given that the respective populations consist of $N_1(t)$ and $N_2(t)$ individuals at time t, the deterministic model for the interaction is taken to be,

$$\left.\begin{aligned} N_1(t+1) &= \frac{\lambda_1 N_1(t)}{1+\alpha_1 N_1(t)+\beta_1 N_2(t)}, \\ N_2(t+1) &= \frac{\lambda_2 N_2(t)}{1+\alpha_2\{N_2(t)/N_1(t)\}}, \end{aligned}\right\} \tag{1·1}$$

where α_1, β_1 and α_2 are parameters > 0, and $\log_e \lambda_1 = r_1 = b_1 - d_1$, $\log_e \lambda_2 = r_2 = b_2 - d_2$ are the intrinsic birth- and death-rates of the two species. For the stationary state, $N_1 = L_1$, $N_2 = L_2$, we have,

$$\left.\begin{aligned} L_1 &= \frac{\alpha_2(\lambda_1-1)}{\beta_1(\lambda_2-1)+\alpha_1\alpha_2}, \\ L_2 &= (\lambda_2-1)L_1/\alpha_2. \end{aligned}\right\} \tag{1·2}$$

It has been shown (Leslie, 1948, § 6) that this discrete-time model is closely related to the continuous-time model, (writing the operator $D \equiv d/dt$),

$$\left.\begin{aligned} DN_1 &= (r_1 - a_1 N_1 - c_1 N_2)N_1 \\ DN_2 &= \left(r_2 - a_2 \frac{N_2}{N_1}\right)N_2 \end{aligned}\right\} \quad (a_1, a_2, c_1 > 0), \tag{1·3}$$

for which the stationary state is

$$L_1 = \frac{a_2 r_1}{c_1 r_2 + a_1 a_2},$$
$$L_2 = r_2 L_1 / a_2.$$
(1·4)

Putting $N_1 = L_1(1 + u_1)$ and $N_2 = L_2(1 + u_2)$, then we have from (1·3) for small u_1 and u_2,

$$Du_1 = -a_1 L_1 u_1 - c_1 L_2 u_2,$$
$$Du_2 = r_2(u_1 - u_2).$$
(1·5)

The equation in D is $\qquad D^2 + (r_2 + a_1 L_1)D + r_2(a_1 L_1 + c_1 L_2) = 0,$

or from (1·4) $\qquad\qquad D^2 + (r_2 + a_1 L_1)D + r_1 r_2 = 0.$ (1·6)

The roots of (1·6), therefore, will be either both negative, or complex with the real part negative, so that the stationary state is stable, and an approach to this state will be made by a series of damped oscillations if

$$(r_2 + a_1 L_1)^2 < 4 r_1 r_2.$$

The properties of this model differ somewhat from those of the classical Lotka–Volterra equations for this type of interaction, viz.

$$DN_1 = (\epsilon_1 - \gamma_1 N_2) N_1$$
$$DN_2 = (-\epsilon_2 + \gamma_2 N_1) N_2 \qquad (\epsilon_1, \epsilon_2, \gamma_1, \gamma_2 > 0).$$
(1·7)

This deterministic system and the stochastic model based upon it have been discussed recently by Bartlett (1957 a). Here there is no damping towards the equilibrium point $L_1 = \epsilon_2 / \gamma_2$, $L_2 = \epsilon_1 / \gamma_1$, and the deterministic path of small cycles around this point is given by the ellipse
$$\epsilon_2 u_1^2 + \epsilon_1 u_2^2 = \text{constant},$$

where $N_1 = L_1(1 + u_1)$, $N_2 = L_2(1 + u_2)$. Consequently, as Bartlett points out, in the stochastic model the effect of random drift, in the absence of any damping factor, must result sooner or later, either in the extinction of the predator, or in the extinction first of the prey, followed in due course by that of the predator from starvation. In the stochastic formulation of this model (1·7), the stationary state is therefore in a sense unstable. But the presence of a damping term in the model defined by (1·3) would lead to a greater degree of stability, and in the corresponding stochastic model the system might therefore be expected to fluctuate in the region of the equilibrium state, although there might be still a chance of random extinction of one or other species, depending on the degree of variability in numbers in this region. To investigate this point, the stochastic discrete-time model corresponding to (1·1) was programmed for the Elliot–N.R.D.C. computer in the Statistical Department of Rothamsted Experimental Station, and some of the results obtained are given in the following sections.

2. Stochastic model

In a stochastic formulation of this model, a wide variety of possible birth-rate and death-rate functions for the two species could be adopted (cf. Leslie, 1958, § 4). But, clearly, one of the most obvious choices to make is the case when the birth-rate (b) of each species remains constant, and any increase in the numbers of the predator affects the death-rate ($d_1(t)$) of the prey over the interval t to $t + 1$, and vice versa. If, therefore, in (1·1) we define the parameters representing the intrinsic birth- and death-rates of the two species,

$$\lambda_a = e^{b_a - d_a} \quad (a = 1, 2; \ b_a > d_a),$$

and put
$$q_1(t) = 1 + \alpha_1 N_1(t) + \beta_1 N_2(t),$$

$$q_2(t) = 1 + \alpha_2 \{N_2(t)/N_1(t)\},$$

we have in the constant birth-rate type of discrete-time stochastic model (Leslie, 1958, § 5),

$$
\left.
\begin{aligned}
E\{N_a(t+1) \mid N_1(t), N_2(t)\} &= \frac{\lambda_a}{q_a(t)} N_a(t) = \lambda_a(t) N_a(t) \quad (a = 1, 2), \\
\operatorname{var}\{N_a(t+1) \mid N_1(t), N_2(t)\} &= \left(\frac{2b_a}{r_a(t)} - 1\right)(\lambda_a(t) - 1) E\{N_a(t+1)\} \quad (\lambda_a(t) \neq 1) \\
&= 2b_a E\{N_a(t+1)\} \quad (\lambda_a(t) = 1).
\end{aligned}
\right\}
\tag{2.1}
$$

Here it is assumed that the difference between the constant birth-rate and the variable death-rate of each species at time t,

$$r_a(t) = \log_e [\lambda_a/q_a(t)] = b_a - d_a(t) \quad (a = 1, 2)$$

remains constant over the interval t to $t+1$, and that given $N_1(t)$ and $N_2(t)$, then $N_1(t+1)$ and $N_2(t+1)$ are distributed normally and independently with these means and variances, all negative values of $N_a(t+1)$ being attributed to $N_a(t+1) = 0$.

