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Stochastic Differential Equations As Insect Population Models

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ABSTRACT Stochastic differential equations are a potentially important class of models for describing insect population dynamics. Their advantages include ease of use, relative tractability, ease of understanding, and the potential for approximating many types of stochastic variation affecting insect populations. This paper is an exposition for quantitative ecologists on parameter estimation for one–dimensional stochastic differential equations. Stochastic versions of the exponential growth model and the logistic model are developed in detail as examples. Topics discussed include transition distributions and moments, stationary distributions, maximum likelihood estimates, conditional least squares estimates, maximum quasi–likelihood estimates, jackknifing, multiple stable and unstable equilbria, and deterministic chaos.

Life is stochastic. Ecologists have long observed that the abundances of natural populations, and of insect populations in particular, are highly variable (Allee et al. 1949, p. 319, Andrewartha & Birch 1954, p. 358). Field estimates of insect populations typically show large temporal and spatial fluctuations over and above pure sampling errors. Even replicate laboratory populations started under similar initial conditions often display widely varying outcomes, as demonstrated by classic experiments on arthropod systems discussed in most ecology texts.

Traditionally, ecological modelers have used simple differential or difference equations for summarizing the general forces regulating population growth. This deterministic approach in ecology has a rich history dating back to Verhulst's logistic model in the nineteenth century. Occasionally some ecologists have raised questions about the wisdom of ignoring random components of population growth. Most notable were the insect population biologists who warned of the inherent vacillations in field data during the rancorous debates on density dependence vs. independence during the 1950's. The deterministic approach still predominates in population modeling, to the extent that unpredictable fluctuations in insect populations are now fashionably hypothesized to be the result of deterministic forces producing "chaotic" behavior.

Admittedly, stochastic models are sometimes proposed for describing insect population abundances. The mathematical ecology literature contains numerous explanatory discussions of various stochastic processes presented as possible candidates for population models (May 1974a, Goel & Richter–Dyn 1974, Pielou 1977, Ricciardi 1977, Nisbet & Gurney 1982). Almost never, however, are such models actually used to analyze real data sets, with the exception of non–biological time series models. Stochastic models exist mostly as concepts in ecology rather than as serious testable hypotheses about the forces affecting population growth. One reason for

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this state of affairs is that it has not been clear to ecologists just how to apply such models. It has not been clear to statisticians, for that matter; methods for estimating parameters and testing hypotheses in stochastic processes are only recently receiving comprehensive treatment in the statistics literature (for instance, Basawa & Prakasa Rao 1980).

It is the intent of this paper to provide an exposition for quantitative ecologists on the use of stochastic differential equations (SDE's) as population models. SDE's, known also as diffusion processes, offer great potential in population analysis, since they have many desirable statistical properties and are easy to understand, to apply, and to test. I concentrate on one–species models and show explicit ways of estimating parameters in these models from data. As examples, I develop SDE versions of the exponential growth model and the logistic growth model.

The first section of this paper reviews the main statistical properties of SDE's needed for parameter estimation. I present without proof the relevant results for subsequent use in estimation. The next section discusses parameter estimation for time series data using the full time–dependent statistical properties of SDE's. Maximum likelihood (ML) estimates and conditional least squares (CLS) estimates are developed. In the third section, I present SDE–based analysis methods for populations fluctuating around a stable equilibrium. Instead of focusing on a deterministic fixed point equilibrium, the section advocates estimating parameters for a stationary probability distribution for population size. The last section discusses some related topics and points out problems for further research. The topics include: maximum quasi–likelihood estimation, jackknifing, sampling variability, systems with multiple stable and unstable equilibria, and deterministic "chaos" models.

Statistical Properties of SDE's

Deterministic models of single species populations are often in the form of an ordinary differential equation (ODE):

$$dN(t) = N(t)g(N(t))dt. \tag{1}$$

Here $N(t)$ represents a measure of population abundance (density, biomass, numbers, etc.), and $g(N(t))$ represents the per–unit–abundance growth rate. Two examples frequently seen are: (a) the exponential growth model defined by $g(N(t)) = r$ (constant), and (b) the logistic growth model defined by $g(N(t)) = r - (r/k)N(t)$. The logistic may be regarded as an approximation to a more detailed growth model near a stable equilibrium population abundance (Dennis & Patil 1984, Dennis & Costantino 1988).

Many stochastic versions of (1) can be constructed, but a type of stochastic differential equation (SDE) has potential for describing many features of population fluctuations in a relatively simple fashion. The stochastic version of (1) discussed in this paper is the following SDE:

$$dN(t) = N(t)[g(N(t))dt + \sigma h(N(t))dW(t)]. \tag{2}$$

Here $dW(t)$ has a normal distribution with a mean of zero and a variance of dt, $h(N(t))$ is a positive–valued function, and σ is a positive constant. The formulation describes the addition of random perturbations to the per–unit–abundance growth rate, with the function $h(N(t))$ describing any dependence on $N(t)$ of the magnitude of the fluctuations. A useful form for ecological applications is $h(N(t)) = 1$, corresponding to "multiplicative noise", that is, the scale of fluctuations in the overall growth rate $N(t)g(N(t))$ is proportional to $N(t)$. Population trajectories under this model may be simulated by generating a normal (independent) random variable $dW(t)$ during a small time increment dt, calculating the differential $dN(t)$ using (2), and then computing the new population size as $N(t + dt) = N(t) + dN(t)$, etc.

Mathematically, the differential $dN(t)$ is rigorously defined by either an Ito or a Stratonovich stochastic integral (see Soong 1973, Karlin & Taylor 1981, or Horsthemke & Lefever 1984). The above simulation method corresponds to the Ito interpretation, which will be assumed in this paper. The differences between Ito and Stratonovich calculi have generated a lot of colorful copy in the mathematical ecology literature (for instance, Turelli 1977, Feldman & Roughgarden 1975). The differences from the standpoint of modeling are to some extent semantic (Braumann 1983a, Dennis & Patil 1984) and are not of concern to this paper.

