

# The Gamma Distribution and Weighted Multimodal Gamma Distributions as Models of Population Abundance

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## ABSTRACT

The gamma probability distribution is a general model of a population fluctuating around a steady state. We show this using stochastic differential equations (SDEs), constructed by adding white noise to the specific growth rate in deterministic models of population abundance. The gamma is an approximate stationary solution for almost any SDE having an underlying deterministic equilibrium. If the deterministic model possesses multiple stable and unstable equilibria, the approximate stationary solution to the stochastic case is a weighted gamma distribution. Modes of the stationary distribution roughly correspond to the equilibria of the deterministic model. Stochastic forces have effects similar to harvesting. These findings provide: (1) a theoretical basis for certain descriptive uses of the gamma in statistical ecology, (2) a concise graphical summary of the interactions between density dependent and density independent population regulation, (3) a statistical framework for fitting catastrophe-theoretic models to ecological data sets.

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## 0. INTRODUCTION

A gamma, or Pearson type III, distribution has the probability density function (pdf)

$$f(n) = \frac{\alpha^s}{\Gamma(s)} n^{s-1} e^{-\alpha n}, \quad 0 < n < \infty,$$

where  $\alpha$  and  $s$  are parameters ( $0 < \alpha$ ,  $0 < s$ ), and  $\Gamma(\cdot)$  is the gamma function (Patel et al. [46]).

The gamma plays a curious role in statistical ecology. It is a traditional model of population abundance, used purely for mathematical or empirical

convenience, but without any ecological meaning. The gamma is quite successful in this traditional role: it “mixes” well, has only two parameters, and is flexible enough to describe a wide variety of data sets.

For example, the gamma is utilized in a standard sampling model for spatial dispersion. The number of individuals,  $X$ , of a species appearing in a given sampling unit is treated as a Poisson variate with mean abundance  $n$ . The sampling units are then assumed heterogeneous by assigning a gamma distribution to  $n$ , resulting in a negative binomial distribution for  $X$  (e.g., Pielou [54], Boswell et al. [5]). Assigning a distribution to a parameter in this fashion is often termed “mixing” in the statistics literature.

In another example, the gamma is a “species abundance distribution” used in community ecology studies. The mean abundances of species in a collection are assumed to be independent, identically distributed gamma variates. From this assumption springs a whole range of species abundance models used in ecological work, including the negative binomial, extended negative binomial, log series, generalized log series, generalized gamma, Dirichlet, and broken-stick (Pielou [53], Kempton [34], Engen [18], Engen and Taillie [19]).

Recently Costantino and Desharnais [13] have demonstrated that the gamma distribution offers an excellent empirical description for the abundances of laboratory flour beetle (*Tribolium*) populations at steady state. They obtained the gamma as an approximation to the steady-state probability distribution for the stochastic version of a flour-beetle growth model. Their work has shown that the gamma may have a deeper biological meaning.

The purpose of this paper is to suggest a general biological cause for the gamma distribution of population abundance. We show that the gamma is the approximate stationary distribution for the abundance of a population fluctuating around a stable equilibrium. We employ the methods of stochastic differential equations (SDEs) to model the effects of random environmental fluctuations on a population’s growth rate. The result of Costantino and Desharnais [13] is thereby generalized to apply to the stochastic version of almost any population model having a stable equilibrium. We believe the gamma provides a succinct statement of the interactions between density dependent and density independent population regulation.

The paper is organized as follows. The first section sets up the machinery of SDEs, with discussion on ecological and mathematical interpretation of the models. The second section obtains the gamma distribution as the approximate steady-state solution of the SDEs. The exact solutions for various models popular in the ecological literature are compared with the corresponding gamma approximations. The third section discusses the relationships between underlying deterministic models and their stochastic counterparts. The relationships between modes and equilibria, stochastic forces and harvesting, and density dependence and independence are discussed. The

last section examines recent deterministic population models having multiple stable and unstable equilibria. The solutions to the stochastic versions of these models are weighted gamma distributions having multiple modes and antimodes corresponding to the deterministic equilibria. We close the section with some remarks on catastrophe theory and data analysis.

## 1. STOCHASTIC POPULATION-GROWTH MODELS

Deterministic models of population growth often have the general form

$$\frac{dn}{dt} = ng(n), \quad (1)$$

where  $n$  is population density at time  $t$ , and  $g(n)$  is the specific growth rate, assumed an autonomous function of  $n$  (Freedman [23]). If an equilibrium, denoted  $\bar{n}$ , exists, it will be a root of

$$g(\bar{n}) = 0. \quad (2)$$

The equilibrium is locally stable if

$$g'(\bar{n}) < 0, \quad (3)$$

that is, a population perturbed from equilibrium by a moderate amount will ultimately return to size  $\bar{n}$  if  $g(n)$  is decreasing at  $n = \bar{n}$ .

A stochastic version of this model may be constructed by adding “white noise” to  $g(n)$ . We add noise to the specific rate because environmental fluctuations chiefly affect growth or reproduction of individuals belonging to populations. The stochastic model may be written as

$$\frac{dn}{dt} = n[g(n) + h(n)z(t)], \quad (4)$$

where  $z(t)$  is a Gaussian process (white noise) with variability parameter  $\sigma^2$ , and  $h(n)$  is a function specifying any density dependence in the effects of the noise. The noise is assumed density independent in many applications by taking  $h(n) = 1$ . We view the noise as a phenomenological description of the effects of unpredictable environmental fluctuations on the specific growth rate of the population. May [38] and Roughgarden [60] provide good introductions to ecological and genetical uses of these SDEs (see also Goel and Richter-Dyn [24], Capocelli and Ricciardi [8], Tuckwell [63], Ricciardi [58], Ludwig [36], Kiester and Barakat [33], Dennis and Patil [17], Braumann [7], Karlin and Taylor [32]).

The above interpretation of the noise differs from usual usage in ecological studies. Many investigators single out a particular parameter in  $g(n)$ ,

such as  $r$  in the logistic form  $r - (r/k)n$ , and add noise to the parameter. It is important in such studies for the parameter to have a clear biological meaning in order for its noisy version to be useful. We believe the biological meaning of  $r$  and  $k$  in the logistic is still somewhat ambiguous. The parameter  $k$ , for instance, the “environmental carrying capacity,” is measured in units of population density and not in units of some explicit environmental variable. A rigorous derivation of the logistic growth model based on underlying nutrient conditions has been given (Williams [65], Dennis [14]), but it requires some rather restrictive assumptions about how organisms feed. Instead, we view the logistic as an approximation of some more detailed, unspecified, growth model (Section 2). Likewise, the noise fluctuations are not measured in units of environmental factors (such as temperature or nutrient supply) but rather in units of the quantity to which noise is added. We here use noise in a statistical sense as a model of random fluctuations in the specific growth rate caused by a variety of unspecified environmental variables.

Differences of interpretation aside, adding noise to any particular parameter occurring linearly in  $g(n)$  will produce an SDE in the form of (4).