The programmes for this model were similar to those described by Leslie & Gower (1958) for a system of two competing species and little need be said of them here. In particular the same method of random number generation was used and the population parameters could easily be varied. Since the results consisted largely of long trajectories of the population numbers of the two species at succeeding instants of time, an additional programme was written to construct distributions of these population numbers direct from the output tapes.

3. Theoretical variances and covariance of the system

The theoretical variances and covariance of the population numbers, when such a system is fluctuating in the region of the stationary state, may be estimated, to a first approximation, in the following way. The equations (2·1) may be written in the form

$$N_a(t+1) = f_a(N_1, N_2, t) + Z_a(t+1) \quad (a = 1, 2) \tag{3.1}$$

in which the first term is the deterministic part of the process defined by (1·1); and the $Z_a(t+1)$ are independent normal variables with zero means, and variances, $\sigma^2(Z_a) \sim 2b_a L_a$, when the birth-rate of each species remains constant, and the system is in the region of the stationary state (L_1, L_2) defined by (1·2). By applying the usual δ-technique (cf. Leslie & Gower, 1958, § 5), we have as a first approximation from (3·1), the set of equations for determining $\operatorname{var}(N_1(t)) = \sigma_1^2$, $\operatorname{var}(N_2(t)) = \sigma_2^2$ and $\operatorname{cov}(N_1(t), N_2(t)) = \sigma_{12}$,

$$
\left.
\begin{aligned}
\sigma_1^2 &= \left(\frac{\partial f_1}{\partial N_1}\right)^2 \sigma_1^2 + 2\left(\frac{\partial f_1}{\partial N_1}\right)\left(\frac{\partial f_1}{\partial N_2}\right)\sigma_{12} + \left(\frac{\partial f_1}{\partial N_2}\right)^2 \sigma_2^2 + 2b_1 L_1, \\
\sigma_2^2 &= \left(\frac{\partial f_2}{\partial N_1}\right)^2 \sigma_1^2 + 2\left(\frac{\partial f_2}{\partial N_1}\right)\left(\frac{\partial f_2}{\partial N_2}\right)\sigma_{12} + \left(\frac{\partial f_2}{\partial N_2}\right)^2 \sigma_2^2 + 2b_2 L_2, \\
\sigma_{12} &= \left(\frac{\partial f_1}{\partial N_1}\right)\left(\frac{\partial f_2}{\partial N_1}\right)\sigma_1^2 + \left[\left(\frac{\partial f_1}{\partial N_1}\right)\left(\frac{\partial f_2}{\partial N_2}\right) + \left(\frac{\partial f_1}{\partial N_2}\right)\left(\frac{\partial f_2}{\partial N_1}\right)\right]\sigma_{12} + \left(\frac{\partial f_1}{\partial N_2}\right)\left(\frac{\partial f_2}{\partial N_2}\right)\sigma_2^2,
\end{aligned}
\right\}
\tag{3.2}
$$

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the partial differential coefficients being evaluated for $N_1 = L_1$, $N_2 = L_2$. Thus, from (1·1) and (1·2), we have

$$f_1 = \frac{\lambda_1 N_1}{1 + \alpha_1 N_1 + \beta_1 N_2},$$

$$f_2 = \frac{\lambda_2 N_2}{1 + \alpha_2 N_2 / N_1},$$

and

$$\left(\frac{\partial f_1}{\partial N_1}\right)_{L_1 L_2} = 1 - \frac{\alpha_1 L_1}{\lambda_1}, \quad \left(\frac{\partial f_2}{\partial N_2}\right)_{L_1 L_2} = \frac{1}{\lambda_2},$$

$$\left(\frac{\partial f_1}{\partial N_2}\right)_{L_1 L_2} = -\frac{\beta_1 L_1}{\lambda_1}, \quad \left(\frac{\partial f_2}{\partial N_1}\right)_{L_1 L_2} = \frac{(\lambda_2 - 1)^2}{\alpha_2 \lambda_2}.$$

It is also useful to have the equations for determining the variances and covariance for the analogous continuous-time model. From (1·5), writing $c_1 = k a_1$, we have the linear stochastic system for small u_1 and u_2,

$$\left.\begin{aligned} \delta u_1 &= -a_1 (L_1 u_1 + k L_2 u_2)\,\delta t + \delta \xi, \\ \delta u_2 &= r_2 (u_1 - u_2)\,\delta t + \delta \phi, \end{aligned}\right\} \tag{3·3}$$

in which the independent variables $\delta \xi$ and $\delta \phi$ have zero means, and variances $(2b_1/L_1)\,\delta t$ and $(2b_2/L_2)\,\delta t$, respectively, when the birth-rate of each species is assumed to remain constant and the system is in the region of the state (L_1, L_2). From $u_1 + \delta u_1$, $u_2 + \delta u_2$, we finally obtain, by squaring and taking the cross-product, the equations for the variances and covariance $(\sigma_1^2, \sigma_2^2, \sigma_{12})$ of u_1 and u_2,

$$\left.\begin{aligned} L_1 \sigma_1^2 &= \frac{b_1}{a_1 L_1} - k L_2 \sigma_{12}, \\ \sigma_2^2 &= \frac{b_2}{r_2 L_2} + \sigma_{12}, \\ (a_1 L_1 + r_2)\,\sigma_{12} &= r_2 \sigma_1^2 - k a_1 L_2 \sigma_2^2. \end{aligned}\right\} \tag{3·4}$$

