THEORETICAL POPULATION BIOLOGY 5, 345–357 (1974)

A Study of Some Diffusion Models of Population Growth

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Received January 23, 1973

The stochastic differential equations of many diffusion processes which arise in studies of population growth in random environments can be transformed, if the Stratonovich stochastic calculus is employed, to the equation of the Wiener process. If the transformation function has certain properties then the transition probability density function and quantities relating to the time to first attain a given population size can be obtained from the known results for the Wiener process. Some other random growth processes can be derived from the Ornstein–Uhlenbeck process. These transformation methods are applied to the random processes of Malthusian growth, Pearl–Verhulst logistic growth and a recent model of density independent growth due to Levins.

1. INTRODUCTION

In order to study the growth of populations under fluctuating conditions, the differential equation satisfied by the continuous approximation to the population size, as a function of time, may be converted to a stochastic differential equation by considering a growth rate or any other parameter to be a random process. If $N(t)$ is the random process, representing the size of the population, generated by randomization of the parameter $n(t)$, then the stochastic equation satisfied by $N(t)$ is often of the form

$$dN(t)/dt = f(N(t)) + g(N(t))\, n(t). \tag{1}$$

Having established a stochastic equation for the growth of the population, one is then primarily interested in determining the transition probability density function (pdf), defined through

$$p(N, t \mid N_0)\, dN = \Pr\{N < N(t) \leqslant N + dN \mid N(0) = N_0\}, \tag{2}$$

whenever this quantity affords a complete description of the process. From the transition pdf one can calculate the mathematical expectation and variance of the population size at various times and also the probability of ultimate extinction. We will only be concerned in this paper with populations whose stochastic equations are of the form of (1).

In the study of population growth in random environments it is usually assumed that the quantity $n(t) = w(t)$, a stationary, delta-correlated, Gaussian process (white noise); for then, if $f(N)$ and $g(N)$ in (1) satisfy a uniform Lipschitz condition in N and there exists a constant C such that

$$|f(N)| \leqslant C(1 + N^2)^{1/2},$$
$$0 \leqslant g(N) \leqslant C(1 + N^2)^{1/2}, \tag{3}$$

then it has been shown (Doob, 1953; Jaswinski, 1970) that $N(t)$ is mean-square continuous and Markov so that $p(N, t \mid N_0)$ does provide a complete description of the process. (We also note that a monotonic function of a Markov process is Markov (Gihman and Skorohod, 1972)). Furthermore $N(t)$ is a diffusion process because its transition pdf satisfies the (forward) Kolmogorov equation

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial N}[K(N)p] + \frac{\sigma^2}{2}\frac{\partial^2}{\partial N^2}[g(N)^2 p], \tag{4}$$

where σ^2 is the variance parameter of $w(t)$.

A problem arises, however, in that the drift term, $K(N)$, depends upon the rules employed for the integration of the original stochastic differential equation. Of the two methods of integration, the Ito and Stratonovich calculi, the latter is generally held (Gray and Caughey, 1965; Jaswinski, 1970; Wonham, 1970; but see also Mortensen, 1969) to be more appropriate for the integration of equations which model random processes occurring in 'physical' problems. We will adopt this approach here so that the first infinitesimal moment is given by (Stratonovich, 1963)

$$K(N) = f(N) + \mu g(N) + (1/2)\,\sigma^2 g(N)\,g'(N), \tag{5}$$

where μ is the mean value of $w(t)$.

It can be seen, even for quite simple functions $f(N)$ and $g(N)$, that the Kolmogorov equation, obtained when (5) is substituted in (4), may appear quite difficult to solve analytically. However, we will see that in many cases there exists a simple integral transformation which will give rise to one of the two well-known processes, the Wiener process (WP) and the Ornstein–Uhlenbeck process (OUP). This will enable us to obtain $p(N, t \mid N_0)$ in closed form.