Strictly speaking, models such as (4) must be defined in terms of a stochastic integral, two common definitions being the “Ito” and the “Stratonovich” calculi (see, for example, Mortensen [42]). The difference between the two calculi has caused some controversy in ecology (Feldman and Roughgarden [20]), but is mostly semantic (Braumann [6]). Accordingly, we shall here list results from both calculi with the help of an “Ito-Stratonovich indicator” variable,  $\omega$ :

$$\omega = \begin{cases} \sigma^2 & \text{if Ito calculus is used;} \\ \sigma^2/2 & \text{if Stratonovich calculus is used.} \end{cases}$$

Of primary interest is the pdf of  $n$  at time  $t$ , denoted  $f(n, t)$ . According to the usual theory for these stochastic models,  $f(n, t)$  satisfies a partial differential equation of the form

$$\frac{\partial f(n, t)}{\partial t} = \frac{1}{2} \frac{\partial^2 [v(n)f(n, t)]}{\partial n^2} - \frac{\partial [m(n)f(n, t)]}{\partial n}, \quad (5)$$

where  $v(n) = \sigma^2 n^2 [h(n)]^2$  and  $m(n) = ng(n) + (\sigma^2 - \omega)nh(n)[h(n) + nh'(n)]$ . For many models,  $f(n, t)$  approaches a limiting, stationary pdf, denoted  $f(n)$ , as  $t \rightarrow \infty$ . The population then attains a stochastic equilibrium. Setting  $\partial f(n)/\partial t = 0$  in (5) gives Wright’s [67] formula for the equilibrium

pdf ( $0 < n < \infty$ ):

$$f(n) = \psi \exp \left( \frac{2}{\sigma^2} \int \frac{1}{n} \left\{ \frac{g(n)}{[h(n)]^2} \right\} dn - \frac{2\omega}{\sigma^2} \log n - \frac{2\omega}{\sigma^2} \log h(n) \right). \quad (6)$$

Here  $\psi$  is a constant found by setting the area under the curve  $f(n)$  equal to one.

The difference between Ito and Stratonovich calculus manifests itself in equilibrium in the form of weighted distributions. A weighted distribution has a pdf,  $f_w(n)$ , of the form

$$f_w(n) = \frac{w(n)f(n)}{E[w(N)]}, \quad (7)$$

where  $w(n)$  is a weight associated with each value of  $n$ , and  $f(n)$  is a pdf (Rao [57], Patil and Rao [48,49]). Denoting the Ito and Stratonovich equilibrium pdfs by  $f_I(n)$  and  $f_S(n)$  respectively, we find from (6) that

$$f_S(n) = \frac{nh(n)f_I(n)}{E[N_I h(N_I)]}, \quad (8)$$

with  $N_I$  being the Ito random variable for the population size. The Stratonovich pdf is thus just a weighted version of the Ito pdf.

Furthermore, a Stratonovich variable is a size biased Ito variable under the special case of density independent noise. Taking  $h(n) = 1$  in (8) gives

$$f_S(n) = \frac{nf_I(n)}{E[N_I]}, \quad (9)$$

which is the pdf for the size biased Ito variable (Patil and Rao [49]). A result following immediately from (9) is that

$$\frac{1}{E[1/N_S]} = E[N_I], \quad (10)$$

where  $1/E[1/N_S]$  is the harmonic mean of the Stratonovich variable.

The *qualitative* predictions of the two calculi under density independent noise will always agree at equilibrium. Note that when  $h(n) = 1$ ,  $f(n)$  (6) takes the form

$$f(n) = \psi e^{a \log n + b(n)}, \quad (11)$$

where  $a = -2\omega/\sigma^2$ , and  $b(n) = (2/\sigma^2) \int [g(n)/n] dn$ . This pdf belongs to

the log-exponential family of pdfs defined by Patil and Ord [47]. The log-exponential family has the “form invariance” property: the size biased version always retains the same form as the original pdf. Thus, if the Ito calculus predicted a certain type of equilibrium distribution, such as a gamma, lognormal, etc., the Stratonovich calculus would predict the same type (provided both pdfs exist).

## 2. THE GAMMA DISTRIBUTION

### THE GAMMA APPROXIMATION

A suitable approximation to (6) exists in the case where the deterministic model (1) has a stable equilibrium. In other words, an approximate probability distribution is available for the size of a population fluctuating around a single steady state. The Taylor series expansions about  $\bar{n}$  of certain terms in the exponent of (6) give [noting (2)]:

$$\begin{aligned} \frac{g(n)}{[h(n)]^2} &= \frac{g(\bar{n})}{[h(\bar{n})]^2} + (n - \bar{n}) \left\{ \frac{g'(\bar{n})}{[h(\bar{n})]^2} - \frac{2g(\bar{n})h'(\bar{n})}{[h(\bar{n})]^3} \right\} \\ &\quad + \text{higher-order terms} \\ &\approx (n - \bar{n}) \frac{g'(\bar{n})}{[h(\bar{n})]^2}; \\ \log h(n) &= \log h(\bar{n}) + (n - \bar{n}) \frac{h'(\bar{n})}{h(\bar{n})} + \text{higher-order terms.} \end{aligned}$$

Using these approximations in (6) gives the gamma pdf:

$$f(n) \approx \psi n^{s-1} e^{-\alpha n}, \quad 0 < n < \infty, \quad (12)$$

where

$$\begin{aligned} \alpha &= \frac{2}{\sigma^2 h(\bar{n})} \left[ \omega h'(\bar{n}) - \frac{g'(\bar{n})}{h(\bar{n})} \right], \\ s &= \frac{-2\bar{n}g'(\bar{n})}{\sigma^2 [h(\bar{n})]^2} + 1 - \frac{2\omega}{\sigma^2}. \end{aligned}$$

The normalization constant is  $\psi = \alpha^s / \Gamma(s)$ . Conditions for the existence of this pdf are  $s > 0$  and  $\alpha > 0$ . The mean population size under the gamma is  $s/\alpha$ , while the most likely population size (mode), denoted  $\tilde{n}$ , is  $(s-1)/\alpha$ . The typical shape of the gamma is unimodal and skewed on the right (Figure 1), though the distribution is J-shaped when  $0 < s \leq 1$ . The exponential distribution is a special case of the gamma when  $s = 1$ .

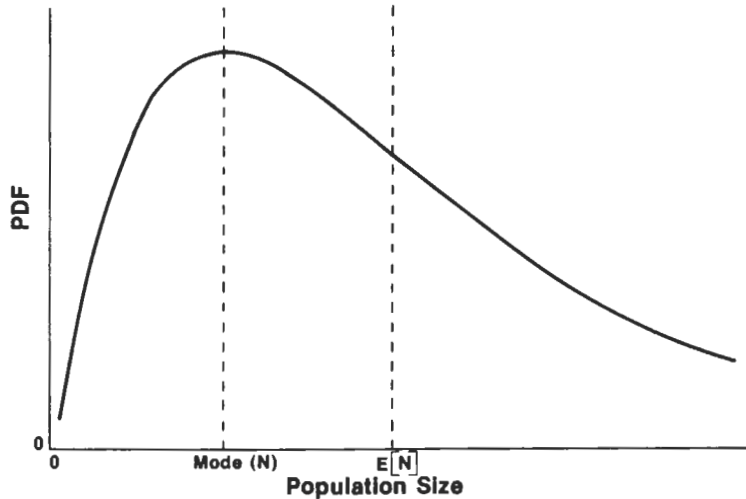


FIG. 1. The pdf for the gamma distribution plotted as a function of population size. The expected population size,  $E[N]$ , is greater than the most likely population size (mode).