Since $N_1 = L_1(1 + u_1)$, $N_2 = L_2(1 + u_2)$, we then have

$$\mathrm{var}\,(N_1) = L_1^2\,\mathrm{var}\,(u_1), \quad \mathrm{var}\,(N_2) = L_2^2\,\mathrm{var}\,(u_2), \quad \mathrm{cov}\,(N_1, N_2) = L_1 L_2\,\mathrm{cov}\,(u_1, u_2),$$

which can be contrasted with the variances and covariance for the discrete-time model given by (3·2). The relationships between the parameters of the two types of model are

$$r_a = \log_e \lambda_a \quad (a = 1, 2), \qquad a_1 = \alpha_1 r_1 / (\lambda_1 - 1) \qquad \text{and} \qquad k = \beta_1 / \alpha_1;$$

while the constant birth-rates b_1 and b_2, and the stationary values, L_1 and L_2, are naturally the same for each model. In regard to the differences between the two models, it is perhaps worth noting that the variances estimated by means of (3·4) are always less than those obtained by the solution of (3·2), so that the use of the discrete-time model leads to an enhanced degree of variation when a particular system is fluctuating in the neighbourhood of the equilibrium level (cf. Bartlett, Gower & Leslie, 1960). By reducing the unit of time adopted in the discrete-time model, however, it is always possible to make the variances of the two types of model more in agreement.

4. Fluctuations in the neighbourhood of the stationary state

The behaviour of this type of system in the region of the stable stationary state may be illustrated by the results obtained from a realization which was computed for 1000 steps, taking as the numerical values of the parameters in (2·1)

$$\lambda_1 = 1{\cdot}2574, \quad b_1 = 0{\cdot}2577, \quad \lambda_2 = 1{\cdot}1892, \quad b_2 = 0{\cdot}2521,$$

$$\alpha_1 = 0{\cdot}0005148, \quad \beta_1 = 0{\cdot}0018018 \quad \text{and} \quad \alpha_2 = 0{\cdot}2838,$$

which from (1·2) give a stationary state of $L_1 = 150$, $L_2 = 100$. Starting with the initial values of $N_1(0) = 500$ for the prey, and $N_2(0) = 20$ for the predator, these processes rapidly approached their equilibrium levels, in the region of which they then continued to oscillate
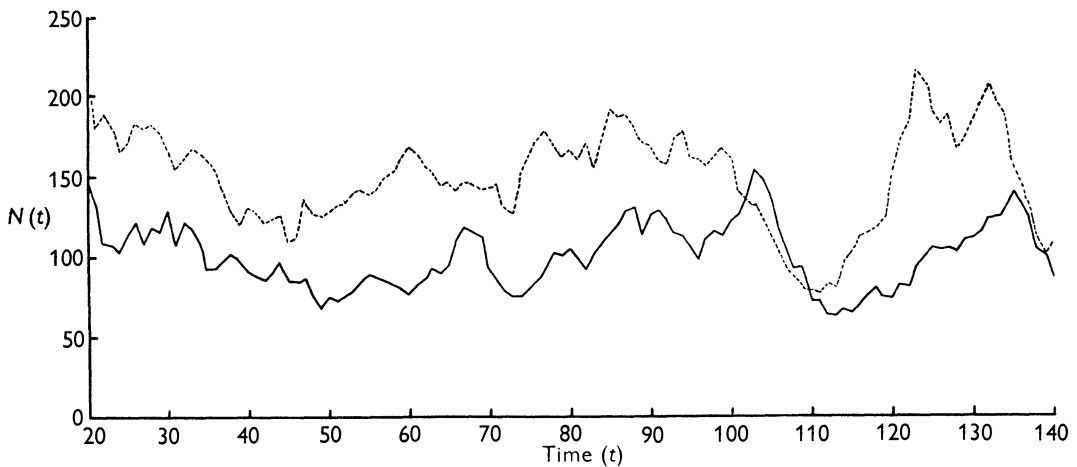

Fig. 1. Fluctuations of a predator–prey system in the region of the stable stationary state. ————, the number of prey (equilibrium level $L_1 = 150$); ————, the number of predators (equilibrium level $L_2 = 100$).

in an irregular fashion. As an example, the changes in numbers are illustrated in Fig. 1 for the period of time from $t = 20$ to $t = 140$. It will be seen that there is no regularity in the oscillations, and that at times there is a tendency for quite a pronounced excursion to be made away from the region of the stationary state, for example, in Fig. 1 the course of events from about $t = 100$ to $t = 120$, when a large fall in the numbers of the prey is followed shortly afterwards by a similar type of fall in numbers of the predator. The general picture is somewhat different from that of a system of two competing species with a stable stationary state (Leslie & Gower, 1958), where any drift away from the equilibrium level seems to take place in opposite directions owing to the negative correlation which exists between the two species in that type of system. In the case of the predator–prey type of interaction, the correlation is positive in sign.

Theoretically, it might be expected that the stationary distribution of such a two-species system would be approximately bi-variate normal in form, with variances and covariance given by (3·2), (Bartlett, Gower & Leslie, 1960). The bivariate distribution of $N_1(t)$ and $N_2(t)$ is given in Appendix Table 1 for the last 800 steps in this realization. The observed means were $\bar{N}_1 = 149{\cdot}74$ and $\bar{N}_2 = 97{\cdot}09$, compared with the deterministic stable state of $L_1 = 150$, $L_2 = 100$; while the observed variances and covariance (computed by the machine from the

individual observations and not from the grouped data), together with the values expected theoretically both for the discrete-time model, and for its continuous-time equivalent, were:

| | Expected | | Observed |
	Continuous-time model	Discrete-time model	Discrete-time model
var (N_1)	432	546	635·6
var (N_2)	170	228	214·0
cov (N_1, N_2)	+37·2	+56·6	+63·6

Considering that the expected values are based on the theory of small fluctuations and so cannot be exactly correct, the agreement in the case of the model actually used seems very satisfactory.

