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SIAM Journal on Applied Mathematics, Volume 33, Issue 2 (Sep., 1977), 256-266.

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SIAM Journal on Applied Mathematics

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PROBABILITY OF EXTINCTION IN A STOCHASTIC COMPETITION*

MARC MANGEL AND DONALD LUDWIG†

Abstract. When noise is present, the outcome of the competition between two species is no longer a deterministic function of the initial population sizes. An approximate value is given for the probability that a specified species will become extinct, conditioned on the initial population sizes. The calculation involves the asymptotic solution of the Kolmogorov backward equation. The theory is compared with Monte Carlo experiments for the case of flour beetle competition. It is also shown that the theory can be used to describe threshold fluctuations in nerves.

Introduction. The competition between two species is often represented by a pair of coupled differential equations. When the model is deterministic, the outcome of the competition can be predicted from the sizes of the initial populations. If there is a stochastic component to the competition, however, the outcome becomes a random variable. The results of the competition must then be expressed in terms of probabilities.

The experiments of Park (1954) as interpreted by Neyman, Park and Scott (1956) provide the classic example of a competition modified by stochastic factors. Leslie and Gower (1958), Bartlett, Gower and Leslie (1960) and Barnett (1962) constructed Monte-Carlo schemes to model stochastic competition. Barnett (1962), in particular, investigated the qualitative dependence of the probability that a specified species becomes extinct as a function of the initial population sizes. The present treatment offers an alternative approach through the asymptotic solution of the diffusion equation obeyed by the conditional probability.

In § 2, the Kolmogorov backward equation for this probability is given. A one dimensional example, for which the diffusion equation can be solved exactly, is presented in § 3. The solution involves the error function. This result is generalized in § 4 by means of a variation of the ray method developed by Cohen and Lewis (1967) for the solution of parabolic equations. In § 5, the "ray expansion" is simplified near the deterministic separatrix, which separates two domains of attraction. The result is a Riccati equation, which is solved in § 6. The solution is used to generate contours of equal probability in the plane. The competition between two species of flour beetle is considered in § 7. The theoretical results are compared with Monte Carlo experiments (Barnett (1962)). In § 8, the same procedure is applied to threshold fluctuations in nerve (Lecar and Nossal, (1971)). It will be shown that the method and results of Lecar and Nossal (1971) are a special case of the method presented here.

1. Noise and the dynamics of competing species: An example. The following pair of equations has been used to model competition between two species (May,

* Received by the editors March 18, 1976, and in revised form September 29, 1976.

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1973). A less symmetric system is treated in § 7.

$$(1.1) \quad \frac{dx^1}{dt} = x^1(1 + \alpha - x^1 - \alpha x^2),$$

$$(1.2) \quad \frac{dx^2}{dt} = x^2(1 + \alpha - x^2 - \alpha x^1).$$

The point $(1, 1)$ is an equilibrium of this system. When the equations are linearized around $(1, 1)$, the eigenvalues are $-1 \pm \alpha$. If $|\alpha| < 1$, then $(1, 1)$ is a stable node. If $|\alpha| > 1$, then $(1, 1)$ is a saddle point. In Fig. 1, the phase portrait for the case of a saddle point is sketched. Two trajectories lead to the saddle point. All other trajectories lead to one or the other of the two equilibrium points on the coordinate axes. The trajectories which enter the saddle point (labeled I) form the separatrix.

If the competition were deterministic, and if the process were to begin at point A, it would end at O_2 . Similarly, if it were to begin at point B, it would end at O_1 . When noise is present, however, the two population sizes will fluctuate and the separatrix might be crossed several times. We shall consider the case of Gaussian white noise.

We want to calculate the probability that a competition beginning at $P_0(x^1, x^2)$ will end at O_2 and to study the qualitative behavior of this probability as a function of P_0 . The region of major interest is the vicinity of the separatrix. Far from the separatrix, for example point C in Fig. 1, it is unlikely that noise of small intensity will affect the outcome of the competition. However, in those competitions which begin near the separatrix, noise can markedly affect the outcome, since the populations may be driven back and forth across the separatrix by the noise.