2. The Transformation Method

A. Transformed Wiener Processes

Suppose $f(N) = 0$, so that Eq. (1), with $n(t) = w(t)$, becomes simply

$$dN(t)/dt = g(N(t))\, w(t). \tag{6}$$

The transformation

$$Y(N) = \int^{N} g(N')^{-1}\, dN', \tag{7}$$

previously utilized by Lax (1966), yields a random process satisfying

$$dY(t)/dt = w(t), \tag{8}$$

providing the integral in (7) exists. Ordinary integration rules apply because we are using the Stratonovich calculus. Equation (8) is the stochastic equation satisfied by the Wiener process. Suppose further that $N(t) \in (N_1, N_2)$ and that the function $Y(N)$ has range $(-\infty, \infty)$. Then the transition pdf of $Y(t)$ for an initial value Y_0 is

$$p_y(Y, t \mid Y_0) = \frac{1}{(2\pi\sigma^2 t)^{1/2}} \exp\left[\frac{-(Y - Y_0 - \mu t)^2}{2\sigma^2 t}\right]. \tag{9}$$

Now, providing the function defined by (7) is strictly monotonic and has a continuous nonzero derivative on (N_1, N_2), the transition pdf of $N(t)$ is immediately found to be

$$p(N, t \mid N_0) = \frac{|g(N)|^{-1}}{(2\pi\sigma^2 t)^{1/2}} \exp\left[\frac{-\left(\int_{N_0}^{N} g(N')^{-1} dN' - \mu t\right)^2}{2\sigma^2 t}\right]. \tag{10}$$

The boundaries $+\infty$ and $-\infty$ of the Wiener process are natural in the sense of Feller (1952). The above transformation preserves the nature of the boundaries so that N_1 and N_2 are natural boundaries for the process $N(t)$; this means that there is zero probability that they will be reached in a finite time.

Since the function $Y(N)$ is strictly monotonic we can also easily find the probability density function of the time of first passage T, of the process $N(t)$ to a value $N^* \in (N_1, N_2)$, given an initial value N_0. Using the known result for the Wiener process (Cox and Miller, 1965) gives the following expression for this density:

$$\phi(N^*, t \mid N_0) = \frac{\left|\int_{N_0}^{N^*} g(N')^{-1} dN'\right|}{(2\pi\sigma^2 t^3)^{1/2}} \exp\left[\frac{-\left(\int_{N_0}^{N^*} g(N')^{-1} dN' - \mu t\right)^2}{2\sigma^2 t}\right]. \tag{11}$$

The mean and variance of T together with the probability that a given value N^* will ever be reached can also be obtained from the known results for the WP.

B. *Transformed Ornstein–Uhlenbeck Processes*

If the function $f(N)$ has the special form indicated by the equation,

$$\frac{dN(t)}{dt} = g(N(t))\left[w(t) - \beta \int^{N(t)} g(N^1)^{-1} dN^1\right], \qquad \beta > 0, \tag{12}$$

then the change of variable (7) yields a process satisfying

$$dY(t)/dt = -\beta Y(t) + w(t). \tag{13}$$

This is the stochastic differential equation of the OUP. Using the known transition pdf for this process (on the whole real line) and making the same assumptions about (7) as we did for transformations of the WP, we find (Uhlenbeck and Ornstein, 1930) that the transition pdf of $N(t)$ is

$$p(N, t \mid N_0) = \frac{e^{\beta t} \mid g(N)\mid^{-1}}{(\pi\sigma^2(e^{2\beta t} - 1)/\beta)^{1/2}} \times \exp\left[\frac{-\left(e^{\beta t}\int^N g^{-1} dN' - \int^{N_0} g^{-1} dN' - \mu \int_0^t e^{\beta t'} dt'\right)^2}{\sigma^2(e^{2\beta t} - 1)/\beta}\right] \tag{14}$$

where $\int g^{-1} dN'$ has been used as an abbreviation for $\int g(N')^{-1} dN'$.

