

Extinction dynamics of age-structured populations in a fluctuating environment

(demography/ecology/life history/stochastic model/diffusion process)

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ABSTRACT We model density-independent growth of an age- (or stage-) structured population, assuming that mortality and reproductive rates fluctuate as stationary time series. Analytical formulas are derived for the distribution of time to extinction and the cumulative probability of extinction before a certain time, which are determined by the initial age distribution, and by the infinitesimal mean and variance, μ and σ^2 , of a diffusion approximation for the logarithm of total population size. These parameters can be estimated from the average life history and the pattern of environmental fluctuations in the vital rates. We also show that the distribution of time to extinction (conditional on the event) depends on the magnitude but not the sign of μ . When the environmental fluctuations in vital rates are small or moderate, the diffusion approximation gives accurate estimates of cumulative extinction probabilities obtained from computer simulations.

The theory of extinction times for single populations has applications in diverse fields, including paleontology, island biogeography, community ecology, and conservation biology. Various analytical models have been constructed to estimate extinction times, probabilities of extinction, or both for a population subject to stochastic variation in demographic parameters (e.g., refs. 1–7). Two sources of random variation in population growth can be distinguished: first, demographic stochasticity caused by finite population size, in which each individual independently experiences age-specific probabilities of survival and reproduction; and second, environmental stochasticity, which affects the vital rates of all individuals similarly. Demographic stochasticity is important only in small populations, since chance variation in vital rates among individuals tends to average out in large populations (greater than about 100 individuals), whereas environmental factors can produce substantial fluctuations in demographic parameters in populations of any size. In natural populations subject to substantial abiotic and biotic perturbations, environmental stochasticity is usually far more important than demographic stochasticity in causing extinction (6, 7). Previous analytical models of stochastic population growth and extinction either lacked age structure or dealt only with demographic stochasticity (1–7).

Here we analyze the extinction dynamics of a population subject to environmental fluctuations in age-specific birth and death rates. The theory of population growth developed by Cohen (8, 9) and Tuljapurkar and Orzack (10, 11) is used to derive a diffusion approximation for the logarithm of total population size in a population subject to density-independent fluctuations in vital rates.

THE MODEL

Assumptions. A standard model of density-independent growth in an age- (or stage-) structured population specifies

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a recursion formula for the numbers of individuals in each age class or developmental stage at time $t + 1$ in terms of those at the previous time t ,

$$\mathbf{n}(t + 1) = \mathbf{A}(t)\mathbf{n}(t), \quad [1]$$

where $\mathbf{n}(t)$ is a column vector with entries representing the numbers of (female) individuals of each type at time t and $\mathbf{A}(t)$ is a square projection matrix with nonnegative entries $A_{ij}(t)$ that determine the number of individuals of type i produced at time $t + 1$ per individual of type j at time t . For an age-structured population, $\mathbf{A}(t)$ is the familiar Leslie matrix with age-specific fecundity rates in the top row, age-specific survival probabilities along the subdiagonal, and zeros elsewhere (12, 13). We assume that the projection matrices change with time such that each of the entries, or vital rates, compose a stationary time series.

Under a mild assumption on the life history (nonperiodic fertilities), regardless of the initial population vector $\mathbf{n}(0)$, the probability distribution of the natural logarithm of total population size asymptotically approaches a normal distribution (2, 10, 14). For most life histories the rate of approach to normality will be sufficiently fast that even for short times the changes in logarithmic population size can be accurately approximated as a diffusion process with constant infinitesimal mean μ and infinitesimal variance σ^2 (10).

Initial Age Distribution. The initial age distribution can have a substantial effect on extinction probabilities because individuals of different ages contribute unequally to future population growth. The influence of the initial age distribution can be approximated in the following manner. Consider a sample path of the stochastic process from time 0 to time t , expressed as a product of t projection matrices (Eq. 1). Standard demographic reasoning applied to the stochastic case (e.g., ref. 15, page 51) indicates that asymptotically

$$\mathbf{n}(t) \approx R(0, t)(\mathbf{v}(0) \cdot \mathbf{n}(0))\mathbf{u}(t), \quad [2]$$

where $R(0, t)$ is a scalar representing the growth of the matrix product and $\mathbf{v}(0)$ and $\mathbf{u}(t)$ are the dominant left and right eigenvectors of the matrix product, normalized so that $\mathbf{v}(0) \cdot \mathbf{u}(t) = 1$. Both $\mathbf{v}(0)$ and $\mathbf{u}(t)$ geometrically converge to stationary distributions that are independent of t . In addition, it is possible to show by using the methods of Tuljapurkar and Lee (personal communication), that $\mathbf{v}(0) = \mathbf{v} + O(\varepsilon^2)$, where \mathbf{v} is the dominant left eigenvector of the average projection matrix and ε measures the size of the deviations of the vital rates from the average matrix. Hence, for small noise, assuming $\mathbf{u}(t)$ is normalized so that $\sum_i u_i(t) = 1$, the initial total reproductive value in the population, $V_0 = \mathbf{v} \cdot \mathbf{n}(0)$, gives an accurate approximation of the effect of initial age distribution on the total population size at time t .