The gamma distribution is thus a general model of a population fluctuating around a stable equilibrium. May [38] discusses a normal-distribution approximation to  $f(n)$  aimed primarily toward analyzing multispecies stochastic models. May's approach has the advantage of mathematical tractability for such multispecies problems. The flour-beetle data of Costantino and Desharnais [13], however, reveal a distinct right-skewness in the distributions of single species abundances at equilibrium. The gamma model preserves this empirical property of skewness. In addition, it has the added advantage of a positive range, whereas under a normal distribution, population abundance may take negative values. Nonetheless, the gamma and the normal distributions will be similar if the intensity of the stochastic forces (as measured by  $\sigma^2$ ) is very small.

*THE LOGISTIC MODEL*

The logistic equation is a Taylor series approximation near equilibrium to any deterministic model of the form (1). Specifically, expanding  $g(n)$  around  $\bar{n}$ , we have

$$\begin{aligned} \frac{dn}{dt} &= n [ g(\bar{n}) + (n - \bar{n}) g'(\bar{n}) + \dots ] \\ &\approx rn - \frac{r}{k} n^2, \end{aligned} \tag{13}$$

where  $r = -\bar{n}g'(\bar{n})$  and  $k = \bar{n}$ . The logistic model has a colorful history in

ecology (Hutchinson [31]). The above Taylor-series approach attributes no particular significance to the parameters  $r$  and  $k$  beyond being the intercepts for the vertical and horizontal axes of the linear approximation to  $g(n)$ .

As May [38] and others have noted, the stochastic version of the logistic with density independent noise yields the gamma as an exact result. Specifically, using  $g(n) = r - (r/k)n$  and  $h(n) = 1$  in (4) produces the gamma pdf (12) exactly, with  $\alpha = 2r/(k\sigma^2)$  and  $s = (2r/\sigma^2) + 1 - (2\omega/\sigma^2)$ . The mean and the mode of the distribution become  $E[N] = k[1 + (\sigma^2/2 - \omega)/r]$  and  $\bar{n} = k(1 - \omega/r)$ . The expected population size would thus be equal to (Stratonovich) or slightly less than (Ito) the deterministic equilibrium,  $k$ . The mode falls below  $k$ .

#### A FLOUR-BEETLE MODEL

Costantino and Desharnais [13] studied some stochastic versions of a model describing growth of flour-beetle populations (Lloyd [35]):

$$\frac{dn}{dt} = n(\lambda e^{-\beta n} - \mu). \quad (14)$$

A model in discrete time similar to (14) is known in the fisheries literature as the Ricker model (after Ricker [59]). A stable equilibrium exists at  $\bar{n} = (1/\beta)\log(\lambda/\mu)$ . Costantino and Desharnais approximate unwieldy exact stationary distributions for stochastic versions of (14) by gamma distributions. With  $h(n) = 1$ , the exact stationary distribution for (4) using (14) is

$$f(n) = \psi n^{-\theta_1 - 1} e^{-\theta_2 E_1(\theta_3 n)}, \quad 0 < n < \infty, \quad (15)$$

where  $\theta_1 = (2\mu/\sigma^2) + (2\omega/\sigma^2) - 1$ ,  $\theta_2 = 2\lambda/\sigma^2$ ,  $\theta_3 = \beta$ , and  $E_1(\cdot)$  is the exponential-integral function (Abramowitz and Stegun [1]). The gamma approximation (12) gives  $\alpha = 2\beta\mu/\sigma^2$ ,  $s = (2/\sigma^2)[\mu\log(\lambda/\mu) - \omega] + 1$ . The exact pdf (15) has a mode at  $\bar{n} - (1/\beta)\log(1 + \omega/\mu)$ , whereas the gamma has a mode at  $\bar{n} - (1/\beta)(\omega/\mu)$ , which reasonably approximates the exact mode when  $\omega/\mu$  is small. Evaluating  $\psi$  in (15) requires numerical integration.

#### FISHERIES MODELS

May et al. [41] examine the stochastic behavior of numerous models popular in the fisheries-harvesting literature, including (14) above. Two of the models are

$$\frac{dn}{dt} = n \left[ \frac{\lambda}{\beta + n} - \mu \right], \quad (16)$$

$$\frac{dn}{dt} = n[\lambda\beta - \lambda\log n]. \quad (17)$$



The discrete-time (“stock-recruitment”) version of (16) is called the Beverton-Holt model (Beverton and Holt [4]), and (17) is due to Fox [22]. A stable equilibrium exists for (16) at  $\bar{n} = (\lambda/\mu) - \beta$ , and for (17) at  $\bar{n} = e^\beta$ . Exact equilibrium distributions resulting in the stochastic cases using  $h(n) = 1$  are, respectively, the beta type II (of which the  $F$  distribution is a special case) given by

$$f(n) = \psi n^{\theta_1 - \theta_2 - 1} (\beta + n)^{-\theta_1}, \quad 0 < n < \infty, \quad (18)$$

where  $\theta_1 = 2\lambda/(\beta\sigma^2)$ ,  $\theta_2 = (2\mu/\sigma^2) + (2\omega/\sigma^2) - 1$ , and  $\psi = \beta^{\theta_2} \Gamma(\theta_1) / [\Gamma(\theta_1 - \theta_2) \Gamma(\theta_2)]$ ; and the lognormal:

$$f(n) = \psi n^{-1} \exp\left[-\frac{(\log n - \theta_1)^2}{2\theta_2}\right], \quad 0 < n < \infty, \quad (19)$$

where  $\theta_1 = \beta + [\sigma^2/(2\lambda)] - (\omega/\lambda)$ ,  $\theta_2 = \sigma^2/(2\lambda)$ , and  $\psi = 1/\sqrt{\theta_2 2\pi}$ . The gamma approximation to (18) would have  $\alpha = (2\mu/\sigma^2)(\mu/\lambda)$  and  $s = [(2\mu/\sigma^2)(1 - \beta\mu/\lambda)] + 1 - (2\omega/\sigma^2)$ . The mode of the gamma at  $\bar{n} - (\lambda/\mu)(\omega/\mu)$  would approximate the true mode of (18) at  $\bar{n} - (\lambda/\mu)[\omega/(\mu + \omega)]$  for small  $\omega$ . Approximating (19) by a gamma distribution would set

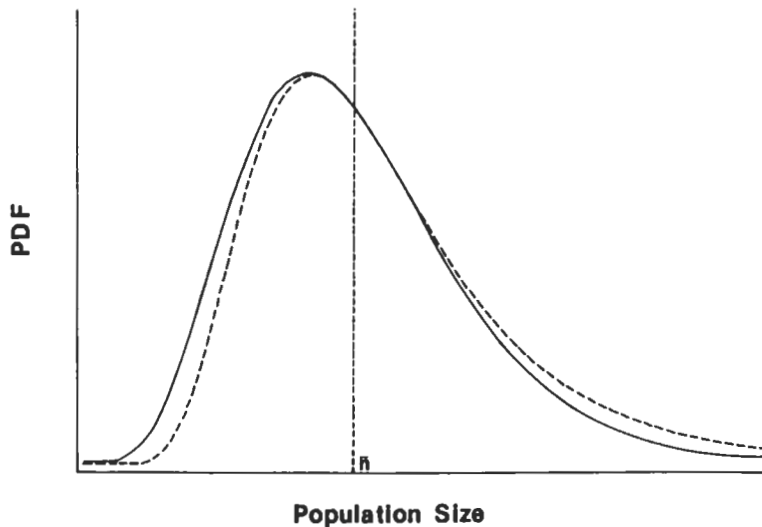


FIG. 2. The beta type-II pdf (dashed curve) compared with the gamma approximation (solid curve). The vertical dashed line gives location of the deterministic equilibrium from the model (16).