For samples as large as 800, taking $g_1 \sim m_3/m_2^{\frac{3}{2}}$ and $g_2 \sim [(m_4/m_2^2) - 3]$, we have (applying Sheppard's corrections in computing the moments) for the marginal distribution of N_1 in Appendix Table 1,

$$g_1 \sim +0·322 \pm 0·087, \quad g_2 \sim -0·035 \pm 0·173,$$

and for that of N_2, $g_1 \sim +0·121 \pm 0·087, \quad g_2 \sim -0·201 \pm 0·173.$

The skewness coefficient for the second species is not much different from zero, while that for the first species is 3·7 times the standard error given, suggesting a degree of positive skewness in the marginal distribution of N_1. These standard errors, however, are the classical values, viz. $\sigma(g_1) = \sqrt{(6/n)}$, ignoring the serial correlation between the successive values of both $N_1(t)$ and $N_2(t)$. They are therefore underestimates of the correct values (Bartlett *et al.* 1960). In any case the degree of skewness is not very marked, and broadly speaking, we can regard the distribution given in Table 1 as being approximately bivariate normal in form.

5. THE CHANCES OF RANDOM EXTINCTION

In the numerical system used as an illustration in the previous section, the chance of one or other of the species becoming extinct appears to be negligible, at least in terms of any ordinary time scale, once their numbers are in the region of their equilibrium levels. For instance, to take the predatory species which has the smaller numbers as an example; the order of magnitude of the mean passage time to extinction is likely to be inversely proportional to the probability of the zero state, or in terms of a normal distribution, using the observed mean and variance for this species, of the order of $1·4 \times 10^{11}$ units of time. It might be expected, therefore, that this system would continue to oscillate around the equilibrium level in an irregular fashion for a comparatively lengthy period. But, in other systems, this may not be so, and the chances of extinction may then become appreciable.

This point is relevant to the results obtained by Gause (1934) in his experiments with the two Protozoa, *Didinium nasutum* and *Paramecium caudatum*. The latter species is devoured by the former, and the amount of food required by *Didinium* is very great. His first experiments were carried out in a relatively small microcosm (the upper asymptote in numbers of the *Paramecia*, when living alone, being of the order of 100 individuals), and the introduction of small numbers of *Didinium* at varying intervals of time after the prey was followed by an intense multiplication of the predator, which devoured all the prey and afterwards themselves perished. There was also a considerable degree of variability in numbers between replicates of the same age (Gause, 1934, Chapter VI and Appendix, Table 6).

Suppose, then, we have a relatively small environment in which a species of prey is established, and which is then invaded by a small group of predators. For simplicity it will be assumed in the model that the intrinsic rates of increase and the birth-rates of both species are the same, and that in (2·1) we put

$$\lambda_1 = \lambda_2 = 1 \cdot 25, \quad b_1 = b_2 = 0 \cdot 25, \quad \alpha_1 = 0 \cdot 001.$$

These values of λ_1 and α_1 lead to a logistic upper-asymptote in numbers of the prey, if it were living alone, of 250 individuals. When it is assumed that the birth-rates of both species remain constant, the remaining parameters, β_1 and α_2, in (1·1) and (2·1), define the magnitude of the effect which the numbers of each species have on the death-rate of the other. β_1 might be termed the 'relative voracity' of the predator in regard to the prey, since for a given value of N_2, the greater the value of this parameter, the more the death-rate of the prey is affected during a unit of time; and α_2 represents the sensitivity of the predator to the relative density in numbers of the two species, i.e. for a given value of the ratio N_2/N_1, the greater the value of α_2, the more the death-rate of the predator is affected. Consider three systems in which β_1 and α_2 are varied slightly, which together with the values of the other parameters given above lead to the following stationary states:

System	β_1	α_2	L_1	L_2
(i)	0·015	0·375	22·7	15·2
(ii)	0·025	0·500	18·5	9·3
(iii)	0·050	0·250	4·9	4·9

Some realizations were computed for each of these three systems, taking in each case $N_1(0) = 200$, $N_2(0) = 15$ as the initial conditions, i.e. it was assumed that the prey was well established in this imaginary environment, when it was invaded by a small group of predators. The results were as follows.

System (i)

The computations were carried on for 399 steps, at the end of which time neither species was eliminated, though at one point the predator was very close to extinction, having been reduced to only one individual surviving on two successive occasions. Neglecting the first ten steps, during which time an approach was being made to the region of the stationary state, the observed means for the remaining 389 observations were $\bar{N}_1 = 25 \cdot 33$ and $\bar{N}_2 = 12 \cdot 96$; while the observed variances and covariance compared with the theoretical expectations derived from (3·3) were

	Expected	Observed
var (N_1)	101	137·3
var (N_2)	37·7	33·35
cov (N_1, N_2)	$+19\cdot7$	$+22\cdot02$

This very good agreement between the theoretical and observed variances was of interest, since in this type of discrete-time stochastic model, the assumption made in applying (2·1) that the $N_a(t+1)$ ($a = 1, 2$), for given $N_a(t)$ are distributed normally, might be expected to break down in the region of small numbers. The observed distributions of N_1 and N_2 are given in Appendix Table 2, from which it can be seen that these departed appreciably from the normal, there being a pronounced positive skewness in each case. However, with no knowledge of the form of distribution which might be expected in such systems when numbers are small, it is difficult to know what reliance can be placed on this observed bivariate distribution.