Infinitesimal Mean and Variance. For "small" fluctuations in the vital rates, the analytical framework in Tuljapurkar (11) can be used to derive approximations for the constant asymptotic rates of change in mean and variance of the prob-

ability distribution of the logarithm of population size. We present for simplicity only the case of serially independent environments, although his general formulas include terms describing serial correlation of fluctuations in the vital rates. The infinitesimal mean, μ , also known as the long-run growth rate of the population, and the infinitesimal variance, σ^2 , are

$$\mu \approx \ln \lambda_0 - \sigma^2/2 \quad [3]$$

and

$$\sigma^2 \approx \lambda_0^{-2} \delta^T C \delta, \quad [4]$$

where λ_0 is the dominant eigenvalue of the average projection matrix A (containing the average vital rates A_{ij}) and δ is a column vector (and δ^T its transpose) of sensitivity coefficients that can be expressed as $\partial \lambda_0 / \partial A_{ij} = v_i u_j$, in which v_i and u_j are elements of the dominant left and right eigenvectors of A , normalized as above (16). C is the variance-covariance matrix of fluctuations in the elements of $A(t)$. (μ here is equivalent to a in refs. 10 and 11 and to $\ln \lambda$ in refs. 8, 9, and 14).

Another way of obtaining estimates of the infinitesimal mean and variance in the diffusion approximation for logarithm of population size is by numerical simulation of the stochastic process. The total population size at time t obeys the recursion equation $N(t+1) = \lambda(t)N(t)$ where the values of the realized geometric growth rate, $\lambda(t)$, are determined by the projection matrix for the age-structured population (Eq. 1). Defining $x(t) = \ln N(t)$ and $r(t) = \ln \lambda(t)$, the recursion for the natural logarithm of total population size, $x(t+1) = r(t) + x(t)$, has the solution for a particular sample path $x(t) = x(0) + \sum_{i=0}^{t-1} r(i)$. The $r(i)$ have serial correlation caused by the time lag or "momentum" inherent in age-structured populations, in addition to possible environmentally induced autocorrelation in the vital rates. Therefore, as $t \rightarrow \infty$

$$t^{-1}E[x(t) - x(0)] \rightarrow \bar{r} = \mu \quad [5]$$

and

$$t^{-1}\text{Var}[x(t) - x(0)] \rightarrow \sigma_r^2 \left[1 + 2 \sum_{\tau=1}^{\infty} \rho(\tau) \right] = \sigma^2, \quad [6]$$

where the expectation and variance are across sample paths. \bar{r} and σ_r^2 are respectively the mean and variance of $r(t)$, and $\rho(\tau)$ is the serial correlation of $r(t)$ with $r(t+\tau)$ (refs. 8–10, 14, 17).

Alternatively, μ and σ^2 can be accurately estimated from a single sufficiently long sample path since the realized growth rates compose a stationary ergodic time series. However, because the realized growth rates are autocorrelated (even with serially independent environments), σ^2 must be calculated over segments of the sample path that are much longer than the characteristic autocorrelation time. One could also compute the infinitesimal variance as $\sigma^2 = 2(\ln \lambda_0 - \mu)$, given a numerical estimate of μ . Either of these methods of estimating σ^2 is simpler than direct computation of the autocorrelation function in Eq. 6.

Diffusion Equation. Let x represent the natural logarithm of total population size, and $x_0 = \ln V_0$ be its adjusted initial value at time $t = 0$. The probability that log population size will be x at time t , starting from x_0 , is defined as $p \equiv p(x, t|x_0)$, which for most life histories quickly approaches the solution of the diffusion equation for the Wiener process (18, 19)

$$\partial p / \partial t = -\mu \partial p / \partial x + (\sigma^2/2) \partial^2 p / \partial x^2, \quad [7]$$

with the initial condition $p(x, 0|x_0) = \delta(x - x_0)$, the Dirac delta function located at x_0 . In the absence of an extinction boundary (absorbing barrier) Eq. 7 has natural boundaries at $-\infty$ and $+\infty$ and the solution is a normal distribution with mean $x_0 + \mu t$ and variance $\sigma^2 t$ (18), as described by the asymptotic results given above.