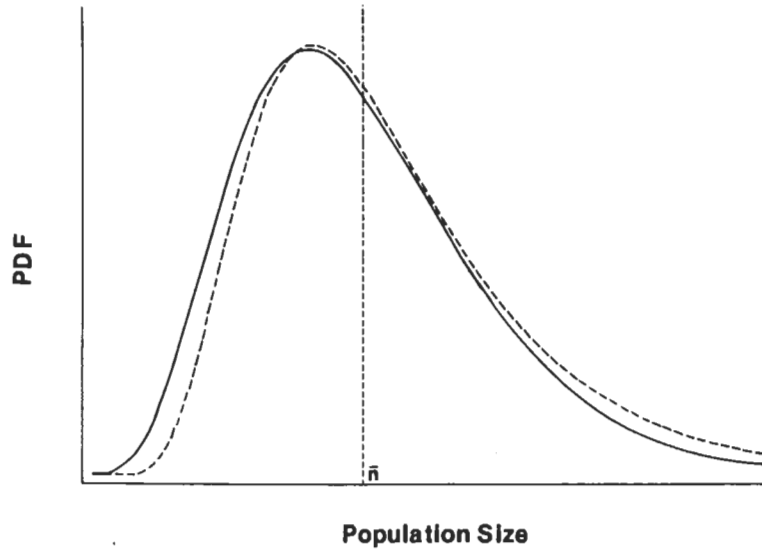


FIG. 3. The lognormal pdf (dashed curve) compared with the gamma approximation (solid curve). The vertical dashed line gives location of the deterministic equilibrium from the model (17).

$\alpha = (2\lambda/\sigma^2)e^{-\beta}$  and  $s = (2\lambda/\sigma^2) - (2\omega/\sigma^2) + 1$ . While the lognormal model (19) has a mode at  $\bar{n}(e^{-\omega/\lambda})$ , the gamma mode at  $\bar{n}(1 - \omega/\lambda)$  would be close by when  $\omega$  is small compared to  $\lambda$ . The gamma approximations to both the beta type II (Figure 2) and the lognormal (Figure 3) resemble the exact distributions very closely.

In most practical instances, one would not be able to discriminate between these exact distributions and the gamma on the basis of fit to a given data set. The distributions are shaped similarly and tend to describe data equally well (or poorly). Further information would be necessary to distinguish among specific underlying forms for  $g(n)$  in these models. In the absence of such information, the gamma would seem a logical choice because of its generality.

#### SPECIES ABUNDANCE DISTRIBUTIONS

R. A. Fisher conceived of using the gamma model as an underlying common model of abundance for a collection of species (Fisher et al. [21]). F. Preston, on the other hand, utilized the lognormal in a similar role (Preston [55,56]). That the gamma has some underlying basis as a general equilibrium model for population size lends credence to Fisher's instinct. The lognormal (19) as an equilibrium model is not so convincing, though: (17) has

the unbiological property that  $g(n) \rightarrow \infty$  as  $n \rightarrow 0$ . However, as a *nonequilibrium* model, the lognormal does indeed have desirable properties. If the simple exponential-growth equation,  $dn/dt = \lambda n$ , is made stochastic with  $h(n) = 1$ , then the nonequilibrium pdf  $f(n, t)$  is equal to (19), with  $\theta_1 = \log n_0 + \lambda t + [(\sigma^2/2) - \omega]t$ ,  $\theta_2 = \sigma^2 t$ . Thus, Preston's model seems meaningful for pioneer, colonizing communities, whereas Fisher's model seems more appropriate for mature, equilibrium communities (Dennis and Patil [17]).

Interestingly, the Ito-Stratonovich difference occurs in the form of a weighted distribution in this nonequilibrium lognormal model. Specifically,

$$f_S(n, t) = \frac{n^{1/2} f_I(n, t)}{E[(N_I(t))^{1/2}]} \quad (20)$$

Several interrelationships between arithmetic means, geometric means, harmonic means, and modes result:  $E[N_I] = \exp\{E[\log N_S]\}$ ,  $\exp\{E[\log N_I]\} = 1/E[1/N_S]$ , and  $1/E[1/N_I] = \tilde{n}_S$ , where  $\tilde{n}_S$  is the mode of the Stratonovich pdf. The semantic differences between the Ito and Stratonovich approaches for this simple exponential growth model are amusing: most common measures of central tendency for the Ito version equal other such measures for the Stratonovich version.

#### BAYESIAN STATISTICS

Bayesian statistical analysis (see Hogg and Craig [27]) has not gained much favor among ecologists, in contrast to the widespread attention it receives in the statistics literature. Quantifying and incorporating subjective beliefs into data analysis is a statistical procedure that practicing scientists rightly regard with skepticism. While not advocating wholesale use of Bayesian methods, we would like to point out how the gamma population model might help eliminate some of the subjectivity involved. An example follows.

Consider a problem of estimating the mean population density of a species. Random plots of unit area are sampled, and the numbers of organisms in each plot,  $x_1, x_2, \dots, x_m$  say, are recorded. A common statistical model would take these values to be a random sample from a Poisson distribution with parameter  $n$ . The statistical method for estimating  $n$  most familiar to ecologists uses the sample mean,  $\hat{n} = (\sum x_i)/m$ , which is the maximum-likelihood estimate.

A Bayesian approach would have the investigator summarize prior knowledge about the value of  $n$  into a probability distribution (the prior distribution) for  $n$ . A convenient prior distribution in Bayesian analysis has traditionally been the gamma, since its conjugacy with the Poisson distribution produces estimates that are mathematically easy to handle. Through the use of the Bayes rule of conditional probability, the distribution of  $n$

conditional upon the data (the posterior distribution) is obtained. One then typically picks, as an estimate (or rather, predictor) of  $n$ , the average value of  $n$  given the data. This estimate becomes  $\hat{n}_B = (\sum x_i / m)m / (m + \alpha) + (s/\alpha)\alpha / (m + \alpha)$  when the prior distribution is gamma with parameters  $\alpha$  and  $s$ . The operational problem with this approach is the subjectivity involved in using the gamma prior distribution and picking the numerical values of  $\alpha$  and  $s$ .

For some studies, it may be reasonable to assume the population is at steady state. Information from previous population monitoring, for instance, may support such an assumption. The gamma distribution is then a theoretical model of the population's abundance. Under these circumstances, incorporation of a gamma prior distribution into current population estimates seems reasonable rather than subjective. Data on previous abundances of the population, such as the mean and variance of previous abundances, may be used to estimate  $\alpha$  and  $s$  in a prior gamma distribution. The above Bayesian estimate  $\hat{n}_B$  is seen to be a weighted average of the maximum-likelihood estimate  $\hat{n}$  and the mean,  $s/\alpha$ , of the prior distribution. If an apparent anomalous value of  $\hat{n}$  turned up in a continued monitoring study, the past equilibrium history of population abundance would carry some weight in the estimate  $\hat{n}_B$ . However, most of the weight will be carried by  $\hat{n}$  if the sample size  $m$  is large.