System (ii)

The predator became extinct in each of the five realizations which were computed for this system. In one case the prey also vanished at the same time as the predator, and in another its numbers were reduced to only one individual. In this region of a stochastic logistic process, the probability of random extinction should be roughly of the same order of magnitude as that of a simple birth and death process with parameters corresponding to the intrinsic rate of increase of the particular species, viz. $\log \lambda = b - d$; so that if only one individual is left surviving, the probability that the prey population would in turn become extinct, is appreciable in this numerical example, being $P(0) \sim d/b = 0 \cdot 11$. In other words, the disappearance of the predator before the prey may not necessarily mean that the latter species will be able to persist.

System (iii)

Out of 19 realizations with the initial numbers $N_1(0) = 200$, $N_2(0) = 15$, the prey was eliminated by the predator in 9 cases, which would result inevitably in the disappearance also of the predator. In the remaining 10, the predator became extinct before the prey; but
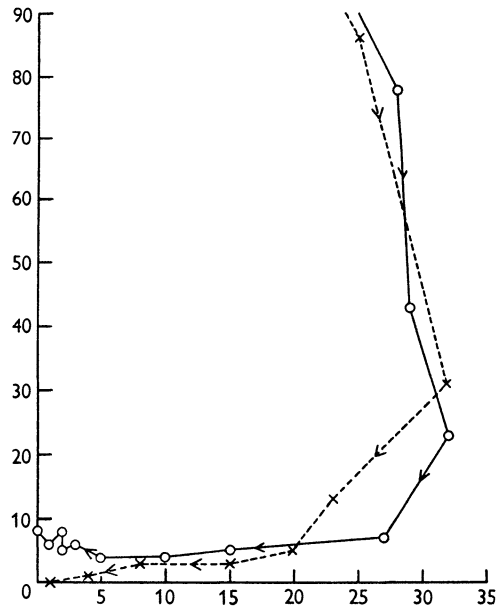
Fig. 2. Representative trajectories for System (iii), for which the deterministic stable state is $L_1 = L_2 \sim 5$. The initial conditions were for the prey, $N_1(0) = 200$, and for the predator, $N_2(0) = 15$, but in order to save space, a few of the initial steps in each realization are omitted from the figure.

in five of these cases the prey at this time was reduced to such low numbers, for example, either one or two individuals, that its ability to persist became problematical. There appeared to be little difference between the times taken for either predator or prey to become extinct, the combined mean passage time to extinction being $\bar{t} = 20 \cdot 3 \pm 2 \cdot 99$ units of time. The (N_1, N_2) trajectories differed somewhat, depending on the length of time the interaction persisted, but a pair of replicates are illustrated in Fig. 2, for which the passage time to zero was of the same order as the mean value. In broad outline the pattern is very similar to the trajectories observed by Gause (1934) in his experiments, not only with *Didinium*

and *Paramecium*, but also with other species of Protozoa, for example, *Paramecium bursaria* and *Bursaria truncatella* (Gause, 1935).

The results with these three numerical systems suggest that, in a limited environment, in which there is no immigration from outside, the persistence of both species in a predator–prey interaction depends very greatly on the relations between the various parameters for the two species, and that the chances of random extinction are very sensitive to relatively small changes in these parameters. If the magnitudes of the intrinsic rates of increase of the two species, the relative 'voracity' of the predator, and so forth, are not happily adjusted in between themselves, it appears doubtful whether in a very simplified type of system both species will be able to persist for very long, and the probability of random extinction then becomes a dominant feature of the interaction.

6. WHEN ONLY A FRACTION OF THE PREY POPULATION IS EXPOSED TO RISK

In developing the type of model we have used so far, one tacit assumption has been made, namely, that in some way or other the entire prey population is exposed to the risk of capture by the predator. The background environment in which the interaction takes place is assumed to be in a sense 'homogeneous', and the predator and prey populations freely intermingle. Suppose, however, that this is not so, and that because of some 'heterogeneity' of the environment, only a fraction of the prey population is exposed to risk during any one unit of time. One way in which this might occur would be if the configuration of some type of vegetation formed a 'cover' for the prey, which protected it from the predator. Thus, Gause (1934) has pointed out the importance of a refuge in enabling the prey to survive in his experiments with various species of Protozoa, although the predator might still become extinct. But, apart from 'cover' in its literal sense, a variety of different situations can be imagined as regards the environment, or the habits of the two species, which would result in the interaction being confined to only a fraction of the total prey population.

Suppose, for simplicity, that a fraction k ($0 \leqslant k \leqslant 1$) of the prey population is exposed to risk of capture by the predator, and that this fraction remains constant for a particular system. Then, in a more generalized model in the place of (1·1) and (2·1), the deterministic part of the process may be written,

$$\left. \begin{aligned} E\{N_1(t+1) \mid N_1(t), N_2(t)\} &= \left[\frac{(1-k)\lambda_1}{1+\alpha_1 N_1(t)} + \frac{k\lambda_1}{1+\alpha_1 N_1(t) + \beta_1 N_2(t)} \right] N_1(t), \\ E\{N_2(t+1) \mid N_1(t), N_2(t)\} &= \frac{\lambda_2 N_2(t)}{1+(\alpha_2/k)\{N_2(t)/N_1(t)\}}. \end{aligned} \right\} \tag{6·1}$$

When $k = 1$, this system reduces to (1·1), and when $k = 0$, i.e. when none of the prey population are exposed to risk, the predator cannot survive, and the system becomes a simple logistic model for the prey population when living alone.