Since the boundaries $+\infty$ and $-\infty$ are natural for the OUP we again find that the boundaries N_1 and N_2 are natural for the process $N(t)$. If, however, either $Y(N_1)$ or $Y(N_2)$ is finite, then the corresponding boundary points for both $Y(t)$ and $N(t)$ will be regular. At such a boundary various boundary conditions may be imposed such as those for absorbing or reflecting barriers. In particular, suppose that $Y(N) \in [0, \infty)$ and that the origin is regarded as an absorbing barrier. Providing $\mu = 0$ we can still obtain a closed form expression for the transition pdf of $N(t)$:

$$p(N, t \mid N_0) = \frac{e^{\beta t} \mid g(N)\mid^{-1}}{(\pi\sigma^2(e^{2\beta t} - 1)/\beta)^{1/2}} \left\{\exp\left[\frac{-\left(e^{\beta t}\int^N g^{-1} dN' - \int^{N_0} g^{-1} dN'\right)^2}{\sigma^2(e^{2\beta t} - 1)/\beta}\right] - \exp\left[\frac{-\left(e^{\beta t}\int^N g^{-1} dN' + \int^{N_0} g^{-1} dN'\right)^2}{\sigma^2(e^{2\beta t} - 1)/\beta}\right]\right\}. \tag{15}$$

3. Application to Models of Population Growth

1. *Malthusian Growth*

This example of a stochastic growth process is included, even though it has been much studied (Gray and Caughey, 1965; Lewontin and Cohen, 1969; Goel, Maitra and Montroll, 1971; Capocelli and Ricciardi, 1974), because it provides a simple demonstration of the above transformation method. The stochastic differential equation is simply

$$dN(t)/dt = r(t)\,N(t), \qquad N_0 \in (0, \infty). \tag{16}$$

If $r(t)$, the random growth rate, is a white noise, then $N(t)$ is a diffusion process and the transformed variable, obtained from (7), is $Y(t) = \log N(t)$, which is a WP on $(-\infty, \infty)$. Thus from (10) we find that the transition pdf of $N(t)$ is

$$p(N, t \mid N_0) = \frac{N^{-1}}{(2\pi\sigma^2 t)^{1/2}} \exp\left[\frac{-\left(\log \dfrac{N}{N_0} - \mu t\right)^2}{2\sigma^2 t}\right], \qquad N > 0. \tag{17}$$

The mathematical expectation of the population size at time t is

$$E(N(t)) = N_0 e^{(\mu+\sigma^2/2)t}, \tag{18}$$

and its variance is

$$\mathrm{Var}(N(t)) = N_0^2 e^{2\mu t} e^{\sigma^2 t}(e^{\sigma^2 t} - 1). \tag{19}$$

On calculating the value of $\Pr\{N(t) > N_1\}$, where $0 < N_1 < \infty$, we find that the probability of ultimate extinction is unity if $\mu < 0$, zero when $\mu > 0$, and $\frac{1}{2}$ if $\mu = 0$. These results support the view that the Stratonovich calculus leads to more meaningful results in a 'physical' problem than the Ito calculus. The latter, when applied to the stochastic equation (16), indicates that populations may go extinct with probability one even for certain positive values of the mean growth rate μ. We note, finally, that as $t \to \infty$, $N(t)$ does not possess a stationary distribution; the probability density function accumulates either at arbitrarily small values of N ($\mu < 0$) or arbitrarily large values ($\mu > 0$) or both ($\mu = 0$).

2. *Pearl–Verhulst Logistic Growth*

When, as is usually the case, there are factors which limit the population size, the simplest model is provided by the equation

$$dN(t)/dt = r(t)\,N(t)\,(1 - N(t)/K), \qquad N_0 \in (0, K), \tag{20}$$

where K, a positive constant, is called the carrying capacity. As a stochastic differential equation, (20) has been studied by Levins (1969) but the transition pdf was not obtained explicitly. May (1973) has studied a version of this equation, regarding K as a random process, with a view to determining the limiting distribution of $N(t)$.