The two examples of SDE's considered here arise from the exponential growth and the logistic growth deterministic models. The exponential growth SDE is defined by

$$dN(t) = N(t)rdt + \sigma N(t)dW(t), \tag{3}$$

and the SDE version of logistic growth becomes

$$dN(t) = N(t)[r - (r/k)N(t)]dt + \sigma N(t)dW(t). \tag{4}$$

Both models use $h(N(t)) = 1$.

A stochastic process $N(t)$ defined by an SDE in the form (2) is known as a diffusion process. Such diffusion processes have the Markov property and are continuous functions of time (see Karlin & Taylor 1981). Two functions are particularly important for obtaining statistical properties of diffusion processes. They are the infinitesimal mean, denoted $m(n)$, and the infinitesimal variance, $v(n)$, given by

$$m(n) = \lim_{\Delta t \to 0}(1/\Delta t)E[N(t+\Delta t) - N(t) \mid N(t) = n] = ng(n); \tag{5}$$

$$v(n) = \lim_{\Delta t \to 0}(1/\Delta t)E[\{N(t+\Delta t) - N(t)\}^2 \mid N(t) = n] = \sigma^2 n^2 [h(n)]^2. \tag{6}$$

The infinitesimal mean and variance for the exponential SDE (3) are $m(n) = rn$ and $v(n) = \sigma^2 n^2$, while those for the logistic SDE (4) become $m(n) = n[r - (r/k)n]$ and $v(n) = \sigma^2 n^2$.

Several properties of SDE's or diffusion processes make them valuable for modeling applications. First, the Markov property allows the formulation of explicit likelihood functions for fitting the models to data. Second, many statistical properties such as transition distributions and moments, or approximations thereof, are straightforwardly derived; these properties are useful for fitting the models to data or for studying the dynamic behavior of the models. Third, many other types of stochastic processes, such as birth–death processes, stochastic difference equations, or branching processes, can be approximated by SDE's through scaling techniques (see Karlin & Taylor 1981, p. 168). Finally, if $N(t)$ is a diffusion process, then a transformation $X(t) = f(N(t))$ is also a diffusion process, provided $f(N(t))$ is a continuous, strictly increasing (or decreasing) function. The infintesimal mean and variance of $X(t)$ are given by

$$m_X(x) = v_N(n)f''(n)/2 + m_N(n)f'(n), \tag{7}$$

$$v_X(x) = v_N(n)[f'(n)]^2, \tag{8}$$

where $n = f^{-1}(x)$ (Karlin & Taylor 1981, p. 173). This property often permits the transformation of a novel diffusion process into a known process with well–studied statistical properties.

All the essential properties of a diffusion process $N(t)$ governed by an SDE (2) are embodied in the transition probability density function (pdf) of the process. The transition pdf, denoted $p(n,t|n_0)$, is a pdf with time t and initial population abundance $N(0) = n_0$ appearing as parameters. The area under the transition pdf between a and b gives the probability that the population is in the interval (a,b] at time t, given that $N(0) = n_0$:

$$\Pr[a < N(t) \leq b] = \int_a^b p(n,t|n_0)dn. \tag{9}$$

The transition pdf is a solution to a partial differential equation known as the Fokker–Planck or forward equation,

$$\partial p/\partial t = (1/2)\partial^2[vp]/\partial n^2 - \partial[mp]/\partial n, \tag{10}$$

where $p = p(n,t|n_0)$, $v = v(n)$, and $m = m(n)$. The solution must obey the initial condition $p(n,0|n_0) = \delta(n - n_0)$ (i.e. $\Pr[N(0) = n_0] = 1$); $\delta(x)$ is the Dirac delta function which is zero everywhere except for a "spike" of infinite height at $x = 0$ such that the area under $\delta(x)$ is 1. When appropriate, the solution $p(n,t|n_0)$ must also obey boundary conditions relating to integrability and to reflection or absorption of the process at the edge of its range. The Fokker–Planck equation has been solved for many specific SDE models; solution details and examples are provided by Goel & Richter–Dyn (1974), Karlin & Taylor (1981), Gardiner (1985), and Risken (1984).

The transition pdf or suitable approximation is needed to fit an SDE to time series data using ML estimation.

The transition pdf for the exponential growth SDE (3) is easily obtained using the transformation $X(t) = \log N(t)$. The transformation formulas (7) and (8) yield constant infinitesimal mean and variance for the process $X(t)$:

$$m_X(x) = r - \sigma^2/2, \tag{11}$$

$$v_X(x) = \sigma^2. \tag{12}$$

These are the infinitesimal moments of a Wiener process (Brownian motion) with drift. A well–known result gives a normal transition distribution for $X(t)$ (e.g. Ricciardi 1977, p. 58): $X(t) \sim \text{normal}(x_0 + (r - \sigma^2/2)t,\ \sigma^2 t)$, where $x_0 = \log n_0$. Thus, the distribution of $N(t)$ is lognormal with transition pdf given by

$$p(n,t\,|\,n_0) = [n(\sigma^2 t 2\pi)^{1/2}]^{-1} \exp\{-[\log n - \log n_0 - (r - \sigma^2/2)]^2/(2\sigma^2 t)\},$$

$$0 < n < \infty. \tag{13}$$

This highly skewed distribution starts as a spike at n_0 and spreads rapidly as t increases.

The process $N(t)$ governed by the logistic SDE (4) can be transformed into a process with a linear infinitesimal mean through the Bernoulli transformation $X(t) = 1/N(t)$. The infinitesimal moments (7) and (8) for $X(t)$ are

$$m_X(x) = (r/k) - (r - \sigma^2)x, \tag{14}$$

$$v_X(x) = \sigma^2 x^2. \tag{15}$$

As Prajneshu (1980) pointed out, these infinitesimal moments correspond to a process introduced by Wong (1964). Wong (1964) provided an expression for the transition pdf of $X(t)$, and Prajneshu (1980) transformed the pdf to obtain the transition pdf of $N(t)$.