For the stationary state (L_1, L_2) of (6·1), we have for the predatory species

$$\left. \begin{aligned} L_2 &= \frac{k(\lambda_2 - 1)}{\alpha_2} L_1; \end{aligned} \right.$$

while that of the prey is given by the positive root of the equation,

$$\left. \begin{aligned} L_1^2 + \left[\frac{1-(1-k)\lambda_1}{\alpha_1} + \frac{1-k\lambda_1}{B} \right] L_1 - \frac{\lambda_1 - 1}{\alpha_1 B} &= 0, \end{aligned} \right\} \tag{6·2}$$

where

$$B = \alpha_1 + \frac{k\beta_1(\lambda_2 - 1)}{\alpha_2}.$$

The theoretical variances and covariance of the stochastic model for this type of system in the region of the stationary state may be obtained from (3·3), in a similar way to those of the original model, allowing for the alterations in the functions f_1 and f_2.

It is of interest to consider the effect of allowing the value of the constant k to vary in a system with a given set of the remaining parameters in (6·1), more particularly in regard to the chances of random extinction. As an illustration, take the System (iii) of the previous section, for which

$$\lambda_1 = \lambda_2 = 1·25, \quad \alpha_1 = 0·001, \quad \beta_1 = 0·050,$$

$$b_1 = b_2 = 0·25, \quad \alpha_2 = 0·250.$$

In this case it is known from the realizations already computed that the interaction cannot persist for very long, when $k = 1$. Suppose, now, that k is allowed to vary, and that a particular system with constant k is in the region of the stationary state (L_1, L_2) given by (6·2). If, as an approximation, we assume that $N_1(t)$ and $N_2(t)$ are both distributed normally about means given by this state, then the mean passage time to zero for each species should be, very roughly, of the order of magnitude

$$\Theta_a(0) \sim \sqrt{(2\pi)}\, \sigma_a\, e^{L_a^2/2\sigma_a^2} \quad (a = 1, 2),$$

where the variance σ_a^2 is obtained from (3·3). The following are the stationary states (L_1, L_2) and the estimated values of $\Theta_a(0)$ for a system with the basic parameters given above, over a range of values of k $(0 \leqslant k \leqslant 1)$.

	Stationary state		Order of magnitude of the mean passage time to zero in units	
k	L_1	L_2	$\Theta_1(0)$	$\Theta_2(0)$
0	250·0	0	$5·8 \times 10^{40}$	—
0·05	230·1	11·5	$9·8 \times 10^{34}$	$6·2 \times 10^2$
0·10	194·0	19·4	$6·0 \times 10^{25}$	$1·3 \times 10^4$
0·15	155·7	23·4	$7·4 \times 10^{17}$	$4·8 \times 10^4$
0·20	125·0	25·0	$1·2 \times 10^{13}$	$6·5 \times 10^4$
0·25	90·7	22·7	$1·5 \times 10^8$	$1·7 \times 10^4$
0·35	50·4	17·6	$2·4 \times 10^4$	$1·5 \times 10^3$
0·50	23·3	11·6	$3·3 \times 10^2$	$1·6 \times 10^2$
0·65	12·8	8·3	76	58
0·80	8·1	6·5	37	34
1·00	4·9	4·9	20	21

It will be seen that, as might be expected, the stationary numbers of the prey (L_1) steadily increase as a smaller fraction of the population is exposed to risk; while those of the predator (L_2) steadily increase with decreasing k up to a maximum which, in this particular example, is reached in the region of $k = 0·20$. The estimates of $\Theta_a(0)$, which must not be taken too literally, change very rapidly as k decreases. Taking the figures for the predator, which is the species having the smaller numbers, it appears that the approximate maximum mean passage time to extinction is reached at $k \sim 0·20$, when it is about 3000 times greater than in the case of the original system with $k = 1$. These estimates of $\Theta_a(0)$ suggest that in this particular system both species would persist for a comparatively long time when some 10–35 % of the prey population were exposed to risk, in contrast with the relatively rapid extinction of one or other species as this fraction approaches unity.

It was of interest, experimentally, to see how far some of these figures could be confirmed in practice. Taking $k = 1$ in the model, 100 realizations were computed, starting each time

with the initial numbers $N_1(0) = N_2(0) = 5$, i.e. the nearest integers to the deterministic stationary state. In 51 of the replicates the predator disappeared before the prey, the mean passage time to the zero state being $\bar{t} = 19\cdot61 \pm 2\cdot27$ units. In the remaining 49 the prey became extinct before the predator, with $\bar{t} = 19\cdot25 \pm 2\cdot55$. The distributions of the individual times to extinction were very skew, the longest time recorded being in the $t = 76\text{--}79$ class.* But these mean figures are in excellent agreement with those given in the table above. It is also of interest to note that these mean times may be very little affected by the initial numbers adopted in this particular system, as was illustrated in the previous section (System iii), when with $N_1(0) = 200$, $N_2(0) = 15$, the combined mean passage time to extinction for 19 replicates was $t \sim 20$ units.

When $k = 0\cdot8$ in this system, the 'normal' approximation suggests that the mean passage time to zero should be of the order of 35 steps for both species. In 50 realizations using this value of k, and taking as the initial state $N_1(0) = 8$, $N_2(0) = 7$, the predator became extinct in 38 cases, with $\bar{t} = 43\cdot55 \pm 6\cdot36$; while in the remaining 12, the prey disappeared in $\bar{t} = 50\cdot17 \pm 11\cdot48$ steps. Both of these means are somewhat greater than the expected figure, but the distributions of the individual times were even more skew than in the preceding examples when $k = 1$, the interaction on one occasion persisting for 172–175 steps before the predator became extinct. In general, however, these computed mean times to extinction for the two values of k are in reasonably good agreement, at least as regards orders of magnitude, with those derived from the normal approximation.