### 3. RELATIONSHIPS BETWEEN STOCHASTIC AND DETERMINISTIC MODELS

#### MODES AND EQUILIBRIA

There is an important relationship between the equilibria of a deterministic system and the modes of the stationary pdf in the stochastic system (Cobb [11]). The relationship has significant implications for population dynamics. In Cobb's [11] terminology, a *mode* is a local maximum of  $f(n)$ , an *antimode* is a local minimum, and a *pole* is a point where  $f(n) \rightarrow \infty$ . Modes and antimodes of (6), denoted  $\tilde{n}_i$ , are found by solving for the roots of  $d \log f(n) / dn = 0$ :

$$g(\tilde{n}) - \omega h(\tilde{n}) [h(\tilde{n}) + \tilde{n}h'(\tilde{n})] = 0. \quad (21)$$

Whether a mode  $\tilde{n}$  is greater or less than a corresponding deterministic steady state  $\bar{n}$  [from (2)] will depend on specific properties of the density dependent noise modulation term,  $h(n)$ . The fact that (2) may have only one root  $\bar{n}$  does not preclude the existence of several roots to (21). A multimodal distribution could arise from a deterministic system with a single equilibrium, while a system with multiple equilibria might produce a unimodal distribution.

The gamma would approximate the true distribution of population size only near a single stable equilibrium. However, various deterministic models receiving wide attention in the ecological literature possess multiple stable and unstable equilibria (see review by May [40]). Intuitively, one might expect a stable equilibrium in a deterministic system to influence the location of the locally most likely population size in the stochastic system. Also, an unstable equilibrium should determine one of the locally least likely population sizes. This is indeed the case when the noise is density independent. In fact, the effect of density independent noise added to models like (1) is similar to the effect of harvesting.

#### NOISE AND HARVESTING

Models of commercial renewable resources frequently assume a population growing according to (1) suffers harvesting at a rate  $\epsilon n$ , where  $\epsilon$  is a constant harvesting effort (Clark [10]). Thus,

$$\frac{dn}{dt} = ng(n) - \epsilon n. \quad (22)$$

An equilibrium is then found as a root of

$$g(\bar{n}) - \epsilon = 0. \quad (23)$$

A stable harvesting equilibrium from (23) will be less than the stable equilibrium from the unexploited population (2). Likewise, an unstable harvesting equilibrium will be greater than the unstable, nonharvesting equilibrium.

Consider now a stochastic population growing (without harvesting) according to (4) with  $h(n) = 1$ . A mode of the stationary pdf for population size is then, from (21), a root of

$$g(\bar{n}) - \omega = 0. \quad (24)$$

The mode of the stochastic model is identical to the equilibrium of a deterministic population harvested at a constant effort  $\omega$ , as is clear from comparing (24) and (23). Thus, a population experiencing density independent environmental fluctuations is most likely to be found below its deterministic steady state.

#### DENSITY INDEPENDENCE AND DENSITY DEPENDENCE

These SDE models provide a concise summary of the interactions between density independent and density dependent population regulation. The famous controversy over whether density independent or density dependent

forces are predominantly responsible for population regulation divided ecologists for many years (see for instance, Colinvaux [12]). Contemporary ecological theory has come to rest heavily on the importance of density dependence (Roughgarden [60], Hutchinson [31], May [39]). Applied ecologists in resource management, by contrast, have frequently found the field data to be too scattered for the density dependent models to be useful. For instance, the recent willingness of fisheries scientists to adopt a density independent approach to the analysis of recruitment distributions (Hennemuth et al. [26]) shows there is still life in the controversy.

The SDE (4) with  $h(n) = 1$  represents a quantitative refinement of Horn's [29] graphical "resolution" to the issue of density independence versus density dependence. Displayed in Figure 4 are a logistic growth rate (13) and a "harvesting" term  $\omega n$  contrasted as functions of  $n$ . Their intersection provides the location of the mode to the stationary gamma pdf. Horn [29] presented a similar figure, only the linear term  $\omega n$  was a deterministic removal rate representing deaths from density independent causes, and the intersection was a deterministic equilibrium. The refinement represented by Figure 4 is to treat only density dependent forces as deterministic, with the density independent environmental factors affecting a population stochastically. In engineering parlance, density dependence is the underlying "signal," and density independence is the "noise." The result puts the most likely

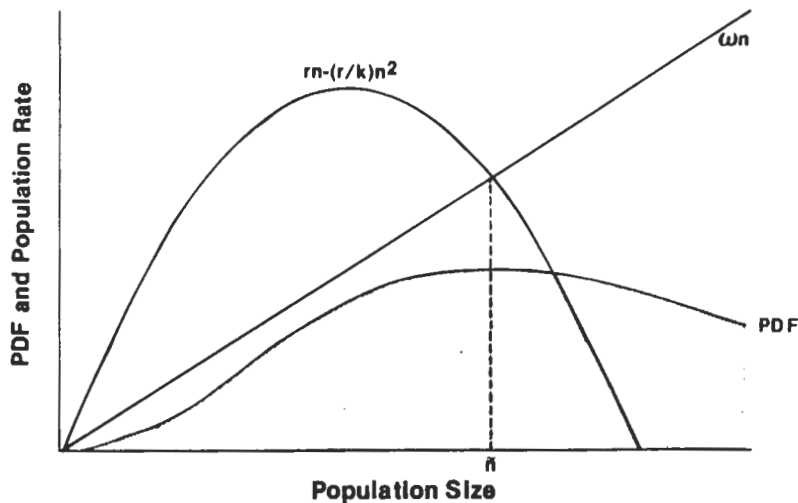


FIG. 4. The relationship between density dependent and density independent population regulation. The curve  $rn - (r/k)n^2$  is the growth rate from the underlying deterministic model of density dependent regulation. The intensity of stochastic density independent forces (environmental fluctuations) is the line  $\omega n$ . Intersection of the curve and line provides the location of the mode of the gamma distribution of population size.

population size,  $\bar{n}$ , below the equilibrium that would pertain in the absence of stochastic effects. Also,  $\sigma^2$ , the scaling parameter in the noise, is in some sense a measure of the intensity or unpredictability of the stochastic forces. Recalling that  $\omega$  is proportional to  $\sigma^2$  shows the mode to be decreasing with increasing environmental variability. Additionally, the variance of the stationary gamma pdf, given by  $\text{Var}(N) = s/\alpha^2 = [\sigma^2 k^2 / (2r)][1 + (\sigma^2/2 - \omega)/r]$ , increases with increasing  $\sigma^2$ . Extreme population sizes, large and small, would be more likely with increasing environmental fluctuations.