Unfortunately, the resulting transition pdf for the logistic SDE is extremely complicated, involving an integral of functions of complex variables. Computing it is not out of the question, but is hardly within the scope of routing insect population analyses. Fortunately, though, one can obtain suitable approximations for the transition pdf amenable to computing using perturbation methods (details are beyond the scope of this paper; perturbation methods are discussed by Gardiner 1985). One such approximaton is displayed later in this paper (equation (27)). The transition pdf so approximated starts as a spike at n_0 and resembles an S–shaped ridge converging ultimately to a stationary distribution.

If the deterministic population trajectory goverend by (1) approaches a stable point equilibrium, a corresponding SDE (2) may possess a limiting stationary distribution. As t becomes large, the transition pdf $p(n,t|n_0)$ may approach a pdf, denoted $p(n)$, that does not depend on t or n_0. The form of the pdf is given by

$$p(n) = C\exp\{(2/\sigma^2)\int((1/n)g(n)/[h(n)]^2)dn - 2\log n - 2\log h(n)\} \tag{16}$$

(see Dennis & Patil 1984). The constant C is found by setting the area under the curve $p(n)$ equal to one (if the area is infinite, then a stationary distribution for the process does not exist). The exponential growth SDE (3) does not have a stationary distribution, but the logistic SDE (4) does have a stationary distribution. It is a straightforward exercise to use (16) to obtain a stationary gamma distribution, with pdf given by

$$p(n) = [\beta^{\alpha}/\Gamma(\alpha)]n^{\alpha-1}e^{-\beta n}, \quad 0 < n < \infty, \tag{17}$$

for the logistic SDE. Here $\alpha = (2r/\sigma^2) - 1$, $\beta = 2r/(k\sigma^2)$. Just as the deterministic logistic approximates more detailed deterministic models, the gamma distribution (17) can be regarded as an approximate stationary distribution for more detailed SDE models (Dennis & Patil 1984).

Moments of $N(t)$ and other distributional properties of $p(n,t|n_0)$ are useful for summarizing the statistical behavior of the process through time. Moments or other expected values are also needed for estimating parameters with the CLS method. The expected value of a function, $f(N(t))$, of a diffusion process given that $N(0) = n_0$ is itself a function of n_0 and t:

$$E[f(N(t))|N(0) = n_0] = \int_{-\infty}^{+\infty} f(n)p(n,t|n_0)dn = u(n_0,t). \tag{18}$$

Setting $f(n) = n$ gives the time–dependent mean of $N(t)$, $f(n) = n^2$ gives the second moment, etc. Such expectations can be computed directly from (18) using the transition pdf. Alternatively, $u(n_0,t)$ satisfies a partial differential equation known as the backward equation:

$$\partial u/\partial t = (v(n_0)/2)\partial^2 u/\partial {n_0}^2 + m(n_0)\partial u/\partial n_0. \tag{19}$$

The function $u(n_0,t)$ is obtained by solving (19) subject to the condition $u(n_0,0) = f(n_0)$. A derivation of the backward equation from the definition of $u(n_0,t)$ (18) is provided by Karlin & Taylor (1981, p. 214).

For the exponential growth SDE, the νth moment of $N(t)$ defined by $E[(N(t))^{\nu}|N(0) = n_0] = u_{\nu}(n_0,t)$ is obtained straightforwardly from (18) using the lognormal transition pdf (13) and $f(n) = n^{\nu}$:

$$u_\nu(n_0,t) = n_0{}^\nu \exp\{[r - (\sigma^2/2)]\nu t + (\sigma^2/2)\nu^2 t\}. \tag{20}$$

The mean $E[N(t)\,|\,N(0) = n_0]$ of the process given by

$$u_1(n_0,t) = n_0 e^{rt} \tag{21}$$

corresponds to the solution of the deterministic model. However, the mean is not necessarily a good characterization of the behavior of the process. In fact, if $0 < r < \sigma^2/2$, it is easy to demonstrate using the transition pdf (13) that $\Pr[0 < N(t) \leq \epsilon] \to 1$ as $t \to \infty$ for arbitrarily small $\epsilon > 0$ (see, for instance, Dennis & Patil 1988). In biological terms, the SDE predicts virtually certain extinction of the population if σ^2 is large compared with r.

For the transformed process $X(t) = 1/N(t)$, where $N(t)$ is defined by the logistic SDE (4), a recursion expression relates the νth moment of $X(t)$ to the $(\nu-1)^{th}$ moment. Derivation of this relationship is beyond the scope of this paper but is based on a moment result for SDE's (Goel & Richter–Dyn 1974, p. 46). Letting $E[(X(t))^\nu\,|\,X(0) = x_0] = E[(N(t))^{-\nu}\,|\,N(0) = n_0] = u_{-\nu}(n_0,t)$, the relationship is

$$u_{-\nu}(n_0,t) = \exp\{(\nu\sigma^2/2)[\nu - 1 - 2(r-\sigma^2)/\sigma^2]t\}\{n_0{}^{-\nu}$$

$$+ \nu(r/k)\int_0^t \exp\{-(\nu\sigma^2/2)[\nu - 1 - 2(r-\sigma^2)/\sigma^2]w\}u_{-\nu+1}(n_0,w)dw\}. \tag{22}$$

In particular, the mean of $X(t)$ is found by setting $\nu = 1$ and noting that $u_0(n_0,t) = 1$:

$$u_{-1}(n_0,t) = (r/k)/(r-\sigma^2) + [1/n_0 - (r/k)/(r-\sigma^2)]\exp[-(r-\sigma^2)t]. \tag{23}$$

An immediate consequence of (23) is that the harmonic mean of $N(t)$ grows according to a logistic equation. The harmonic mean of $N(t)$ is defined as $1/u_{-1}(n_0,t)$:

$$1/E[1/N(t)\,|\,N(0) = n_0] = k(1 - (\sigma^2/r))/\{1 +$$

$$(1/n_0)[k(1 - (\sigma^2/r)) - n_0]\exp[-(r-\sigma^2)t]\}. \tag{24}$$

In other words, the harmonic mean is a solution of a logistic ODE except with a loss term $\sigma^2 n$ subtracted: $dn/dt = rn - (r/k)n^2 - \sigma^2 n$. It is interesting that this nonlinear SDE (4) preserves a logistic–type trajectory for one of its measures of central tendency.