A further realization was computed for the case of $k = 0\cdot20$, for which, according to the above table, the chance of the predator being able to persist is at a maximum, and starting with the initial numbers of $N_1(0) = 125$, $N_2(0) = 25$, the calculations were carried on for 999 steps. During this time there appeared to be no definite approach to the zero state, although on one occasion the numbers in the predator population fell to only six individuals. The observed means for the 999 observations were $\bar{N}_1 = 120\cdot75$, $\bar{N}_2 = 22\cdot37$, compared with the deterministic stationary state of $L_1 = 125$, $L_2 = 25$; and the variances and co-variance were $\text{var}(N_1) = 345\cdot2$, $\text{var}(N_2) = 37\cdot66$ and $\text{cov}(N_1, N_2) = +8\cdot24$. These observed variances are in very good agreement with the theoretical approximations derived from (3·3), namely $\sigma_1^2 \sim 296$, $\sigma_2^2 \sim 37\cdot4$ and $\sigma_{12} \sim +7\cdot53$. The grouped frequency distribution of N_1 and N_2 is given in Appendix Table 3, and from the marginal distributions we have for the prey species (N_1)

$$g_1 \sim -0\cdot168 \pm 0\cdot077, \quad g_2 \sim -0\cdot089 \pm 0\cdot155,$$

and for the predatory species (N_2)

$$g_1 \sim +0\cdot131 \pm 0\cdot077, \quad g_2 \sim -0\cdot133 \pm 0\cdot155,$$

where the standard errors attached to the estimates are again the classical values, representing lower limits to the correct values. The magnitude of the skewness coefficients suggests that the distribution can be regarded as approximately bivariate normal in form. But, the main point of these results is to confirm that in this system, both species should co-exist for comparatively lengthy periods of time when, owing to some 'heterogeneity' of the environment, the fraction of the prey population exposed to risk is of the order

* In carrying out these computations, the machine was instructed to stop whenever the number of one or other species reached zero, and to record the number of steps taken for this point to be reached. Although the means and variances were computed from the individual figures, the frequency distributions of the times to extinction were finally printed in groups of four units, so that it is impossible to give the exact highest and lowest figure observed.

of 20 %. Naturally, this optimum fraction, which reduces the chance of random extinction of the predator to a minimum, will vary from system to system and may indeed be insufficient to prevent the disappearance of one or other species.

The 'heterogeneity' of the environment is not, however, the only factor which would tend to increase the probability of both species co-existing. The relative dispersion and movements of the two species over an area may also be important. This has been illustrated very elegantly by some experiments by Huffaker (1958) with the mite *Eotetranychus sexmaculatus* as the prey, and the predator mite, *Typhlodromus occidentalis*, in which a number of oranges, arranged in trays in a two-dimensional manifold, were used as the medium on which the prey species could develop. In all his simple universes, the inter-action did not persist for very long, either the predator or prey disappearing as in Gause's experiments with various species of Protozoa, to which we have referred. But, when in Huffaker's experiments partial barriers were included in his universe, the co-existence of the predator and prey was maintained for three successive oscillations of the system. This more complex environment, in which the partial barriers restricted the movements of the species from orange to orange arranged in a two-dimensional grid, made it less likely that the predator would be in contact with the prey at all positions simultaneously. In a stoch-astic model for this type of system it would be necessary to incorporate a spatial grid, with restricted or partially restricted movements of the individuals from cell to cell, as in the model designed by Bartlett (1957b) for studying theoretically the development of a measles epidemic in a community. In terms of the simplified models used here, the nearest approach one could make to such a system would be to consider that the fraction k of the prey popula-tion exposed to risk was not a constant, but a variable; although at first sight it is not easy to see what form of functional dependence of k on the relative numbers of the two species should be adopted in the model. Generally speaking, however, it seems likely from the results for constant k given in this section, that even in the case of variable k, provided that this variability is not too extreme, the likelihood of both species being able to co-exist would be greatly increased.

REFERENCES

BARTLETT, M. S. (1957a). On theoretical models for competitive and predatory biological systems. *Biometrika*, **44**, 27–42.

BARTLETT, M. S. (1957b). Measles periodicity and community size. *J.R. Statist. Soc.*, A, **120**, 48–70.

BARTLETT, M. S., GOWER, J. C. & LESLIE, P. H. (1960). A comparison of theoretical and empirical results for some stochastic population models. *Biometrika*, **47**, 1–11.

GAUSE, G. F. (1934). *The Struggle for Existence*. Baltimore: Williams and Wilkins.

GAUSE, G. F. (1935). Vérifications expérimentales de la théorie mathématique de la lutte pour la vie. *Actualités Sci.* no. 277, 1–61. Paris: Hermann.

HUFFAKER, C. B. (1958). Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia*, **27**, 343–83.

LESLIE, P. H. (1948). Some further notes on the use of matrices in population mathematics. *Biometrika*, **35**, 213–45.

LESLIE, P. H. (1958). A stochastic model for studying the properties of certain biological systems by numerical methods. *Biometrika*, **45**, 16–31.

LESLIE, P. H. & GOWER, J. C. (1958). The properties of a stochastic model for two competing species. *Biometrika*, **45**, 316–30.

APPENDIX I

For convenience, the bivariate distributions of N_1 and N_2 in the region of the stationary state for the three systems, to which reference has been made in the text, are given all together in this appendix. These grouped frequency distributions were tabulated by hand from the typed lists of results for each series, the marginal totals being checked by the distributions of each species (grouped in pairs of integers, 0–, 2–, 4–, 6–, etc.) recorded by the machine. It should be noted, however, in this connexion that all the variances and covariances given in the text were calculated on the machine from the individual results in each series, and not from the grouped data. They are therefore, in a sense, exact. The following were the values of the parameters used in computing the processes.