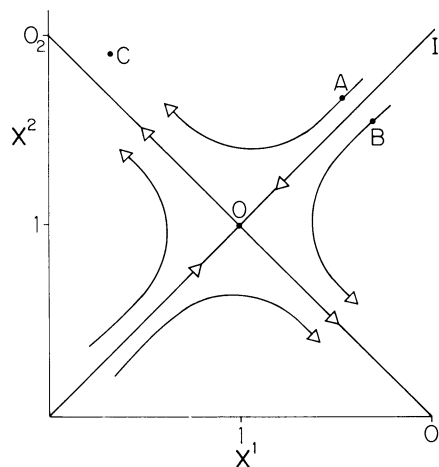


FIG. 1. A phase plane portrait of the system of equations (1.1)–(1.2). The point O is a saddle point. The trajectory labeled I is the only trajectory leading to the saddle point. All other trajectories lead to one or the other of the two equilibrium states on the coordinate axes.

2. The backward equation. Let X be the vector of population sizes. Instead of the deterministic assumption that $dX/dt = b(X)$, we assume that if $X(t) = x$, then dX is normally distributed with mean $b(x) dt$ and covariance $\varepsilon a(x) dt$. Symbolically, X will satisfy the Ito equation (Ito and McKean (1965)):

$$(2.1) \quad dX = b(x) dt + \sqrt{\varepsilon a(x)} dW.$$

The functions $b(x)$ and $\varepsilon a(x)$ are characterized by the following conditional expectations (Feller, (1971)):

$$(2.2) \quad b^i = \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} E[X^i(t + \Delta t) - X^i(t) | X^j(t) = x^j, j = 1, \dots, n],$$

$$(2.3) \quad \varepsilon a^{ij} = \lim_{\Delta t \rightarrow 0} \frac{1}{\Delta t} E[(X^i(t + \Delta t) - X^i(t))(X^j(t + \Delta t) - X^j(t)) | X^k(t) = x^k, \\ k = 1, \dots, n].$$

Transition probabilities can be associated with (2.2) and (2.3) (Feller (1971)). Let $Q_t(x, y) dy$ be the probability that $y \leq X(t) \leq y + dy$ given that $X(0) = x$. Then if $u(t, x)$ is defined by

$$(2.4) \quad u(t, x) = \int Q_t(x, y) u_0(y) dy,$$

$u(t, x)$ is the conditional expectation of $u_0(X(t))$ on the hypothesis that $X(0) = x$. In the case of competing species, $u(t; x^1, x^2)$ might be the probability that in a competition starting with x^i individuals of species i , species 1 is extinct by time t .

According to Feller (1971, p. 334) u satisfies the backward equation:

$$(2.5) \quad u_t = \frac{\varepsilon}{2} a^{ij} u_{ij} + b^i u_i.$$

We use the convention that repeated indices are summed from 1 to n . Generally, the coefficients a^{ij} and b^i will be complicated functions of x , so that (2.5) cannot be solved exactly. Our goal is to obtain time independent, approximate solutions of (2.5).

3. A simple example: Repulsion from the origin. Consider the following one dimensional model equation

$$(3.1) \quad \frac{dx}{dt} = x, \quad x(0) = x_0, \quad -1 \leq x \leq 1.$$

The process is arbitrarily stopped at $x = \pm 1$. The solution of (3.1) is:

$$(3.2) \quad x = x_0 e^t.$$

The origin is the only equilibrium of this system. It is unstable. If x_0 is known, the position of the particle at any time t can be calculated from (3.2). This process is a one dimensional analogue of the process described in § 1.

When noise is present, it is impossible to know the position of the particle exactly. Let $u(t, x)$ be the probability that a particle starting at the point x has

reached $x = 1$ by time t . If $a = 2$ then u satisfies

$$(3.3) \quad u_t = \varepsilon u_{xx} + xu_x \quad u(t, -1) = 0, \quad u(t, 1) = 1.$$

The time independent solution of (3.3) is obtained by two quadratures and is

$$(3.4) \quad u(x) = \frac{\int_{-1}^x e^{-y^2/(2\varepsilon)} dy}{\int_{-1}^1 e^{-y^2/(2\varepsilon)} dy}.$$

Thus the solution is an error function. We note that $u(0) = \frac{1}{2}$. It will be seen that this result generalizes in the two dimensional case: the value of $u(x)$ when starting at the saddle point is $\frac{1}{2}$.