The mean of $N(t)$ defined by $u_1(n_0,t) = E[N(t)\,|\,N(0) = n_0]$ does not obey a logistic equation. The mean of $N(t)$ has been derived by Hamada (1981) and is a complicated expression involving

numerous intractable integrals. An approximation for $u_1(n_0,t)$ can be obtained from the backward equation (19) using singular perturbation methods:

$$u_1(n_0,t) \approx k/[1 + ((k-n_0)/n_0)e^{-rt}] + (\sigma^2/2)(k/r)[1 + ((k-n_0)/n_0)e^{-rt}]^{-3} *$$

$$\{[1 - (2k/n_0)]e^{-2rt} + (2k/n_0)e^{-rt} - 1 - 2r[(k-n_0)/n_0]te^{-rt}\}. \tag{25}$$

Wiesak (1988) has given a rigorous justification of this approximation as well as for the following one (26). The mean of N(t) has the familiar sigmoid shape, but is less than the solution of the deterministic logistic. Additionally, an approximation for the second moment is

$$u_2(n_0,t) \approx \{k/[1 + ((k-n_0)/n_0)e^{-rt}]\}^2$$

$$+ (\sigma^2/2)(k/r)^2 2r[1 + ((k-n_0)/n_0)e^{-rt}]^{-4}\{[-(4k/n_0) + (5/2)]e^{-2rt}$$

$$+ [(4k/n_0)-2]e^{-rt}-(1/2)+r[((k-n_0)/n_0)e^{-rt}-1]((k-n_0)/n_0)te^{-rt}\}. \tag{26}$$

With these two moments, one can approximate the transition pdf for the stochastic logistic with a time–dependent gamma distribution having matching moments. Let $\alpha(n_0,t) = u_1^2/[u_2 - u_1^2]$, $\beta(n_0,t) = u_1/[u_2 - u_1^2]$, where u_1 and u_2 are given by (25) and (26). Then the transition pdf given by

$$p(n,t|n_0) = [\beta^\alpha/\Gamma(\alpha)]n^{\alpha-1}e^{-\beta n}, \quad 0 < n < \infty, \tag{27}$$

where $\alpha = \alpha(n_0,t)$ and $\beta = \beta(n_0,t)$, satisfies the initial condition $p(n,0|n_0) = \delta(n-n_0)$, has first two moments identical to (25) and (26), and approaches the exact stationary gamma pdf (17) as t becomes large.

Time–Dependent Analysis

Suppose an insect population is observed at times $0, t_1, t_2, \ldots, t_q$. the recorded observations of population size will be denoted $n(0) = n_0$, $n(t_1) = n_1, \ldots, n(t_q) = n_q$, and the time intervals (not necessarily equal) between observations denoted $t_1 - 0 = \tau_1$, $t_2 - t_1 = \tau_2, \ldots, t_q - t_{q-1} = \tau_q$. A recommended way of fitting an SDE to such observations is ML estimation.

ML estimation typically requires an approximate or exact transition pdf for the process N(t) governed by the SDE (2). The SDE will generally contain one or more unknown parameters; the vector of unknown parameters will be denoted by θ. The initial population size n_0 can be regarded as fixed in many population studies; the ML estimates developed here are consequently conditioned on n_0. The likelihood function $\ell(\theta)$ is defined as the joint pdf for $N(t_1), N(t_2), \ldots,$

$N(t_q)$, given $N(0) = n_0$, evaluated at observations $n_1, n_2, \ldots, n_q$. Since $N(t)$ is a Markov process with stationary transition probabilities (pdf of n_i given n_{i-1} depends only on τ_i, not t_{i-1}), the likelihood function is a product of transition pdfs:

$$\ell(\theta) = \prod_{i=1}^{q} p(n_i, \tau_i | n_{i-1}; \theta). \tag{28}$$

Here $p(n_i, \tau_i | n_{i-1}; \theta) \equiv p(n_i, \tau_i | n_{i-1})$ is the transition pdf defined by (9) evaluated at n_i, τ_i, and n_{i-1} (likelihood of system moving to n_i from n_{i-1} in a time interval of τ_i); the above notation emphasizes the dependence on the unknown parameters in θ. The ML estimates, $\hat{\theta}$, of the parameters in θ are the parameter values jointly maximizing $\ell(\theta)$ or $\log \ell(\theta)$.

ML estimation for the exponential growth SDE (3) was studied by Braumann (1983b) for the case of equal time intervals between observations: $\tau_1 = \tau_2 = \ldots = \tau_q$. It is straightforward to generalize his results for unequal intervals. The SDE has two unknown parameters: r and σ^2. It is somewhat more convenient to reparameterize by letting $\mu = r - \sigma^2/2$ and finding estimates of μ and σ^2 instead. Using the transition pdf (13), the log–likelihood function becomes

$$\log \ell(\mu, \sigma^2) = \sum_{i=1}^{q} \log p(n_i, \tau_i | n_{i-1}; \mu, \sigma^2) = -\sum_{i=1}^{q} \log[n_i(\tau_i 2\pi)^{1/2}] - (q/2)\log \sigma^2$$

$$- [1/(2\sigma^2)] \sum_{i=1}^{q} (1/\tau_i)[\log(n_i/n_{i-1}) - \mu\tau_i]^2. \tag{29}$$

It is an easy exercise to set partial derivatives of $\log \ell(\mu, \sigma^2)$ with respect to μ and σ^2 equal to zero and solve for the ML estimates:

$$\hat{\mu} = \{\sum_{i=1}^{q} \log(n_i/n_{i-1})\} / \sum_{i=1}^{q} \tau_i = [\log(n_q/n_0)]/t_q; \tag{30}$$

$$\hat{\sigma}^2 = (1/q) \sum_{i=1}^{q} (1/\tau_i)[\log(n_i/n_{i-1}) - \hat{\mu}\tau_i]^2. \tag{31}$$

The ML estimate for r becomes $\hat{r} = \hat{\mu} + (\hat{\sigma}^2/2)$.