Applying the transformation (7) again yields a WP on $(-\infty, \infty)$, and since the assumptions of Section 2 are satisfied by the function

$$Y(N) = \int^{N} [N'(1 - N'/K)]^{-1}\, dN' \tag{21}$$

we have, from (10), for $0 < N < K$,

$$p(N, t \mid N_0) = \frac{KN^{-1}(K - N)^{-1}}{(2\pi\sigma^2 t)^{1/2}} \exp\left[\frac{-\left(\log\left\{\dfrac{N(K - N_0)}{N_0(K - N)}\right\} - \mu t\right)^2}{2\sigma^2 t}\right], \tag{22}$$

with $p(N, t \mid N_0)$ vanishing at the natural boundaries, $N = 0$ and $N = K$. Again the process does not attain a proper stationary distribution as $t \to \infty$.

The mathematical expectation and variance of $N(t)$ have not been found in closed form. However, series expansions for these quantities can be obtained by the use of Taylor series over the appropriate ranges of convergence. Thus we find that the integral

$$E(N(t)) = \frac{K}{(2\pi\sigma^2 t)^{1/2}} \int_{-\infty}^{\infty} (1 + e^{-y})^{-1} \exp\left[\frac{-(y - y_0 - \mu t)^2}{2\sigma^2 t}\right] dy \tag{23}$$

where $y_0 = \log[N_0/(K - N_0)]$, can be computed from the series

$$E(N(t)) = \frac{K}{2} \sum_{k=0}^{\infty} (-)^k \left\{\left[1 - \Phi\left(\frac{bk}{2} - \frac{a}{b}\right)\right] \exp\left[k\left(\frac{b^2 k}{4} - a\right)\right] + \left[1 - \Phi\left(\frac{b(k+1)}{2} + \frac{a}{b}\right)\right] \exp\left[(k+1)\left(\frac{b^2(k+1)}{4} + a\right)\right]\right\}. \tag{24}$$

In this formula $a = \log[N_0/(K - N_0)] + \mu t$, $b = (2\sigma^2 t)^{1/2}$ and

$$\Phi(x) = \frac{2}{\pi^{1/2}} \int_0^x e^{-Z^2} dZ. \tag{25}$$

Similarly the variance can be computed from (24) and the series

$$E(N(t)^2) = \frac{K^2}{2} \sum_{k=0}^{\infty} (-)^k (1 + k) \left\{\left[1 - \Phi\left(\frac{bk}{2} - \frac{a}{b}\right)\right] \exp\left[k\left(\frac{b^2 k}{4} - a\right)\right] + \left[1 - \Phi\left(\frac{b(k+2)}{2} + \frac{a}{b}\right)\right] \exp\left[(k+2)\left(\frac{b^2(k+2)}{4} + a\right)\right]\right\}. \tag{26}$$

To obtain some insight into the long term behavior of the population described by the random process $N(t)$ satisfying the stochastic equation (20), we examine the quantity

$$\Pr\{N_1 < N(t) \leqslant N_2 \mid N(0) = N_0\} = \int_{N_1}^{N_2} p(N, t \mid N_0)\, dN$$

$$= \mathcal{N}\left(\frac{\log\left\{\frac{N_2(K-N_0)}{N_0(K-N_2)}\right\} - \mu t}{(\sigma^2 t)^{1/2}}\right) - \mathcal{N}\left(\frac{\log\left\{\frac{N_1(K-N_0)}{N_0(K-N_1)}\right\} - \mu t}{(\sigma^2 t)^{1/2}}\right) \quad (27)$$

where $\mathcal{N}(x)$ is the normal distribution function. From this formula we see that $\Pr\{N(t) > N_1\}$ approaches zero as $t \to \infty$ if $\mu < 0$; approaches unity if $\mu > 0$; and approaches $\frac{1}{2}$ if $\mu = 0$. Thus if the intrinsic growth rate, $r(t)$, is positive, on average, then the probability of extinction is zero whereas if that quantity is negative, on average, extinction occurs with probability one. The pdf of $N(t)$ accumulates near either the right or left end of the interval $(0, K)$. This phenomenon is the same as found by Kimura (1954, 1964) in the effect of random fluctuations in selection coefficient on gene frequency distributions. In fact we note that (20) is the same, if we put $X = N/K$, as the stochastic equation satisfied by the (random) gene frequency $X(t)$ in the case of no dominance, a problem recently treated by Gillespie (1972). We intend to discuss the applications of the methods of this paper to problems in population genetics in another publication.