#### 4. WEIGHTED, MULTIMODAL GAMMA DISTRIBUTIONS

A variety of deterministic population models have multiple stable and unstable equilibria (examples include Volterra [64], Odum and Alee [44], Philip [52], Takahashi [62], Clark [9], Noy-Meir [43], Peterman [50], May [40], Huberman [30], Ludwig et al. [37], Berryman [2], [3], Dennis [16]). Such models frequently take the form (1) modified by an additional term  $p(n)$ :

$$\frac{dn}{dt} = n[g(n) - p(n)]. \quad (25)$$

Here  $p(n)$  is a specific rate describing the effects of predation, harvesting, Allee effects such as rare matings, or other forces. We adopt the minus sign in (25) as a convention because  $p(n)$  is most frequently some type of removal rate. In predator-prey studies,  $np(n)$  is the "functional response" (Holling [28]) of the predation rate to the abundance of prey,  $n$ . When (25) is altered into a stochastic model, the function  $p(n)$  is manifested as a weight function in the stationary distribution.

##### WEIGHTED GAMMA DISTRIBUTIONS

The stochastic version of (25) becomes

$$\frac{dn}{dt} = n[g(n) - p(n) + h(n)z(t)], \quad (26)$$

by analogy to the original stochastic model (4) without the removal rate. The stationary pdf for this model,  $f_p(n)$  say, is a weighted version of the pdf from the original model:

$$f_p(n) = \frac{w(n)f(n)}{E[w(N)]}, \quad 0 < n < \infty, \quad (27)$$

where  $f(n)$  is given by (6), and

$$w(n) = \exp\left\{-\frac{2}{\sigma^2} \int \frac{p(n)}{n[h(n)]^2} dn\right\}. \quad (28)$$

Evaluating  $E[w(N)]$  will usually require numerical integration.

The most frequent applications assume density independent noise, giving  $h(n) = 1$  and  $w(n) = \exp\{-(2/\sigma^2) \int [p(n)/n] dn\}$  in (27). Also, if  $g(n)$  in (26) is the logistic term  $r - (r/k)n$ , then  $f(n)$  is a gamma distribution [see (12)], and  $f_p(n)$  is a weighted gamma distribution:

$$f_p(n) = \frac{[\alpha^s/\Gamma(s)]n^{s-1}e^{-\alpha n}w(n)}{E[w(N)]}, \quad 0 < n < \infty, \quad (29)$$

where  $\alpha = 2r/(k\sigma^2)$ , and  $s = (2r/\sigma^2) + 1 - (2\omega/\sigma^2)$ . Depending on the form of the weighting function  $w(n)$  in (29), the pdf may display unimodal or multimodal shapes. For such models, modes and antimodes will be roots of

$$r - \frac{r}{k}\bar{n} - p(\bar{n}) - \omega = 0. \quad (30)$$

A few examples follow. The examples assume the model is in the form (26), with  $h(n) = 1$  and  $g(n) = r - (r/k)n$ .

#### CONSTANT-EFFORT HARVESTING

The Schaefer [61] harvesting model uses  $p(n) = \varepsilon$ , as in (22). The stochastic version has a stationary gamma pdf:

$$f_p(n) = \frac{\alpha^{s-\gamma}n^{s-\gamma-1}e^{-\alpha n}}{\Gamma(s-\gamma)}, \quad 0 < n < \infty. \quad (31)$$

Here  $\gamma = 2\varepsilon/\sigma^2$ . The single mode at  $k(1 - \varepsilon/r - \omega/r)$  is less than the mode without harvesting ( $\varepsilon = 0$ ), which in turn is less than the deterministic equilibrium without harvesting ( $\omega = 0$ ,  $\varepsilon = 0$ ). May et al. [41] provide additional results on this model.

#### CONVEX REMOVAL RATE

A frequently used predation model takes  $p(n) = \lambda/(\beta + n)$ , a convex function of  $n$ . Then  $np(n)$  is the familiar type-II functional response in predator-prey theory (Holling [28]). Here  $\lambda$  is the upper maximum at which the predators' feeding rate saturates, and  $\beta$  is the population size:  $\beta p(\beta) = \lambda/2$ . Williams [66] demonstrates how this functional response can arise from a wide variety of predation mechanisms. Peterman and Steer [51] discuss its application as a harvest rate. The model also arises in connection with the growth of sexually reproducing populations. The term  $np(n)$  is used to represent the decline in growth rate due to insufficient mating encounters at low population densities (Dennis [15,16]).

The deterministic model (25) displays no, one, or two equilibria (nonzero) depending on parameter values (Dennis [16]). In the case of two equilibria,



one of them is unstable, representing a lower critical density below which the population declines to extinction. The upper equilibrium is stable.

The stationary pdf (29) using  $p(n) = \lambda/(\beta + n)$  is

$$f_p(n) = \psi n^{s-\theta-1} e^{-an} (\beta + n)^\theta, \quad 0 < n < \infty. \quad (32)$$

Here  $\theta = 2\lambda/(\beta\sigma^2)$ ,  $\alpha, s$  are given in (29), and the normalization constant can be expressed as  $\psi^{-1} = \Psi(s - \theta, s + 1, \alpha\beta)\Gamma(s - \theta)\beta^s$ , where  $\Psi$  is a degenerate hypergeometric function (Gradshteyn and Ryzhik [25]; also called a confluent hypergeometric function by Abramowitz and Stegun [1]). A condition for existence of this pdf is  $s - \theta > 0$ . The condition reduces to  $r > \lambda/\beta$  (Stratonovich) or  $r > \lambda/\beta + \sigma^2/2$  (Ito), and if it is not met, the stationary pdf is degenerate at zero, meaning certain extinction. This existence condition corresponds to having only one equilibrium in the deterministic model (25). The lower unstable equilibrium vanishes when  $r > \lambda/\beta$ , since  $r$  and  $\lambda/\beta$  are the vertical-axis intercepts of  $g(n)$  and  $p(n)$ , respectively. Only the upper stable equilibrium would remain. In other words, the pdf (32) exists only if the natural reproductive rate of the deterministic population is always high enough at lower densities to overcome negative effects of the removal rate.

Modes and antimodes of (32), however, behave as if there were an additional harvesting burden on the deterministic population. From (30), modes and antimodes are roots of

$$r - \frac{r}{k} \bar{n} - \frac{\lambda}{\beta + \bar{n}} - \omega = 0. \quad (33)$$

This is a simple quadratic expression with roots,  $\bar{n}_1$  and  $\bar{n}_2$ , given by  $\bar{n} = [-B \pm (B^2 - 4AC)^{1/2}]/(2A)$ , where  $A = -r/k$ ,  $B = r(1 - \beta/k) - \omega$ , and  $C = \beta(r - \omega) - \lambda$ . The pdf (32) has several shapes depending on the values of these roots. For small  $\sigma^2$ , only the root  $\bar{n}_2$  is positive (Figure 5) and the pdf will have one mode (Figure 6). As  $\sigma^2$  increases the root  $\bar{n}_1$  becomes positive (Figure 5), producing an antimode in the pdf (Figure 6). The antimode is a stochastic equivalent of a deterministic critical density, being a point where the population size is unlikely to be found. The two roots merge when  $\omega = r(1 + \beta/k) - 2(\lambda r/k)^{1/2}$  (Figure 5). The corresponding pdf has a "shoulder" (Figure 6). Finally, large values of  $\sigma^2$  make the roots vanish (Figure 5) and yield a declining monotone pdf with a pole at zero (Figure 6).