More realistically, the imposition of an extinction boundary—i.e., certain extinction below a population size of one individual, dictates the boundary condition

$$p(0, t|x_0) = 0. \quad [8]$$

Quantities pertaining to a population declining to any threshold can be obtained by taking x_0 to be the distance from the adjusted initial size to the threshold on the log scale (3). Previously known solutions for the Wiener process with an absorbing barrier (18) merely require a linear transformation of coordinates to apply to the present problem (Eqs. 9–12). The solution to Eqs. 7 and 8 is

$$p(x, t|x_0) = (2\pi\sigma^2 t)^{-1/2} \left[\exp\left\{-\frac{(x - x_0 - \mu t)^2}{2\sigma^2 t}\right\} - \exp\left\{-2\mu x_0/\sigma^2 - \frac{(x + x_0 - \mu t)^2}{2\sigma^2 t}\right\} \right]. \quad [9]$$

The probability of extinction in the interval t to $t + dt$, denoted as $g(t|x_0)dt$, is derived from the rate of decrease of the total probability that the population exists at time t ,

$$g(t|x_0) = -(d/dt) \int_0^\infty p(x, t|x_0) dx \quad [10a]$$

$$= x_0 (2\pi\sigma^2 t^3)^{-1/2} \exp\left\{-\frac{(x_0 + \mu t)^2}{2\sigma^2 t}\right\}. \quad [10b]$$

The cumulative probability that the population becomes extinct before time t is, from Eqs. 9 and 10a,

$$G(t|x_0) = \int_0^t g(t'|x_0) dt' \\ = \Phi \left[\frac{-x_0 - \mu t}{\sigma \sqrt{t}} \right] + \exp\left\{-2\mu x_0/\sigma^2\right\} \left(1 - \Phi \left[\frac{x_0 - \mu t}{\sigma \sqrt{t}} \right] \right), \quad [11]$$

where $\Phi[y]$ is the standard normal probability integral

$$\Phi[y] = (2\pi)^{-1/2} \int_{-\infty}^y \exp\{-z^2/2\} dz.$$

The chance of ultimate extinction is

$$G(\infty|x_0) = \begin{cases} 1 & \text{for } \mu \leq 0 \\ \exp\{-2\mu x_0/\sigma^2\} & \text{for } \mu > 0. \end{cases} \quad [12]$$

Conditional Diffusion Process. When $\mu > 0$ the probability distribution of extinction times, $g(t|x_0)$, is improper because the chance of ultimate extinction is less than one. A proper probability distribution of extinction times can be constructed by dividing the original improper distribution by the chance of ultimate extinction, $g^*(t|x_0) = g(t|x_0)/G(\infty|x_0)$. This represents the conditional probability distribution of extinction times, considering only those sample paths in which the population eventually becomes extinct and excluding sample paths in which extinction never occurs,

$$g^*(t|x_0) = x_0 (2\pi\sigma^2 t^3)^{-1/2} \exp\left\{-\frac{(x_0 - |\mu|t)^2}{2\sigma^2 t}\right\}. \quad [13]$$

Remarkably, the conditional distribution of extinction times when $\mu > 0$ is exactly the same as the distribution of extinction times when $\mu < 0$. Hence, the proper distribution of extinction times depends only on the magnitude and not on the sign of μ .

This result can also be derived directly from the theory of conditional diffusion processes (19), by showing that the infinitesimal mean and variance for the conditional process are the same as those for the unconditional process, since these functions (along with the boundary conditions) completely characterize the behavior of a diffusion process. The infinitesimal variance of the conditional process with $\mu > 0$ is the same as that for the unconditional process with $\mu < 0$ (for which eventual extinction is certain), $\sigma^{2*} = \sigma^2$ and the infinitesimal mean of the conditional process with $\mu > 0$ is

$$\begin{aligned}\mu^* &= \mu + \sigma^2 \partial \ln G(\infty|x) / \partial x \\ &= -\mu,\end{aligned}\quad [14]$$

which is also the same as that for the unconditional process with $\mu < 0$. Hence, the entire behavior of the conditional diffusion process with μ positive is identical to that of the unconditional process with μ negative. In particular, the distribution of extinction times in Eq. 13 is the same for the two processes.