4. An asymptotic solution. In this section, we begin the construction of an approximate asymptotic solution of the two dimensional backward equation

$$(4.1) \quad \frac{\varepsilon}{2} a^{ij} u_{ij} + b^i u_i = 0$$

by generalizing the result obtained in § 3. In (4.1), $u(x^1, x^2)$ is the conditional probability that the line $x^1 = 0$ is crossed before $x^2 = 0$, if the initial value of X is (x^1, x^2) . We assume that the deterministic equations $\dot{X} = b(X)$ are such that when the system is linearized about the critical point X_0 , so that $\dot{X} = B(X - X_0) + f(X)$ where f and its first partial derivatives vanish at X_0 , the matrix B has one positive and one negative real eigenvalue and that the eigenvector corresponding to the negative eigenvalue has positive slope. When these conditions are satisfied, the phase portrait of the system $\dot{X} = b(X)$ near X_0 will be similar to Fig. 1 near 0. We will obtain a local solution of (4.1) near the deterministic separatrix. We also assume that εa is positive definite on the separatrix. A nontrivial system satisfying these assumptions is studied in § 7. When ε is small, the local solution which we will construct will change rapidly as the initial point moves across the separatrix.

The result of the previous section indicates that a possible form of the solution is (using superscript n as an index on $g^n(x)$, $h^n(x)$),

$$(4.2) \quad u = \sum_{n=0} \varepsilon^n g^n(x) E(\psi(x)/\sqrt{\varepsilon}) + \varepsilon^{n+1/2} h^n(x) E'(\psi(x)/\sqrt{\varepsilon}).$$

In (4.2), $E(z) = \int_{-\infty}^z e^{-y^2/2} dy$. The second term is chosen in analogy with the asymptotic solution of diffraction problems (Ahluwalia, Lewis and Boersma (1968)). $E(z)$ satisfies the following equations:

$$(4.3) \quad E'' + zE' = 0$$

and

$$(4.4) \quad E''' + zE'' + E' = 0.$$

The functions $g^n(x)$, $h^n(x)$ and $\psi(x)$ are to be determined.

When the partial derivatives of u are evaluated, equations (4.3) and (4.4) are used to replace E'' and E''' by products of E' and $\psi/\sqrt{\varepsilon}$. After derivatives are evaluated and substituted into (4.1) terms are collected according to powers of ε .

We obtain

$$\begin{aligned}
 (4.5) \quad 0 = & \sum_{n=0} \varepsilon^{n-1/2} E'(\psi/\sqrt{\varepsilon}) (g^n - \psi h^n) \left(b^i \psi^i - \frac{a^{ij}}{2} \psi \psi_i \psi_j \right) \\
 & + \sum_{n=0} \varepsilon^n E(\psi/\sqrt{\varepsilon}) \left(b^i g_i^n + \frac{a^{ij}}{2} g_{ij}^{n-1} \right) \\
 & + \sum_{n=0} \varepsilon^{n+1/2} E'(\psi/\sqrt{\varepsilon}) \left(b^i h_i^n + a^{ij} g_i^n \psi_j + \frac{a^{ij}}{2} g^n \psi_{ij} \right. \\
 & \quad \left. - \psi a^{ij} h_i^n \psi_j + \frac{a^{ij}}{2} h_{ij}^{n-1} - \frac{a^{ij}}{2} h((\psi \psi_i)_j) \right).
 \end{aligned}$$

In (4.5), if the superscript of g^n or h^n is less than zero, that term is set equal to zero.

The leading term of the asymptotic expansion ($n = 0$) is composed of three parts. The leading term will vanish if we set

$$(4.6) \quad b^i \psi_i - \frac{a^{ij}}{2} \psi \psi_i \psi_j = 0, \quad O(\varepsilon^{-1/2}).$$

$$(4.7) \quad b^i g_i^0 = 0, \quad O(1).$$

$$(4.8) \quad b^i h_i^0 + \frac{a^{ij}}{2} g_{ij}^0 \psi_j + a^{ij} g_i^0 \psi_j - h_i^0 a^{ij} \psi \psi_j - \frac{a^{ij}}{2} h^0((\psi \psi_i)_j) = 0, \quad O(\varepsilon^{1/2}).$$