In summary, adding these stochastic effects to the deterministic model substantially alters its dynamical character by amplifying, as it were, the "removal load." Population extinction is certain under the stochastic model for the usual parameter values producing two equilibria in the deterministic case. Even if the population's natural reproductive rate compensates for

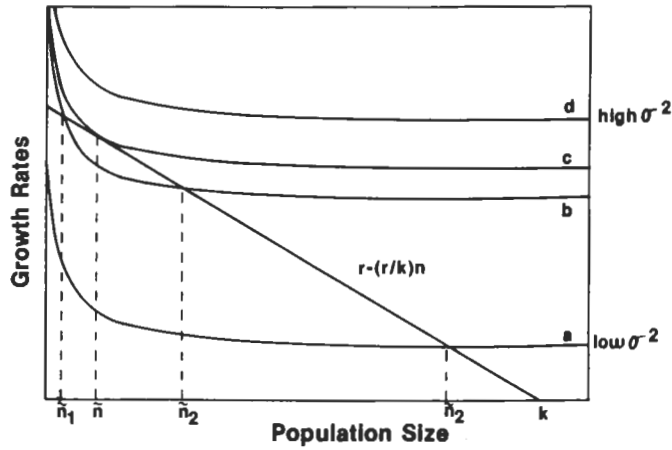


FIG. 5. Intersections of the line  $r - (r/k)n$  with the curve  $\lambda/(\beta + n) + \omega$  provide locations of modes and antimodes in the stationary distribution (32). (a) Low value of  $\sigma^2$  gives only one mode,  $\bar{n}_2$ . (b) Intermediate value of  $\sigma^2$  results in one antimode,  $\bar{n}_1$ , and one mode,  $\bar{n}_2$ . (c) As  $\sigma^2$  increases, mode and antimode merge. (d) No modes or antimodes in the stationary pdf occur for high  $\sigma^2$  values.

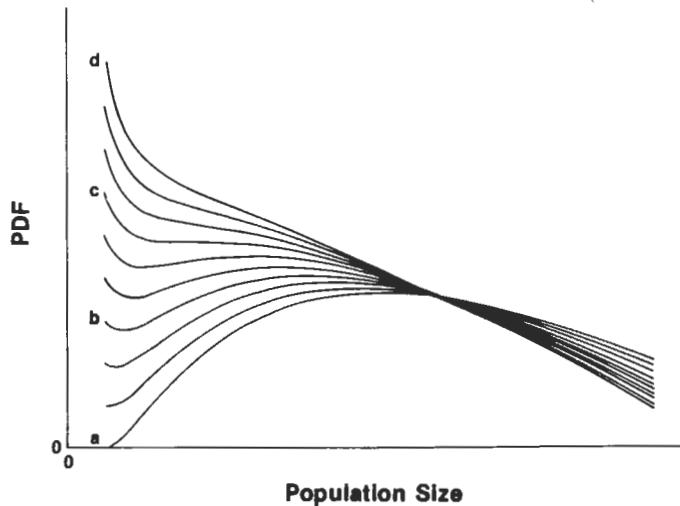


FIG. 6. Shapes of the stationary distribution (32) plotted for various  $\sigma^2$  values. (a) Low  $\sigma^2$ ; one mode. (b) Intermediate  $\sigma^2$ ; one antimode, one mode. (c) Mode and antimode merge into a shoulder. (d) High  $\sigma^2$ ; pdf decreases monotonically.

removal in the deterministic case, the removal rate may be expressed in the stochastic case in the form of the antimode of Figure 6. Periods of population abundance (mode) will be interspersed with periods of chronic rarity (pole at zero). As the stochastic factors become more severe (i.e., increasing  $\sigma^2$ ), rarity, and ultimate extinction, would prevail (Figure 6).

Philip [52] proposed a deterministic model of population growth in the presence of rare matings using the convex removal rate  $p(n) = \lambda e^{-\beta n}$ . The stationary pdf for the stochastic version (26) is, from (29),

$$f_p(n) = \psi n^{s-1} e^{-\alpha n} e^{\gamma E_1(\beta n)}, \quad 0 < n < \infty, \quad (34)$$

where  $\gamma = 2\lambda/\sigma^2$ . Both the deterministic and the stochastic models behave quite similarly to the previous models using  $np(n) = \lambda n/(\beta + n)$ .

*SIGMOID REMOVAL RATE*

Ludwig et al. [37] propose a model of the spruce-budworm system incorporating the sigmoid-shaped term  $np(n) = \lambda n^2/(\beta^2 + n^2)$  representing predation losses. The shape is characteristic of the type-III functional response (Holling [28]). The deterministic model exhibits one, two, or three equilibria depending on parameter values. A single stable equilibrium or two stable equilibria separated by an unstable equilibrium are the most important cases. From (29), the stationary pdf for the stochastic version is

$$f_p(n) = \psi n^{s-1} e^{-\alpha n - \theta \arctan(n/\beta)}, \quad 0 < n < \infty. \quad (35)$$

Here  $\theta = 2\lambda/(\beta\sigma^2)$ , and  $\alpha$  and  $s$  are defined after Equation (29). The constant  $\psi$  must be found by numerical integration.

Modes and antimodes of  $f_p(n)$  are roots to Equation (30). In terms of the parameters in the pdf (35), modes and antimodes are roots to

$$(s-1) - \alpha \tilde{n} - \frac{\theta \beta \tilde{n}}{\beta^2 + \tilde{n}^2} = 0, \quad (36)$$

or, rearranged into a cubic polynomial,  $\tilde{n}^3 + A\tilde{n}^2 + B\tilde{n} + C = 0$ , where  $A = -(s-1)/\alpha$ ,  $B = \beta[\beta + (\theta/\alpha)]$ ,  $C = \beta^2[(s-1)/\alpha]$ . Defining by

$$\Delta = \left(A^3 - \frac{9}{2}AB + \frac{27}{2}C\right)^2 + (3B - A^2)^3, \quad (37)$$

the 16th-century discriminant of Cardan, we have the following shapes of  $f_p(n)$ :

(a)  $\Delta < 0, s > 1$ . The equation (36) has three real roots. If  $s > 1$ , then all three roots must be positive, as no negative values of  $\tilde{n}$  could satisfy Equation (36). Then  $f_p(n)$  would have two modes separated by an antimode.

(b)  $\Delta > 0$ ,  $s > 1$ . Equation (36) has only one positive real root, corresponding to a single mode in  $f_p(n)$ .

(c)  $\Delta = 0$ ,  $s > 1$ . There are only one or two distinct real roots;  $f_p(n)$  has one mode, or a mode and a shoulder.

(d)  $s \leq 1$ . No positive real roots exist to Equation (36). The distribution has a monotone decreasing shape, either with a pole at zero ( $s < 1$ ) or without a pole at zero ( $s = 1$ ).