Moments of Extinction Time Distribution. The distribution of extinction time is of the form known as an inverse Gaussian distribution (20). Its mean and variance are

$$\bar{t} = x_0 / |\mu| \quad \text{and} \quad \sigma_t^2 = x_0 \sigma^2 / |\mu|^3. \quad [15]$$

The mean time to extinction is equal to the logarithm of the adjusted initial population size, divided by the absolute value of the long-run growth rate. It depends on the infinitesimal variance, σ^2 , only through its effect on the long-run growth rate of the population, μ (Eq. 3). The distribution of extinction times is positively skewed, with third central moment $3x_0\sigma^4/|\mu|^5$, so that the mode (the most probable extinction time) is less than the mean. When $\mu = 0$ the moments do not exist, but the mode is at $x_0^2/3\sigma^2$ (5).

COMPUTER SIMULATIONS

Scalar Case. To test the accuracy of the diffusion approximation, apart from complications of age structure, a population with discrete nonoverlapping generations was simulated. The multiplicative growth rate of the population, $\lambda(t)$, was assumed to be a stationary random variable with a log-normal distribution and no serial correlation. Exact values of the infinitesimal mean and variance can then be derived from Eq. 3 with the additional formula $\sigma^2 = \ln(1 + c^2)$, where c is the coefficient of variation of λ (20). Eq. 4 in the scalar case, $\sigma^2 \approx c^2$, is accurate only for small or moderate coefficients of variation in the multiplicative growth rates. Since Tuljapurkar's formulas overestimate σ^2 and underestimate μ , the diffusion approximation employing them overestimates cumulative extinction probabilities given by the simulations (Fig. 1).

The diffusion approximation using exact values of the infinitesimal mean and variance is closer to the simulated extinction probabilities but still slightly overestimates them because the sample paths in the diffusion process are continuous, whereas those in the simulations are discrete: extinction of a continuous sample path occurs at the time the population size first reaches one individual, which generally will not happen at an integer value of elapsed time. There is some chance that a continuous sample path will reach the extinction boundary, but if continued will attain a population size greater than one at the next integer value of time, and persist until the end of the simulation. Such a sample path would be

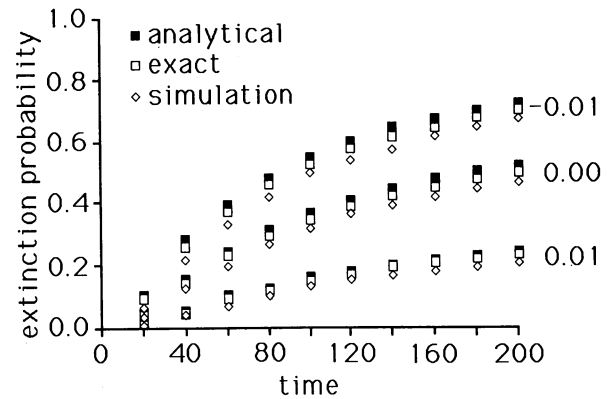


FIG. 1. Cumulative extinction probabilities for a population without age structure. The initial size is 10 individuals, and successive multiplicative growth rates are independent and lognormally distributed, with a mean of 1.033153 and coefficient of variation equal to 0.298275, 0.261828, or 0.215103, corresponding to analytical values of $\mu = -0.01, 0.00,$ or 0.01 . Each point for the stochastic simulations is based on 10,000 sample paths generated independently for each timespan considered; any particular simulated extinction probability, G , has a standard deviation equal to $0.01 [G(1 - G)]^{1/2}$, which always is less than 0.5%. Also shown are two predictions from diffusion approximations (Eq. 11), the first using Eqs. 3 and 4 and the second using the exact expressions for the infinitesimal mean and variance (see text).

counted as an extinction in the diffusion approximation but its discrete analog in the simulation would not.

Age-Structured Populations. Cumulative extinction probabilities were estimated by computer simulation for age-structured populations with different types of life histories with temporally independent fluctuations in the vital rates. These were compared with the analytical approximation by using Eqs. 3, 4, and 11. For all of the life histories we investigated, the analytical approximation accurately predicted the cumulative extinction probabilities when fluctuations in the vital rates were small or moderate. Semianalytical approximations were also made, using an average of numerical estimates of μ obtained as in Eq. 5, from computer simulation of five sample paths (totalling 10^6 time intervals), and setting $\sigma^2 = 2(\ln \lambda_0 - \mu)$. This approximation provides estimates of extinction probabilities with accuracy matching that of the exact diffusion results in the scalar case (Fig. 2).