Equation (4.6) is analogous to the eikonal equation of optics (see below). Note that it is not approximate; we have not ignored any terms involving $h^n(x)$ or $g^n(x)$. Thus ψ can be determined to any order of accuracy, independent of $g^n(x)$ and $h^n(x)$. Since $b^i \partial/\partial x^i = d/dt$ equation (4.7) indicates that g^0 is constant on the separatrix. We require that $g^0 E(\infty) = 1$. Then equation (4.7) implies that g^0 is identically $1/E(\infty)$. Once g^0 and ψ are known, h^0 may be calculated by using (4.8). The terms involving g_{ij}^0 and h_{ij}^0 are absorbed by the equations for g^1 and h^1 which are similar to equations (4.7) and (4.8).

First we consider (4.6). This equation can be put into a form similar to the eikonal equation (Ludwig (1975)) by the transformation

$$(4.9) \quad \phi = -\frac{1}{2} \psi^2 \quad \text{or} \quad \phi_i = -\psi \psi_i.$$

This transformation yields

$$(4.10) \quad \frac{a^{ij}}{2} \phi_i \phi_j + b^i \phi_i = 0.$$

Equation (4.10) is analogous to (3.1.3) of Ludwig (1975). The appearance of the eikonal equation in solutions of the diffusion equation was previously noted by Cohen and Lewis (1967) and Ventsel and Freidlin (1970). The eikonal equation corresponds to a Hamiltonian

$$(4.11) \quad H(x, p) = \frac{1}{2} a^{ij} p_i p_j + b^i p_i$$

with associated Lagrangian

$$(4.12) \quad L(x) = \frac{1}{2} a_{ij} (b^i - \dot{x}^i)(b^j - \dot{x}^j),$$

where $a_{ij} = (a^{ij})^{-1}$.

According to Hamilton–Jacobi theory, $\phi(x)$ can be characterized as the minimum value of the integral of the Lagrangian, taken over all paths joining the point x and a given initial point x_0 . If x_0 is chosen to be the saddle point, then $\phi \equiv 0$ on the separatrix, since $L(x)$ will vanish identically if $\dot{x}^i = b^i$. Hence, we shall set $\psi \equiv 0$ on the separatrix. Solutions of this type will exhibit a sharp transition across the separatrix, for small ε .

The $O(1)$ term of expansion (4.2) is similar to the Fresnel integral, which appears in the theory of diffraction. The intensity of light observed in diffraction by an edge is

$$(4.13) \quad I(x) = \int_0^x e^{-(\pi/2)iy^2} dy$$

Neglecting diffraction effects, one expects light on one side of the shadow and total darkness on the other. The actual transition is given by the Fresnel integral (4.13). In the present case, the deterministic theory predicts certain extinction (darkness) for one of the species. The more exact stochastic solution is given by (4.2).

Now consider (4.8). Since $b^i = dx^i/dt$, $b^i h_i^0 = dh^0/dt$ where t indicates differentiation along the separatrix. Also $\psi = 0$ on the separatrix so that (4.8) becomes

$$(4.14) \quad \frac{dh^0}{dt} - \frac{a^{ij}}{2} h^0 \psi_i \psi_j = -\frac{a^{ij}}{2} g^0 \psi_{ij}.$$

At the saddle point, $dh^0/dt = 0$ since $b^i = 0$. Thus, at the saddle point

$$(4.15) \quad h^0 = C = g^0 a^{ij} \psi_{ij} / (a^{ij} \psi_i \psi_j).$$

The solution of (4.14) is

$$(4.16) \quad h^0 = \frac{\int_t^\infty + \frac{a^{ij}}{2} g^0 \psi_{ij} \exp \left[+ \int_t^\infty \frac{a^{ij}}{2} \psi_i \psi_j dt'' \right] dt' + C}{\exp \left[+ \int_t^\infty \frac{a^{ij}}{2} \psi_i \psi_j dt' \right]}$$

with the integration constant given by (4.15).