The remarks of the last paragraph concerning the probability of extinction and the qualitative long term behavior of the transition pdf actually apply to random growth processes restricted to the interval $(0, K)$ and obeying the general stochastic equation

$$\frac{dN(t)}{dt} = r(t)N(t)^m \left(1 - \frac{N(t)}{K}\right)^n, \qquad N_0 \in (0, K), \quad (28)$$

where $m \geqslant 1$ and $n \geqslant 1$ are positive integers. When $m = 1$, for example, the transformed process, obtained from (7),

$$Y(N) = \log \frac{N}{K-N} + \sum_{i=1}^{n-1} \binom{n-1}{i} i^{-1} \left(\frac{N}{K-N}\right)^i, \quad (29)$$

is a Wiener process on $(-\infty, \infty)$. We continue our discussion, however, of the logistic process (20).

It is interesting to consider the long term behavior of the process $N(t)$ satisfying (20) when the Ito calculus is used, even though the resulting Kolmogorov equation has not been solved analytically. We can, nevertheless, answer questions about the long term behavior of the process using the following argument.

Providing N_0 and N are much smaller than K, the logistic process approximates the Malthusian random process. Then the transition pdf for the (Ito) logistic random process is approximately the same as the (Ito) transition pdf of the random Malthusian process. The conclusion to be drawn is that a population satisfying (20) with N_0 small will go extinct with probability one if $\mu < \frac{1}{2}\sigma^2$.

As pointed out already, the first passage time pdf is given by the expression (11) where we now put $g(N) = N(1 - N/K)$. Furthermore, the mean and variance of T are known (Cox and Miller, 1965):

$$E(T) = \frac{1}{\mu} \log \left[\frac{N^*(K - N_0)}{N_0(K - N^*)}\right], \tag{30}$$

$$\mathrm{Var}(T) = \frac{\sigma^2}{2\mu^3} \log \left[\frac{N^*(K - N_0)}{N_0(K - N^*)}\right], \tag{31}$$

where $0 < N_0 < N^* < K$ and $\mu > 0$. One can also calculate the probability, $\Pi(N^*)$, that the population ever attains the size N^*, from

$$\Pi(N^*) = \begin{cases} 1, & \text{if } \mu \geqslant 0, \\ \left[\dfrac{N^*(K - N_0)}{N_0(K - N^*)}\right]^{2\mu/\sigma^2}, & \text{if } \mu < 0. \end{cases} \tag{32}$$

TABLE I

Calculated Values of $E(T)$, $\mathrm{Var}(T)$, $\Pi(N^*)$ and Pr{Ext.} for the Logistic Random Growth Process when $K = 1000$, $\sigma^2 = |\mu|$, and $N_0 = 1$[a]

	$E(T)$	$\mathrm{Var}(T)$	$\Pi(N^*)$	Pr{Ext.}
$\mu = +1$, $N^* = .5K$	6.91 (4.60)	3.45 (2.30)	1	0
$\mu = -1$, $N^* = .5K$	—	—	1.0×10^{-6} (1.0×10^{-4})	1
$\mu = +1$, $N^* = .9K$	9.10 (6.79)	4.55 (3.40)	1	0
$\mu = -1$, $N^* = .9K$	—	—	1.2×10^{-8} (1.3×10^{-6})	1

[a] Figures in parentheses are for $N_0 = 10$ when these quantities are different from those for $N_0 = 1$. No entry indicates that the quantity does not exist.