DISCUSSION

Our results show that the extinction dynamics of density-independent age-structured populations in a fluctuating environment can be accurately modeled as a diffusion process for the natural logarithm of total population size. For this purpose only three parameters need to be estimated. These are the initial total reproductive value in the population, obtained from the average life history and the initial age structure, and the infinitesimal mean and variance, μ and σ^2 , which can be calculated analytically for small or moderate fluctuations in the vital rates (Eqs. 3 and 4). For large fluctuations in the vital rates, when coefficients of variation are on the order of one or larger, accurate estimates of extinction dynamics can be obtained semianalytically by first estimating μ from simulation of a single very long sample path and then solving Eq. 3 for σ^2 . The semianalytical method predicts cumulative extinction probabilities that are at most a few percent greater than those given by the simulations (Figs. 1 and 2).

The analytical formulas demonstrate that in density-independent populations the dynamics of extinction, conditional on the event, depend only on the magnitude and not the sign of the long-run growth rate, μ . For example, the expected time until extinction, $x_0/|\mu|$ (which has the same form as for

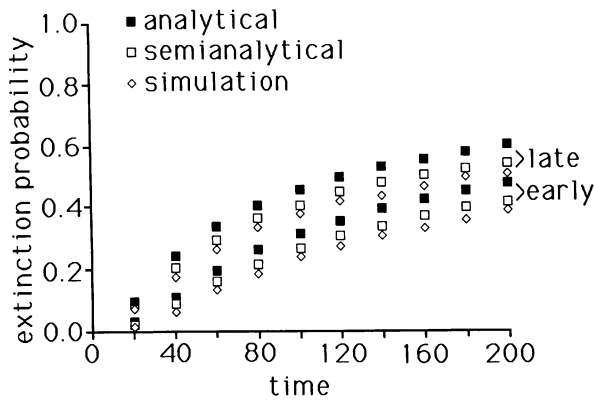


FIG. 2. Cumulative extinction probabilities for a population with two age classes. The survivorship of the first age class was assumed to be 1.0 at all times, and both age classes had equal fertilities, which were lognormally distributed and completely cross-correlated in their fluctuations (but serially independent), with a mean of 0.525 and coefficient of variation 0.381061, corresponding to an analytical value of $\mu = 0$. Two initial age structures were investigated, with 10 individuals in the first age class and 0 in the second age class (early), or vice versa (late). Each point for the stochastic simulations is based on 10,000 independent sample paths. Two diffusion approximations are also presented: the first is analytic, using Eqs. 3 and 4 with $\mu = 0$; the second is semianalytic, using a numerical estimate of $\mu = 0.00231$ (see text).

a declining population in a constant environment, with $\sigma^2 = 0$), depends only on the natural logarithm of the initial total reproductive value in the population and on the absolute value of the long-run growth rate [not on σ^2 except as this influences μ (Eq. 3)]. Invariance of the expected first passage time to the sign of the deterministic force is a general property of conditional diffusion processes (19, 21).

The extinction of a population with high positive μ is expected to be rapid, when it occurs, although eventual extinction is a low-probability event (Eq. 12). This result can be explained as follows. When μ is positive there is a deterministic force acting to increase the population size. If the population goes extinct, it is most likely to happen near the beginning of the sample path (in a series of time intervals with unusually low population growth), before the population attains a size large enough that the same environmental sequence would not cause extinction. The more positive the long-run growth rate, the more rapid and extreme must be the intervals of low growth in order to overcome the opposing deterministic force.

If the long-run growth rate of the population at low densities is positive, the population may become limited by increased mortality or decreased fecundity. Such density-dependent effects may alter the distribution of age structure in a fluctuating environment and greatly complicate the dynamics, unless population density affects all elements of the projection matrix equally (13). It is therefore difficult to derive general quantitative results about the distribution of extinction times in density-dependent age-structured populations. However, two qualitative features are worth noting, assuming that the dynamics can be approximated as a diffusion process. First, if the initial population size is much smaller than the modal size and population growth is initially density-independent, then for short times the probabilities of extinction should be closely approximated by the preceding

density-independent formulas. Second, if μ is positive and of substantial magnitude, the distribution of extinction times should be approximately exponential, given that the population starts from the modal size (22). In this case the population size typically would fluctuate for a very long time around the modal value, before making a relatively rapid transition to small sizes and becoming extinct. The expected duration of the final transition from the modal population size to extinction (conditional on not exceeding the modal value) would approximately equal the expected time for the reverse process of growth from low population size to the modal value (conditional on not becoming extinct) (21).

In a separate paper we will analyze the implications of stochastic demography for conservation biology policy and discuss ways of estimating the extinction probabilities from incomplete information on the life history. We emphasize here that application of diffusion approximations for estimating extinction probabilities in density-independent age-structured populations can result in a great saving of effort in comparison with purely numerical procedures, which must involve many thousands of independent simulations.

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