5. Expansion near the separatrix. The function ϕ , or ψ , is still undetermined. An approximate evaluation of ϕ is given by its expansion in the vicinity of the separatrix (Ludwig (1975)). A point near the separatrix may be written as $x = x_0 + \delta x$, where x_0 is a point on the separatrix and δx is a small distance. For points on the separatrix $\phi = \psi = 0$. In addition, since $\phi = -\frac{1}{2}\psi^2$, on the separatrix $\phi_i = 0$.

At a point in the vicinity of the separatrix, ϕ_i is expanded as

$$(5.1) \quad \phi_i(x) = \phi_{ik} \delta x^k + \frac{1}{2} \phi_{ikl} \delta x^k \delta x^l + O((\delta x)^3).$$

Similarly, $b^i(x)$ is written

$$(5.2) \quad b^i(x) = b^i(x_0) + b^i_{,k} \delta x^k + O((\delta x)^2).$$

When these expansions are substituted into (4.10) we obtain

$$(5.3) \quad \frac{a^{ij}}{2} \phi_{ik} \delta x^k \phi_{jl} \delta x^l + b^i \phi_{ik} \delta x^k + b^i_{,k} \delta x^k \phi_{il} \delta x^l + \frac{1}{2} b^i \phi_{ikl} \delta x^k \delta x^l + O((\delta x)^3) = 0.$$

After collecting powers of δx , we have

$$(5.4a) \quad b^i \phi_{ik} \delta x^k = 0.$$

$$(5.4b) \quad \left(\frac{a^{ij}}{2} \phi_{ik} \phi_{jl} + \frac{1}{2} b^i_{,k} \phi_{il} + \frac{1}{2} b^i_{,k} \phi_{ik} + \frac{1}{2} b^i \phi_{ikl} \right) \delta x^k \delta x^l = 0.$$

Since ϕ and $\nabla \phi$ are zero on the separatrix, their tangential derivatives are zero. Thus, (5.4a) is satisfied. The left hand side of (5.4b) is a quadratic form. In order to simplify notation, we introduce the matrices

$$(5.5) \quad P = (\phi_{kl}), \quad B = (b^i_{,j}), \quad A = (a^{ij}).$$

Then (5.4b) becomes

$$(5.6) \quad \frac{dP}{dt} + BP + PB^T + PAP = 0,$$

where $d/dt = b^i(\partial/\partial x^i)$ and $(\cdot)^T$ indicates the transpose.

Since the tangential derivatives of ϕ are zero, the only nonzero element of P is ϕ_{nn} , the second normal derivative. Through the introduction of local tangential and normal coordinates along the separatrix, the matrix equation (5.6) can be reduced to a simple ordinary differential equation. Let E be the unit normal dyad ($E \equiv \hat{n}\hat{n}$, where \hat{n} is the unit normal vector) and define

$$(5.7) \quad \hat{B} = E^T B E, \quad \hat{A} = E^T A E, \quad \phi_{nn} = E^T P E.$$

The matrix equation (5.6) then becomes

$$(5.8) \quad \frac{d\phi_{nn}}{dt} + \hat{B}\phi_{nn} + \phi_{nn}\hat{B}^T + \phi_{nn}^2 \hat{A} = 0.$$

Equation (5.8) is a single Riccati equation for the second normal derivative of ϕ .

6. Solution of the Riccati equation. In this section, we will solve the Riccati equation (5.8) and show how the solution can be used to generate contours of equal probability in the (x^1, x^2) plane.

Equation (5.8) is solved by introducing $z = 1/\phi_{nn}$,

$$(6.1) \quad \frac{dz}{dt} - z(\hat{B} + \hat{B}^T) = \hat{A}.$$

The solution of (6.1) is obtained by the use of an integrating factor. Then ϕ_{nn} is

$$(6.2) \quad \phi_{nn} = \frac{-\exp\left[\int_t^\infty (\hat{B} + \hat{B}^T) dt'\right]}{\int_t^\infty A \exp\left[\int_{t'}^\infty (\hat{B} + \hat{B}^T) dt''\right] dt' + c}.$$

The constant of integration is determined by the requirement that the solution be regular at the saddle point ($t = \infty$).