TABLE II

The Same Quantities as in Table I with $K = 10^6$, $\sigma^2 = |\mu|$, and $N_0 = 1(10)$

	$E(T)$	$\mathrm{Var}(T)$	$\Pi(N^*)$	Pr{Ext.}
$\mu = +1$, $N^* = .5K$	13.82 (11.51)	6.91 (5.76)	1	0
$\mu = -1$, $N^* = .5K$	—	—	1.0×10^{-12} (1.0×10^{-10})	1
$\mu = +1$, $N^* = .9K$	16.01 (13.71)	8.01 (6.86)	1	0
$\mu = -1$, $N^* = .9K$	—	—	1.2×10^{-14} (1.2×10^{-12})	1

TABLE III

The Same Quantities as in Table I with $K = 1000$, $\sigma^2 = 10|\mu|$, and $N_0 = 1(10)$

	$E(T)$	$\mathrm{Var}(T)$	$\Pi(N^*)$	Pr{Ext.}
$\mu = +1$, $N^* = .5K$	6.91 (4.60)	34.53 (22.98)	1	0
$\mu = -1$, $N^* = .5K$	—	—	.25 (.40)	1
$\mu = +1$, $N^* = .9K$	9.10 (6.79)	45.52 (33.96)	1	0
$\mu = -1$, $N^* = .9K$	—	—	.16 (.26)	1

In Tables I–IV we show the calculated values of $E(T)$, $\mathrm{Var}(T)$, (when they exist), $\Pi(N^*)$, and the probability of ultimate extinction, Pr{Ext.}, for selected and representative values of K, μ, σ^2, N^* and N_0. The following points are supported by a study of the calculated values.

(a) The mean and variance of the time of first reaching a given *fraction* of the carrying capacity is an increasing function of the carrying capacity, for given μ,

TABLE IV

The Same Quantities as in Table I with $K = 10^6$, $\sigma^2 = 10 \mid \mu \mid$, and $N_0 = 1(10)$

	$E(T)$	$\mathrm{Var}(T)$	$\Pi(N^*)$	Pr{Ext.}
$\mu = +1$, $N^* = .5K$	13.82 (11.51)	69.08 (57.56)	1	0
$\mu = -1$, $N^* = .5K$	—	—	.06 (.10)	1
$\mu = +1$, $N^* = .9K$	16.01 (13.71)	80.06 (68.55)	1	0
$\mu = -1$, $N^* = .9K$	—	—	.04 .06	1

σ^2 and N_0 when μ is positive. Similarly, when μ is negative, the probability that the population ever reaches a given *fraction* of the carrying capacity is a decreasing function of the carrying capacity.

(b) For a given carrying capacity and a negative mean growth rate, the increase in the probability of ever reaching a given population size effected by increasing the initial population size is a decreasing function of $\sigma^2/\mid \mu \mid$. That is, the more variable the growth rate for a given mean, the less is the benefit derived from having a larger initial population size.

(c) When μ is negative the probability of ever reaching population sizes which are large relative to the carrying capacity may be quite large when σ^2 is large. One infers that an observation on a real population whose growth rate is fluctuating may yield a result quite close to the carrying capacity even though the population will ultimately become extinct with probability one.

3. *A Model of Malthusian Growth with Random Deaths*

Levins (1969) has considered the stochastic equation

$$dN(t)/dt = rN(t) + \epsilon(t)\,(N(t))^{1/2}, \qquad N_0 \in (0, \infty), \tag{33}$$

where $\epsilon(t)$ is a random process with zero mean and variance parameter $v(1 - v)$, v being the mean viability. The second term in (33) represents the random sampling in the deaths of the adults and in this study this is assumed to be the only source of variability. Thus, regarding r as a constant and $\epsilon(t)$ as a white noise, we can show that $N(t)$ is a Markov process. Furthermore it is related to the