Parameter	Table 1	Table 2	Table 3
λ_1	1·2574	1·25	1·25
b_1	0·2577	0·25	0·25
α_1	0·0005148	0·001	0·001
β_1	0·0018018	0·015	0·050
λ_2	1·1892	1·25	1·25
b_2	0·2521	0·25	0·25
α_2	0·2838	0·375	0·25
k	1·0	1·0	0·20

Table 1

N_1 \ N_2	80–	90–	100–	110–	120–	130–	140–	150–	160–	170–	180–	190–	200–	210–	220–	Total
56–	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1
60–	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
64–	.	2	6	1	2	.	.	2	2	1	1	.	.	.	.	17
68–	.	1	.	3	1	3	.	3	3	.	1	.	.	.	.	15
72–	.	.	1	4	2	6	2	3	4	.	.	.	.	.	.	22
76–	.	.	3	2	7	5	4	4	4	2	1	.	2	.	.	34
80–	.	1	2	9	8	9	7	5	5	6	3	2	4	.	.	61
84–	1	2	.	8	3	11	10	7	5	6	.	3	3	1	1	61
88–	.	.	3	6	14	10	8	8	7	8	4	2	2	.	.	72
92–	.	.	1	8	7	12	8	13	14	13	5	1	1	.	1	84
96–	.	.	2	7	9	20	10	15	13	11	7	1	2	.	.	97
100–	.	.	2	2	5	13	20	13	10	4	6	2	.	2	.	79
104–	.	1	2	2	5	5	12	13	9	6	5	2	.	2	.	64
108–	.	1	.	4	3	8	14	10	6	4	.	3	.	3	.	56
112–	.	.	.	3	2	14	9	6	8	6	5	2	.	1	1	57
116–	.	.	.	1	1	2	5	5	5	3	3	2	.	.	2	29
120–	.	.	.	1	2	5	8	.	1	.	.	.	.	.	.	17
124–	.	.	.	.	1	2	3	2	4	2	1	2	1	.	.	18
128–	.	.	.	.	.	2	1	1	.	1	.	.	.	.	.	5
132–	.	.	.	.	.	1	1	1	3	1	.	.	.	.	.	7
136–	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	3
140–	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
Total	1	9	22	61	72	128	123	112	105	74	42	22	15	9	5	800

Table 2

$N_1 \backslash N_2$	0–	4–	8–	12–	16–	20–	24–	28–	32–	36–	40–	44–	48–	52–	56–	60–	64–	68–	Total
0–	·	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2
2–	·	3	2	4	2	1	1	2	·	·	·	·	·	·	·	·	·	·	12
4–	·	3	2	2	5	5	6	2	·	1	·	·	·	·	·	·	·	·	21
6–	·	·	4	4	8	3	5	6	1	·	2	1	·	·	1	·	·	·	29
8–	·	1	2	5	8	6	11	12	1	1	1	2	1	·	·	·	·	·	39
10–	·	1	1	8	16	15	3	4	4	1	5	1	2	·	·	·	1	·	69
12–	·	·	2	9	14	7	5	3	5	·	6	2	1	1	1	·	·	·	55
14–	·	1	2	4	9	8	5	7	2	3	4	·	1	·	·	2	·	·	46
16–	·	·	1	4	4	4	4	3	5	4	2	1	·	1	·	2	1	1	40
18–	·	·	·	2	·	4	1	2	3	1	2	1	·	·	1	·	·	·	26
20–	·	·	·	2	2	4	·	1	3	2	1	1	·	1	·	·	·	·	17
22–	·	·	·	·	·	2	1	1	·	2	·	·	2	·	·	·	·	·	12
24–	·	·	·	·	1	3	1	3	1	·	·	·	·	·	·	·	·	·	7
26–	·	·	·	·	·	1	1	·	·	2	·	·	·	·	·	·	·	·	7
28–	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	6
30–	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	0
32–	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	1
Total	0	10	17	44	69	64	45	46	25	17	23	9	7	3	3	4	2	1	389

Table 3

N_1 / N_2	60-	66-	72-	78-	84-	90-	96-	102-	108-	114-	120-	126-	132-	138-	144-	150-	156-	162-	168-	174-	Total
6-	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	2
8-	.	.	.	.	.	.	1	1	.	.	1	.	3	2	1	.	.	.	.	.	9
10-	.	1	.	2	.	3	2	3	3	4	3	1	.	.	1	2	.	2	.	.	27
12-	.	.	1	.	2	.	3	4	1	9	3	4	3	2	2	4	1	.	.	.	39
14-	1	3	1	.	1	4	5	5	6	5	7	6	6	8	4	1	.	1	.	.	64
16-	1	1	2	1	1	7	8	7	10	9	7	7	2	6	2	5	1	.	.	.	73
18-	.	1	.	1	1	4	9	11	10	11	8	8	11	11	4	3	2	.	.	.	97
20-	.	1	2	1	3	5	8	15	20	19	9	9	11	9	13	3	2	.	.	.	128
22-	1	.	.	.	4	4	9	16	14	17	13	11	17	16	14	1	.	2	2	.	141
24-	.	1	.	.	.	4	12	3	16	13	19	14	11	14	7	7	1	1	.	1	124
26-	.	.	.	.	1	2	9	11	10	16	10	15	15	6	7	2	1	.	.	.	110
28-	.	.	1	.	.	2	7	5	6	9	6	11	11	3	5	.	1	.	.	.	69
30-	.	.	.	.	1	2	2	5	1	4	2	9	4	7	4	.	.	.	.	.	37
32-	.	.	.	.	.	2	4	1	6	2	9	4	4	2	1	.	.	.	.	.	35
34-	.	.	.	.	.	1	.	1	4	2	7	3	2	2	.	.	.	.	1	.	23
36-	.	.	.	.	1	.	1	2	1	2	2	1	1	.	2	.	.	.	.	.	12
38-	.	.	.	.	.	.	.	.	.	1	2	1	1	.	.	.	.	.	.	.	7
40-	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	2
Total	3	8	7	5	14	40	80	90	108	123	109	105	103	91	67	28	8	6	3	1	999