One can obtain information on the distributions of $\hat{\mu}$ and $\hat{\sigma}^2$ by recalling that $X(t) = \log N(t)$ is Brownian motion with drift. Then, let $Y_i = \log[N(t_i)/N(t_{i-1})] = X(t_i) - X(t_{i-1})$. The variables $Y_1, Y_2, \ldots, Y_q$ are increments of Brownian motion with drift, and are therefore normal, independent, and stationary (e.g. Ricciardi 1977). In fact, if $\underline{Y} = [Y_1, Y_2, \ldots, Y_q]'$ and $\underline{\tau} = [\tau_1, \tau_2, \ldots, \tau_q]'$ are defined as column vectors, the distribution of $\underline{Y}$ becomes a multivariate normal:

$$\underline{Y} \sim \text{normal}(\mu\underline{\tau}, \sigma^2 T). \tag{32}$$

Here $T = \text{diag}(\underline{\tau})$ is a matrix with the elements of $\underline{\tau}$ on the main diagonal and zeros elsewhere. Let $G = \text{diag}(\sqrt{\tau_1}, \ldots, \sqrt{\tau_q})$, that is, $T = G'G$. A transformation of $\underline{Y}$ produces an ordinary normal linear model (e.g. Graybill 1976, p. 207):

$$\underline{Y}^* = G^{-1}\underline{Y} \sim \text{normal}(\mu[\sqrt{\tau_1}, \ldots, \sqrt{\tau_q}]', \sigma^2 I). \tag{33}$$

This is seen to be a model for a simple linear regression without intercept. In practice, one transforms the data by $y_i = \log(n_i/n_{i-1})$, $i = 1, \ldots, q$. The regression approach uses $y_1/\sqrt{\tau_1}$, $y_2/\sqrt{\tau_2}, \ldots, y_q/\sqrt{\tau_q}$ as values of the "dependent variable", $\sqrt{\tau_1}, \ldots, \sqrt{\tau_q}$ as values of the "independent variable", and a linear regression without intercept is performed. The formula (30) for $\hat{\mu}$ is recognized as the slope parameter estimate, and $\hat{\sigma}^2$ (31) is the (biased) ML estimate of the error variance parameter. The unbiased estimate is $q\hat{\sigma}^2/(q-1)$. The usual linear model theory yields the distributions of $\hat{\mu}$ and $\hat{\sigma}^2$: $\hat{\mu} \sim \text{normal}(\mu, \sigma^2/t_q)$, and $q\hat{\sigma}^2/\sigma^2 \sim \text{chisquare}(q-1)$.

Though the approximate transition pdf (27) for the logistic SDE is tractable, closed formulas for the ML estimates of r, k, and σ^2 cannot be obtained. Instead, the likelihood function (28) must be maximized numerically using one of various iterative algorithms (see Press et al. 1986) and a computer. Matrix programming languages such as GAUSS, SAS/IML, or APL make the calculation of ML estimates a fairly straightforward task.

When ML estimation is impractical, an alternative estimation method is conditional least squares. CLS estimates of parameters for an SDE model do not have all the statistical qualities of ML estimates. CLS estimates, like ML estimates, are consistent (i.e. $\hat{\theta}$ tends to be "closer" to θ as the sample size becomes large), asymptotically unbiased, and have asymptotic normal distributions (Klimko & Nelson 1978). However, CLS estimates tend to be less efficient (i.e. they have larger variances) than ML estimates. In addition, practical experience suggests that a bias is often present in CLS estimates for smaller samples. On the other hand, there are some Gauss–Markov style optimality results for certain CLS estimates arising from the theory of estimating equations (Godambe 1985).

The main practical advantage of CLS estimates is ease of calculation. They can often be computed for SDE models using linear or nonlinear regression packages. They make convenient "starter" values for iterative ML calculations.

CLS estimates are based on time–dependent moments or other expected values. Suppose one can write the time–dependent expected value of a function, $X(t) = f(N(t))$, of a diffusion process $N(t)$:

$$\begin{aligned} E[X(t) \mid X(0) = x_0] &= E[f(N(t)) \mid N(0) = n_0] \\ &= u(n_0, t) \equiv u(n_0, t; \theta). \end{aligned} \tag{34}$$

One could obtain the form of u by solving the backward equation (19). Due to the Markov property, $u(n_{i-1},\tau_i;\theta)$ is then the expected value of $f(N(t_i))$ given $N(t_{i-1}) = n_{i-1}$. CLS estimates arise from a sum of squared differences between observed values, $f(n_i)$, and their conditional expected values, $u(n_{i-1},\tau_i;\theta)$:

$$s(\theta) = \sum_{i=1}^{q} [f(n_i) - u(n_{i-1},\tau_i;\theta)]^2. \tag{35}$$

CLS estimates are the values of parameters in θ that jointly minimize $s(\theta)$. Note that many different CLS estimates may be available for a given SDE, based on different forms for the function $f(N(t))$.

CLS estimates for two of the parameters in the logistic SDE (4) can be constructed from the mean of $X(t) = 1/N(t)$ given by (23). Let $\beta_1 = (r/k)/(r-\sigma^2)$, $\beta_2 = r - \sigma^2$, and $f(n) = 1/n$, so that

$$\begin{aligned} u(n_{i-1},\tau_i;\beta_1,\beta_2) &= E[1/N(t_i) \mid N(t_{i-1}) = n_{i-1}] \\ &= \beta_1(1 - e^{-\beta_2\tau_i}) + (1/n_{i-1})e^{-\beta_2\tau_i}. \end{aligned} \tag{36}$$

One could perform a nonlinear regression to find the CLS estimates, i.e. the values of β_1 and β_2 minimizing

$$s(\beta_1,\beta_2) = \sum_{i=1}^{q} [(1/n_i) - u(n_{i-1},\tau_i;\beta_1,\beta_2)]^2. \tag{37}$$

The values $1/n_i$, $i = 1, \ldots, q$, would be entered as the "dependent variable" in a computer package, with the model to be fit given by (36).