OUP because Eq. (33) is of the same form as (12) if $r < 0$. In fact, as observed by Levins, the transformed process $Y = 2N^{1/2}$ satisfies the equation

$$dY(t)/dt = \tfrac{1}{2}rY(t) + \epsilon(t). \tag{34}$$

If r is negative the classical OUP is obtained. In the general case we find that the transition pdf of $N(t)$ is given by

$$p(N, t \mid N_0) = \frac{N^{-1/2}\, e^{-1/2rt}}{\left(2\pi\sigma_v^2 \left(\frac{1 - e^{-rt}}{r}\right)\right)^{1/2}} \left\{ \exp\left[\frac{-2(\sqrt{N}\, e^{-1/2rt} - \sqrt{N_0})^2}{\sigma_v^2 \left(\frac{1 - e^{-rt}}{r}\right)}\right] - \exp\left[\frac{-2(N^{1/2}e^{-1/2rt} + N_0^{1/2})^2}{\sigma_v^2 \left(\frac{1 - e^{-rt}}{r}\right)}\right]\right\}, \tag{35}$$

where $\sigma_v^2 = v(1 - v)$. The origin ($N = 0$) must be regarded as an absorbing barrier because a population which reaches zero must stay there. Hence we have used expression (15) and $p(0, t \mid N_0) = 0$.

As $t \to \infty$ the function defined by (35) vanishes for all finite N and hence no stationary distribution exists, regardless of the sign or absolute magnitude of r. We find that the mathematical expectation of the population size at time t is

$$\begin{aligned} E(N(t)) &= \int_0^\infty Np(N, t \mid N_0)\, dN \\ &= \sigma_v \exp\left\{\frac{-2N_0 r}{\sigma_v^2(1 - e^{-rt})}\right\} \left(\frac{N_0 e^{rt}(e^{rt} - 1)}{2\pi r}\right)^{1/2} \\ &\quad + \left\{N_0 e^{rt} + \frac{\sigma_v^2}{4}\left(\frac{e^{rt} - 1}{r}\right)\right\} \Phi\left(\left(\frac{2N_0 r}{\sigma_v^2(1 - e^{-rt})}\right)^{1/2}\right). \end{aligned} \tag{36}$$

Note that this result is different from that of Levins (1969) who has neglected to treat the origin as absorbing and regarded $Y(t)$ as a process on $(-\infty, \infty)$ instead of $[0, \infty)$. We see from (36) that when $r > 0$, $E(N(t)) \to \infty$ as $t \to \infty$ whereas when $r < 0$, $E(N(t)) \to 0$. When $r = 0$ the asymptotic behavior of (36) is

$$E(N(t)) \underset{t\to\infty}{\sim} \sigma_v (2N_0 t/\pi)^{1/2}, \tag{37}$$

which indicates that in this model the expected population size becomes infinite as $t \to \infty$ when the deterministic part of the process is absent.

To further understand the nature of the process satisfying the stochastic equation (33) we calculate the probability that at time t the population size is between prescribed limits. Such an analysis leads to the result that

$$\Pr\{N(t) > N_1 \mid N(0) = N_0\} = \mathcal{N}\left(\frac{2(k_t N_1^{1/2} + N_0^{1/2})}{V_t^{1/2}}\right) - \mathcal{N}\left(\frac{2(k_t N_1^{1/2} - N_0^{1/2})}{V_t^{1/2}}\right) \tag{38}$$

where $N_1 \in (0, \infty)$ and we have put

$$k_t = e^{-1/2rt}; \qquad V_t = \frac{\sigma_v^2(1 - e^{-rt})}{r}. \tag{39}$$

When $r < 0$ the right side of (38) approaches zero as $t \to \infty$ and we conclude that

$$\Pr\{\text{Ultimate Extinction}\} = 1. \tag{40}$$

When $r \geqslant 0$ we find

$$\Pr\{\text{Ultimate Extinction}\} = 2\mathcal{N}\left(\frac{-2(N_0 r)^{1/2}}{\sigma_v}\right), \tag{41}$$

which is, as might be expected, a decreasing function of N_0 and r. To understand the results (40) and (41) we observe that when $r < 0$ the process is directed towards the origin which is absorbing; hence, ultimately, all populations end up going extinct. When $r > 0$ the process is directed towards large values of the population size but many sample paths end up at zero which is still an absorbing state. Hence the probability of extinction is between zero and one and the larger the initial population size and/or the value of r, the less is the influence exerted by the absorbing barrier at zero population level.