Since $d\phi_{nn}/dt = b^i(\partial\phi_{nn}/\partial x^i)$ and $b^i = 0$ at the saddle point, $d\phi_{nn}/dt = 0$ at the saddle point. Equation (5.8) becomes an algebraic equation for ϕ_{nn} :

$$(6.3) \quad \phi_{nn}(\hat{B} + \hat{B}^T + \phi_{nn}\hat{A}) = 0.$$

Hence the integration constant in (6.2) is given by

$$(6.4) \quad c = \frac{-\hat{A}}{\hat{B} + \hat{B}^T}.$$

Equations (6.2) and (6.4) give the solution of the matrix equation derived in § 5. These equations are used with (4.2) and (4.9) to evaluate the probability of extinction as a function of position. We write

$$\phi(x) = \frac{1}{2}\phi_{nn}(x_0)(\delta n)^2 + O((\delta n)^3).$$

To leading order of ε the approximate probability of extinction is

$$(6.5) \quad u(x) = \frac{1}{\sqrt{2\pi\varepsilon}} \int_{-\infty}^{\sqrt{-\phi_{nn}\delta n}} e^{-y^2/(2\varepsilon)} dy.$$

The probability of extinction will be constant if $\sqrt{-\phi_{nn}\delta n}$ is constant. Hence, we obtain contours of equal probability of extinction at distances proportional to $1/\sqrt{-\phi_{nn}}$.

7. Competition between flour beetles. Barnett, following the initial work of Leslie and Gower (1958) and Bartlett, Gower and Leslie (1960), used a Monte Carlo method to evaluate the outcomes of a model for the experiments of Neyman, Park and Scott. The birth (λ) and death (μ) rates of the two species, *Tribolium castaneum* and *confusum*, were modeled as

$$(7.1a) \quad \lambda_1 = .11 - .0007x^1 - .001x^2,$$

$$(7.1b) \quad \mu_1 = .01,$$

$$(7.1c) \quad \lambda_2 = .08 - .0007x^1 - .0007x^2,$$

$$(7.1d) \quad \mu_2 = .005.$$

The deterministic system corresponding to these rates is

$$(7.2) \quad \frac{dx^1}{dt} = x^1(\lambda_1 - \mu_1) = x^1(.10 - .0007x^1 - .001x^2),$$

$$(7.3) \quad \frac{dx^2}{dt} = x^2(\lambda_2 - \mu_2) = x^2(.075 - .0007x^1 - .0007x^2).$$

The system (7.2)–(7.3) has a critical point at (23.81, 83.33). The critical point is a saddle point and the system satisfies the conditions described at the beginning of § 4.

In his work, Barnett was interested in a relative measure of the length of time to extinction. Consequently, he was not concerned with the lengths of time

between successive changes in population size. On the other hand, in order to evaluate the covariance matrix defined in (2.3), we need to consider the length of time between transitions. We assume that the probability of a change in population size in $(t, t + \Delta t)$ is $\varepsilon \Delta t$, where ε is the reciprocal of the total population at the saddle point. This choice of ε corresponds to scaling the variables by the total population at the saddle. Then, following Bartlett, Gower and Leslie (1960) and Barnett (1962), the transition probabilities, conditional upon a change in population size, are

$$(7.4a) \quad \Pr \{X^1(t + \Delta t) = X^1(t) + 1, X^2(t + \Delta t) = X^2(t)\} = \frac{x^1 \lambda_1}{k}$$

$$(7.4b) \quad \Pr \{X^1(t + \Delta t) = X^1(t) - 1, X^2(t + \Delta t) = X^2(t)\} = \frac{x^1 \mu_1}{k},$$

$$(7.4c) \quad \Pr \{X^2(t + \Delta t) = X^2(t) + 1, X^1(t + \Delta t) = X^1(t)\} = \frac{x^2 \lambda_2}{k},$$

$$(7.4d) \quad \Pr \{X^2(t + \Delta t) = X^2(t) - 1, X^1(t + \Delta t) = X^1(t)\} = \frac{x^2 \mu_2}{k},$$

where

$$X^1(t) = x^1, \quad X^2(t) = x^2 \quad \text{and} \quad k = x^1(\lambda_1 + \mu_1) + x^2(\lambda_2 + \mu_2).$$

With these assumptions, the covariance (2.3) is

$$(7.5) \quad \varepsilon a = \begin{bmatrix} \frac{\varepsilon x^1(\lambda_1 + \mu_1)}{k} & 0 \\ 0 & \frac{\varepsilon x^2(\lambda_2 + \mu_2)}{k} \end{bmatrix}.$$

Integration of (6.2) was performed using a double precision Runge-Kutta routine. Contours of equal probability of extinction of the first species were calculated using the first term in the expansion (4.2). Some of these contours are shown in Fig. 2. To examine the accuracy of the theory, Monte Carlo experiments were performed on a number of test points. In Table 1, the probabilities calculated using the first term and the first two terms of expansion (4.2) are compared with those observed in the simulations.