It is interesting to note that minimizing (37) reduces to a simple linear regression of $1/n_i$ on $1/n_{i-1}$ when the time intervals between observations are equal. When $\tau_1 = \tau_2 = \ldots = \tau_q = \tau$, then (36) can be written as $\theta_1 + \theta_2(1/n_{i-1})$, where $\theta_1 = \beta_1(1 - e^{-\beta_2\tau})$, $\theta_2 = e^{-\beta_2\tau}$.

As an alternative, one could estimate all three parameters r, k, and σ^2 with the CLS method through use of the approximate first moment of N(t) given by (25) using the untransformed data, n_i, $i = 1, \ldots, q$ as the dependent variable, and $u_1(n_{i-1},\tau_i)$ (from (25)) as the model to be fit.

Equilibrium Analysis

The data considered in this section consist of observed sizes of an insect population, or ensemble of populations, fluctuating around an equilibrium. The main idea is to estimate parameters and test the fit of a stationary distribution for population size, instead of concentrating on estimating a fixed point equilibrium. The data are a time series (or group of

time series) of the form $n_1 = n(t_1)$, $n_2 = n(t_2)$, ... , $n_q = n(t_q)$. The methods described here are better when the intervals between observations are large, but the intervals can be small if there are many observations over a long period of time.

The statistical methods are based on the fact that the transition pdf, $p(n,t \mid n_0;\theta)$ approaches a stationary pdf, $p(n;\theta)$ as t becomes large, for some SDE models (16). Thus, as the intervals $\{\tau_i\}$ between observations increase, the time–dependent likelihood function (28) would approach a product of stationary pdfs:

$$\ell(\theta) = \prod_{i=1}^{q} p(n_i;\theta). \tag{38}$$

One computes ML estimates of the parameters in θ by maximizing $\ell(\theta)$ or $\log \ell(\theta)$.

If a chisquare goodness of fit test is desired, or if the time intervals between observations are small, use of a multinomial likelihood is recommended instead of (38). The investigator partitions the positive real line into m abundance classes: $(0, s_1]$, $(s_1, s_2]$, ..., (s_{m-1}, ∞), where $0 < s_1 < \ldots < s_{m-1} < \infty$. Grouped data denoted by $y_1, y_2, \ldots, y_m$ are formed; y_1 is the number of observations that are less than or equal to s_1, y_2 is the number of observations that are greater than s_1 but less than or equal to s_2, etc. Define $\pi_j(\theta)$ as the area under the stationary pdf between s_{j-1} and s_j, $j = 1, \ldots, m$ (where $s_0 = 0$ and $s_m = +\infty$):

$$\pi_j(\theta) = \int_{s_{j-1}}^{s_j} p(n;\theta)dn. \tag{39}$$

Since a diffusion process with a stationary pdf is ergodic, $\pi_j(\theta)$ represents the long–run proportion of time the process spends in the interval $(s_{j-1}, s_j]$. The multinomial likelihood function is

$$\ell(\theta) = C \prod_{j=1}^{m} [\pi_j(\theta)]^{y_j}, \tag{40}$$

where $C = q!/[y_1 ! \, y_2 ! \ldots y_m !]$. The ML estimates are obtained by computing the values of the paramters in θ which maximize $\ell(\theta)$ or $\log \ell(\theta)$. Goodness of fit testing can be accomplished with the Pearson statistic, X^2 or the likelihood ratio statistic, G^2:

$$X^2 = \sum_{j=1}^{m} [y_j - q\pi_j(\hat{\theta})]^2/[q\pi_j(\hat{\theta})], \tag{41}$$

$$G^2 = \sum_{j=1}^{m} y_j \log \{y_j/[q\pi_j(\hat{\theta})]\}. \tag{42}$$

A term in G^2 is understood to be zero if the corresponding count y_j is zero. The statistics X^2 and G^2 have identical large–sample chisquare distributions with degrees of freedom given by m − (# parameters estimated in θ) − 1. The chisquare approximation is adequate when $q\pi_j(\theta) \geq 5$ for at least 80% of the abundance classes (and this should be kept in mind when constructing the classes). If the time intervals between observations are small, then properties of the $\tilde{G}^2$ statistic are unknown at this time. However, under such circumstances X^2 is known to reject the null hypothesis (that the model fits) somewhat too often (Gleser & Moore 1985).

The multinomial likelihood (40) is easily maximized using nonlinear regression packages. The procedure is to use the y_j values as observations on the "dependent variable". Corresponding to each y_j value, $q\pi_j(\theta)$ is computed with programming statements as the model to be fit. Also, weights of $1/[q\pi_j(\theta)]$ are computed (and recomputed every iteration) for each y_j value. This setup "tricks" the nonlinear least squares (Gauss–Newton) algorithm into maximizing the multinomial likelihood (40) (see Jennrich & Moore 1975).

Further details and many numerical examples of stationary distribution analysis have been presented recently by Dennis & Costantino (1988).

Discussion

This section discusses various topics related to SDE analysis and points out problems for further research. The topics include other approaches to statistical inference for SDE's, incorporating sampling variability, models with multiple stable/unstable equilibria, and distinguishing stochasticity from deterministic chaos.

Additional Approaches to Inference.

One alternate approach to parameter estimation for SDE's is through the concept of quasi–likelihood. Quasi–likelihood is finding many uses in statistical theory, particularly in the literature of generalized linear models (McCullagh & Nelder 1983). Suppose x is a vector of observations arising from some stochastic model with a mean vector given by $E[X] = \mu$ and a variance–covariance matrix of $\eta V(\mu)$, where η is a positive constant. The quasi–likelihood function $\ell^*(\mu)$ is defined by a set of partial derivatives:

$$\partial\ell^*(\mu)/\partial\mu = V^{-1}(\mu)(x - \mu). \tag{43}$$

If $\mu = \mu(\theta)$, i.e. μ depends further on a vector θ of underlying parameters, then the maximum quasi–likelihood (MQL) estimate of θ is the solution to $\partial\ell^*(\mu(\theta))/\partial\theta = 0$. By letting $D(\theta) = \partial\mu(\theta)/\partial\theta$ be a matrix of partial derivatives, applying the vector derivative chain rule, and using (43), we have

$$D^T(\theta)V^{-1}(\mu(\theta))[x - \mu(\theta)] = 0 \tag{44}$$

as the system of equations for the MQL estimates of the parameters in θ.