From Eq. (41), setting $N_0 = 1$ and assuming σ_v^2 attains its maximum value of $\frac{1}{4}$ (thus giving the greatest probability of extinction for given values of N_0 and r) we find that the probability of ultimate survival of the population is greater than .9 whenever the growth rate r is greater than the moderately small value of (approximately) 0.17. Finally, we note that when $r = 0$ extinction is certain even though the mathematical expectation of the population size becomes infinite as $t \to \infty$. This phenomenon has been observed previously by Lewontin and Cohen (1969) in their study of the Malthusian random growth process.

Acknowledgments

The author is grateful to Professor L. M. Ricciardi for his help and guidance throughout this work; to Professors J. D. Cowan, R. C. Lewontin, M. Slatkin, and Mr. C. E. Smith for useful discussions and references. Valuable comments from the referee are also appreciated and financial support from an Alfred. P. Sloan Fellowship is acknowledged.

REFERENCES

CAPOCELLI, R. M., AND RICCIARDI, L. M. 1974. A diffusion model for population growth in random environment, *Theor. Pop. Biol.* **5**, in press.

COX, D. R., AND MILLER, H. D. 1965. "The Theory of Stochastic Processes," Wiley, New York.

DOOB, J. L. 1953. "Stochastic Processes," Wiley, New York, London, Sydney.

FELLER, W. 1952. The parabolic differential equations and the associated semigroups of transformations, *Ann. Math.* **55**, 468–519.

GIHMAN, I. I., AND SKOROHOD, A. V. 1972. "Stochastic Differential Equations," Springer–Verlag, New York, Heidelberg, Berlin.

GILLESPIE, J. H. 1972. The effects of stochastic environments on allele frequencies in natural populations, *Theor. Pop. Biol.* **3**, 241–248.

GOEL, N. C., MAITRA, S. C., AND MONTROLL, E. W. 1971. On the Volterra and other non linear models of interacting populations, *Rev. Mod. Phys.* **43**, 231–276.

GRAY, A. H., AND CAUGHEY, T. K. 1965. A controversy in problems involving random parametric excitation, *J. Math. and Phys.* **44**, 288–296.

JASWINSKI, A. H. 1970. "Stochastic processes and Filtering Theory," Academic Press, New York.

KIMURA, M. 1954. Process leading to quasifixation of genes in natural populations due to random fluctuation of selection intensities, *Genetics* **39**, 280–295.

KIMURA, M. 1964. Diffusion models in population genetics, *J. Appl. Prob.* **1**, 177–232.

LAX, M. 1966. Classical Noise IV: Langevin Methods, *Rev. Mod. Phys.* **38**, 541–566.

LEVINS, R. 1969. The effect of random variations of different types on population growth, *Proc. Nat. Acad. Sci.* **62**, 1061–1065.

LEWONTIN, R. C., AND COHEN, D. 1969. On population growth in a randomly varying environment, *Proc. Nat. Acad. Sci.* **62**, 1056–1060.

MAY, R. M. 1973. "Stability and Complexity in Model Ecosystems," Princeton University Press, Princeton, New Jersey.

MORTENSEN, R. E. 1969. Mathematical problems of modeling stochastic nonlinear dynamic systems, *J. Stat. Phys.* **1**, 271–296.

STRATONOVICH, R. L. 1963. "Topics in the theory of random noise," Vol. 1, Gordon and Breach, New York, London.

UHLENBECK, G. E., AND ORNSTEIN, L. S. 1930. On the theory of Brownian motion, *Phys. Rev.* **36**, 823–841.

WONHAM, W. M. 1970. Random Differential Equations in Control Theory, in "Probabilistic Methods in Applied Mathematics," Vol. 2, (A. T. Bharucha-Reid, Ed.), Academic Press, New York and London.