8. Threshold fluctuations in nerve fibers. A nerve fiber stimulated with identical pulses of near threshold intensity will respond with an action potential in a fraction of all trials. Thus, there is a stochastic factor in the excitation of nerve cells (Lecar and Nossal (1971) and the references therein).

Lecar and Nossal (1971) used the V - σ , voltage-conductance, approximation to the Hodgkin-Huxley equations. In the V - σ approximation, the two slow variables of the Hodgkin-Huxley equations, n and h , are ignored. The V - σ equations have three singular points: two stable nodes (one sub-threshold and one suprathreshold) and a saddle point. The saddle point gives rise to a separatrix dividing the V - σ plane into "excited" and "resting" portions.

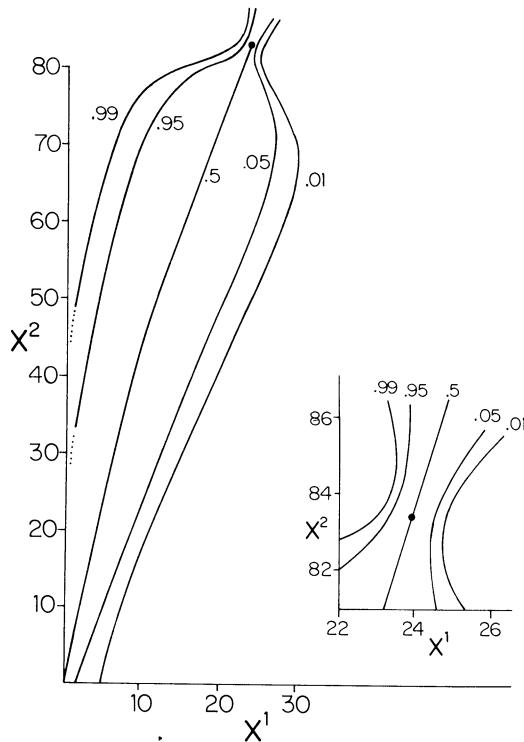


FIG. 2. A phase plane plot of some contours of equal probability of extinction of the first species for the flour beetle competition discussed in § 7

TABLE 1

A comparison of the theoretical and experimental (Monte Carlo) probabilities of extinction for the flour beetle competition described in § 7

Initial Point	Probability of extinction of the first species		
	Theoretical:		Monte Carlo*
	One term	Two terms	
(5,14)	.13	.15	.14 (1825)
(4,7.3)	.06	.06	.05 (2500)
(2,7.1)	.30	.33	.32 (2500)
(3.5,14.2)	.30	.33	.35 (1162)
(3.2,11.3)	.26	.29	.28 (1650)
(2.9,3.1)	.05	.05	.03 (595)
(3.4,5.0)	.05	.05	.04 (1909)
(1.2,4.4)	.30	.33	.34 (1767)

* Numbers in parenthesis indicate the number of Monte Carlo simulations performed.

If noise is added to the V - σ equations, the model mimics certain aspects of the fluctuation in excitability (Lecar and Nossal, 1971). They calculate the probability that the nerve will fire, conditioned on the initial displacement from threshold (Lecar and Nossal, equation (25)). The probability of firing is given by

an error function. The argument of the error function is proportional to the normal projection of the voltage displacement from the separatrix and is inversely proportional to the covariance of the fluctuating variables. Thus, their solution is analogous to (4.2) and (6.2) of this paper. In their analysis, however, only a neighborhood of the saddle point was considered, whereas the method of § 4–§ 6 applies along the entire separatrix. It can be verified that the two results are equivalent, if all of the calculations in § 4–§ 6 are performed at the saddle point.

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