For an SDE model, one can think of a quasi–likelihood as approximating a product of transition pdfs (28). The elements of the vector x in (44) are taken as the observations $f(n_1)$, $f(n_2)$, ..., $f(n_q)$ of a diffusion process $X(t) = f(N(t))$, the corresponding elements in $\mu(\theta)$ are found from $E[f(N(t_i)) \mid N(t_{i-1}) = n_{i-1}] = u_1(n_{i-1},\tau_i;\theta)$ (34), and V becomes a diagonal matrix of conditional variances: $E[\{f(N(t_i))\}^2 \mid N(t_{i-1}) = n_{i-1}] - [u_1(n_{i-1},\tau_i;\theta)]^2 = u_2(n_{i-1},\tau_i;\theta) - [u_1(n_{i-1},\tau_i;\theta)]^2$, say. Also, D becomes a matrix (q rows) of partial derivatives of $u_1(n_{i-1},\tau_i;\theta)$, $i = 1, \ldots q$, with respect to each parameter in θ. Thus, the estimating equations (44) for θ resemble those resulting from finding CLS estimates by minimizing (35), except that the terms in (44) are weighted by (the reciprocals of) the conditional variances.

The calculations to solve (44) can be accomplished with iterative reweighted least squares. From a current set of parameter values, θ_1, the algorithm computes improved values, θ_2, according to

$$\theta_2 = \theta_1 + (D^TV^{-1}D)^{-1}D^TV^{-1}(x - \mu), \tag{45}$$

where D, V, and μ are evaluated at θ_1. In nonlinear regression packages, this amounts to using $f(n_1)$, ..., $f(n_q)$ as observations on the dependent variable, $u_1(n_0,\tau_1;\theta)$, ..., $u_1(n_{q-1},\tau_q;\theta)$ as the model to be fit, with weights of $1/w_1$, ..., $1/w_q$ computed at each iteration, where $w_i = u_2(n_{i-1},\tau_i;\theta) - [u_1(n_{i-1},\tau_i;\theta)]^2$.

MQL appears to be a promising inference approach for stochastic population models. Much research remains to be done concerning the statistical properties of MQL estimates applied to SDE models; I would recommend that Monte Carlo studies be undertaken to examine MQL estimates in comparison to ML and CLS estimates, for specific models such as the stochastic logistic.

Another approach to statistical inference for SDEs involves jackknifing. Recent research by Lele (1988) indicates that jackknifing may be a highly useful way of handling a long–standing problem in stochastic processes: how to estimate the variance of parameter estimates. Lele has shown that jackknifing the linear estimating equations leads to a consistent estimate of the variance–covariance matrix for the parameter estimates. His results applied to SDE models are sketched here briefly. ML, CLS, and MQL estimates of parameters in SDE models are found by solving equations of the form

$$H(\theta) = \sum_{i=1}^{q} h(n_i,n_{i-1},\tau_i;\theta) = 0. \tag{46}$$

For example, in ML estimation h is a vector of partial derivatives of the log–transition pdf, log $p(n_i,\tau_i \mid n_{i-1};\theta)$, with respect to parameters in θ. Let $\hat{\theta}$ denote the estimate resulting from (46). One finds as many as q additional estimates, denoted $\hat{\theta}_j$, $j = 1, 2, \ldots, q$, by solving

$$H_j(\theta) = \sum_{i \neq j}^{q} h(n_i, n_{i-1}, \tau_i; \theta) = 0 \tag{47}$$

where $H_j(\theta)$ represents $H(\theta)$ except with $h(n_j, n_{j-1}, \tau_j; \theta)$ deleted from the sum. The jackknife estimate of θ is

$$(JK)\hat{\theta} = \hat{\theta} - [(q-1)/q]\sum_j(\hat{\theta}_j - \hat{\theta}). \tag{48}$$

We may expect an improvement in any finite sample bias of $\hat{\theta}$ by using $(JK)\hat{\theta}$. The jackknife estimate of $\Sigma(\theta)$, the variance–covariance matrix of $\hat{\theta}$ (or $(JK)\hat{\theta}$), is

$$(JK)\hat{\Sigma}(\theta) = [(q-1)/q]\sum_j(T_j - \overline{T})^2, \tag{49}$$

where $T_j = \hat{\theta}_j - \hat{\theta}$ and $\overline{T} = (\Sigma_j T_j)/q$. Large sample theory provides that $\hat{\theta}$ (or $(JK)\hat{\theta}$) has an asymptotic multivariate normal distribution with mean vector θ and variance–covariance matrix $\Sigma(\theta)$.

In practice, (48) and (49) will be computer–intensive, since they require solving not just one system of nonlinear equations, but up to q + 1 of them! However, the benefits would appear to be well worth the trouble. Lele's results apply to linear estimating equations in general, opening up many valuable applications in spatial analysis, stochastic processes, and statistical distribution modeling.

Sampling Variability.

A problem that has been glossed over in the previous discussions is the question of sampling variability. The abundances of field populations must typically be estimated with samples. The variability from sampling produces variability in the parameter estimates beyond that inherent in the SDE.

One model for incorporating sampling variability is a compound Poisson model. Suppose Y(t) represents the number of insects appearing in a sample at time t. The compound Poisson model would assume a Poisson distribution for Y(t) with a mean of $\lambda N(t)$, where N(t) is itself a stochastic process defined, for example, by an SDE (2), and the proportionality constant λ reflects sampling effort. The sampled abundances $y(t_1), y(t_2), \ldots, y(t_q)$ would constitute a realization of Y(t) and not N(t).

In principle, one can easily write down a probabilistic model (i.e. a joint pdf, and hence a likelihood function) for the sampled abundances. In practice, the expression involves numerous repeated integrals and is not likely to be very useful. Instead, there are ways of dealing with sampling variability in applications. The first is to ignore it. One fits the SDE model directly to

the observations using the methods described earlier. This is a reasonable approach if large samples (e.g. many hundreds) of insects appear in each sample, since the variability from sampling would then be small. For instance, under Poisson sampling, if 400 or more insects appear in a sample, the estimated coefficient of variation from sampling is under 5%. The second is to broaden the conceptual interpretation of the SDE to include sampling. One regards the sample observations (say, numbers of insects caught in pheromone traps at times t_1, t_2, ...) as being generated by a stochastic difference equation having variance components due to population fluctuations and sampling; one then uses an SDE merely as an approximation to that process. The procedure involves fitting the SDE directly to the sample observations; the resulting larger value of the parameter σ^2 conceptually reflects variability due to sampling as well as stochastic population fluctuations. Garcia (1983) incorporated sampling variability into an SDE model of forest growth by transforming the model to a Gaussian (Ornstein–Uhlenbeck) process and incorporating normally distributed sampling error. However, one of the variance parameters was nearly non–identifiable (i.e. data provided little information for its estimation) in his applications.

This problem of how to account for sampling variability is not peculiar to SDE models; it must be confronted with virtually all dynamic models of population abundances. SDE's are proposed here mainly for situations in which actual population fluctuations are the prime source of variability in the observed data. It is my contention that such situations are more numerous in ecological studies than has been previously acknowledged.

Multimodal Models.

Several forest insect systems, including gypsy moth and spruce budworm, have been hypothesized to have two or more stable equilibria (Takahashi 1964, Campbell & Sloan 1978, Ludwig et al. 1978, Berryman 1978). The insects are thought to be held in check at a low–abundance endemic equilibrium by a complex of many predator species. If for some reason the insects increase in abundance beyond a threshold value, however, reproduction gains outpace predation losses. The insects then continue increasing until reaching an upper, epidemic equilibrium where population size is regulated by sheer lack of resources (due to defoliation). Deterministic models in the form of (1) have been proposed to describe such systems (see review by May 1977).

Stochastic forces are likely to play an important role in such systems. Stochastic population fluctuations could provide the initial population increases necessary to move away from a lower stable equilibrium into a basin of attraction to an upper stable equilibrium. Such population outbreaks would occur seemingly at random.

SDE models in the form of (2) can be constructed from deterministic models with multiple stable and unstable equilibria (see Dennis & Patil 1984). One of the more interesting predictions from these SDE models involves the stationary pdf (16) for population abundance. For moderate noise levels, the stationary pdf from such a model may display multiple modes and antimodes corresponding to (though not equal to) the underlying stable and unstable equilibria. For higher

noise levels, the underlying equilibria structure becomes obscured, and a stationary pdf, if it exists at all, may have fewer modes than the number of stable equilibria.

If data on population abundance existed for systems suspected of multiple equilibria, multimodal stationary pdfs such as those listed by Dennis & Patil (1984) could be fitted using the methods discussed in this paper.

Chaos.

Ever since the papers by May (1974b, 1976) and May & Oster (1976) appeared, it has been well–known among mathematical ecologists that simple difference equation models of population growth can display complicated behavior seemingly indistinguishable from a random process. (The same is true for nonlinear differential equation systems of three or more species, as discussed for example, by Schaffer & Kot (1986); the discussion here is restricted to one–species systems.) Indeed, mathematical ecologists had long been steeped in a deterministic traditon, yet had been increasingly confronted with fluctuating population data; the "chaos" hypothesis of population regulation is now regarded as an important contending explanation of unpredictable data.

Chaos can in fact be classified as a type of stochastic behavior. Current thinking by Diaconis and others on the meaning of "randomness" (see Research News, Science Vol. 231, 7 March 1986, p. 1068) views as random a system with output behavior extremely sensitive to initial conditions. That perennial random system, a coin toss, is in principle a deterministic system. However, a tiny change in, say, the initial angular and/or upward velocity of the coin can cause a drastic change in the system output (heads or tails); thus the system may be regarded as random. Another such system is a string of pseudo–random numbers generated on a computer. Change the seed number slightly and a wholly different sequence emerges. Similar things happen in a chaotic deterministic model. Model trajectories differing only slightly in initial conditions diverge from each other exponentially (see review by Grebogi et al. 1987). It is reasonable, then, to contemplate the use of stochastic–based analysis methods on possibly chaotic time series data to see what statistical properties are present.

The statistical properties of SDE models such as the stochastic logistic (4) differ substantially from those of deterministic chaos models (such as the models catalogued by May & Oster 1976). For instance, the concept of a stationary distribution can be applied to the chaotic behavior of a difference equation model. The typical difference equations used as population models possess so–called invariant measures; that is, the long–run abundance frequencies of a chaotic population approach a limiting stationary distribution (see Lasota & Mackey 1985). For instance, the simple difference equation given by $n_{t+1} = 4n_t(1 - n_t)$ has a "stationary distribution" of $p(n) = \pi^{-1}[n(1-n)]^{-1/2}$, $0 < n < 1$. Stationary distributions for other chaos models can seldom be obtained analytically, but it is straightforward to iterate any given model until limiting relative frequencies are obtained. Such exercises carried out to date in my knowledge typically produce U–shaped, multimodal, or irregular stationary distributions for population abundance. By constrast, the logistic SDE produces a unimodal mound–shaped or J–shaped distribution.

Also, a common feature of chaotic behavior is the presence of quasiperiodicity. A chaotic system may have time intervals of seemingly periodic behavior followed by irregularity, or periodicity in which the amplitudes and frequencies undergo gradual precession. "Windows" of actual periodic behavior seem to be abundant in parameter sets corresponding to chaotic regimes (see Grebogi et al. 1987). One–species SDE models, by contrast, do not produce periodic behavior unless periodic forcing terms are included in the models. Time series methods such as spectral analysis can help determine if periodic components are present in the data.

Acknowledgements

This research was supported by the Forest, Wildlife and Range Experiment Station of the University of Idaho (publication no. 362), by a grant from the University of Idaho Research Council (#681–Y508), and by a grant from the USDA–ARS Rangeland Insect Laboratory (#00580401700139).

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