Roots to (30) can be visualized by contrasting the line  $r - (r/k)n$  with the curve  $\lambda n / (\beta^2 + n^2) + \omega$  for varying  $\sigma^2$  values (Figure 7). These different  $\sigma^2$  values produce the assorted shapes of the stationary pdf (Figure 8). Other parameter changes could occur in nature as well. Examples of system parameter changes might be: (1) changes in the abundance of predators (i.e., changes in  $\lambda$  and consequent changes in  $\theta$ ), or (2) changes in the population's food supply (resulting in changes in  $k$  and consequent changes in  $\alpha$ ). In some cases a small parameter change might possibly shift  $\Delta$  or  $s$  from one "shape region" to another, causing drastic changes in the shape of the stationary pdf. Parameter changes in the deterministic system, by contrast, may produce sudden changes in the configuration of the system equilibria. The branch of mathematics known as catastrophe theory is used for classifying these changes of equilibria in deterministic systems and is being applied with increasing frequency to deterministic ecological models. Ludwig et al. [37] provide an example application of catastrophe theory to their deterministic spruce-budworm model.

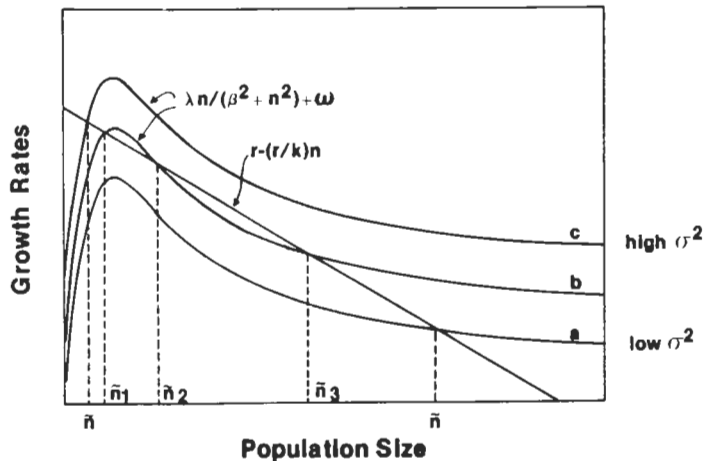


FIG. 7. Intersections of the line  $r - (r/k)n$  with the curve  $\lambda n / (\beta^2 + n^2) + \omega$  provide locations of modes and antimodes in the stationary distribution (35). (a) Low value of  $\sigma^2$  gives only one mode,  $\bar{n}$ . (b) Intermediate value of  $\sigma^2$  gives one antimode,  $\bar{n}_2$ , and two modes,  $\bar{n}_1$  and  $\bar{n}_3$ . (c) High value of  $\sigma^2$  gives one mode,  $\bar{n}$ .

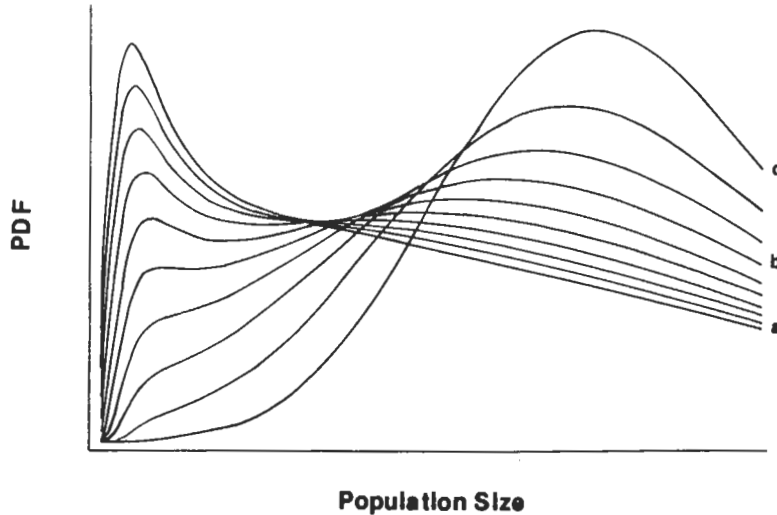


FIG. 8. Shapes of the stationary distribution (35) plotted for various  $\sigma^2$  values. (a) Low  $\sigma^2$ ; one mode. (b) Intermediate  $\sigma^2$ ; one antimode, two modes. (c) High  $\sigma^2$ ; one mode.

*CATASTROPHE THEORY*

Cobb [11] shows how the whole framework of catastrophe theory applies to stochastic equilibrium pdfs with multiple modes. Starting with deterministic models of the form

$$\frac{dn}{dt} = \delta_1 n + \delta_2 n^2 + \delta_3 n^3 + \dots + \delta_j n^j, \tag{38}$$

and introducing white noise into (38), Cobb obtains multimodal pdfs of the exponential family:

$$f_p(n) = \psi n^{\gamma_1 - 1} e^{\gamma_2 n + \gamma_3 n^2 + \dots + \gamma_j n^{j-1}}, \quad 0 < n < \infty. \tag{39}$$

Here  $\gamma_1 = (2\delta_1/\sigma^2) - (2\omega/\sigma^2) + 1$ , and  $\gamma_i = 2\delta_i/[\sigma^2(i-1)]$  for  $i = 2, 3, \dots, j$ . This is a weighted gamma pdf if we write  $\gamma_1 = s + \tau_1$  and  $\gamma_2 = -\alpha + \tau_2$ , where  $\tau_1, \tau_2$  are real numbers. An example of a population model in the form (38) was studied by Volterra [64]:

$$\frac{dn}{dt} = \delta_1 n + \delta_2 n^2 + \delta_3 n^3. \tag{40}$$

An upper stable equilibrium and a lower critical density are predicted. The stochastic version of (40) has the stationary pdf

$$f_p(n) = \psi n^{\gamma_1 - 1} e^{\gamma_2 n + \gamma_3 n^2}, \quad 0 < n < \infty, \tag{41}$$

where  $\gamma_1 = (2\delta_1/\sigma^2) - (2\omega/\sigma^2) + 1$ ,  $\gamma_2 = 2\delta_2/\sigma^2$ ,  $\gamma_3 = \delta_3/\sigma^2$ . This pdf behaves quite similarly to the pdf (32).

The pdf (39) in general may have multiple modes and antimodes. These modes and antimodes may be charted as a surface varying with all the parameters  $\delta_i$ , similar to the equilibrium surface (manifold) of the deterministic model (38). The familiar catastrophe surfaces, such as the fold, cusp, and butterfly, describe the sudden changes in modality of (39) in response to parameter changes. Readers are referred to Cobb ([11] and references therein) for more details.

#### DATA ANALYSIS

Procuring stationary pdfs for SDE models opens new possibilities for analyzing data from systems suspected of having multiple equilibria. In the modeling approach of this paper, the deterministic forces constitute the underlying signal of the system, while the stochastic forces constitute the noise. A stationary pdf forms an explicit frequency distribution for the abundances of an ensemble of populations growing under the same stochastic conditions, or for the long-run history of the abundance of a single population. Data from such situations may be used to estimate the parameters of the stationary pdfs for any proposed deterministic models. Maximum-likelihood techniques for parameter estimation (see Hogg and Craig [27]) allow explicit hypothesis tests for goodness of fit. Furthermore, maximum-likelihood techniques allow use of the likelihood-ratio tests for testing complex models (e.g., multimodal pdfs) against simple models (e.g., unimodal pdfs) contained within the complex ones as special cases. Cobb [11] outlines these procedures for models in the forms (38) and (39). The procedures may of course be used for other pdfs as well, though extensive computing will often be required using maximization algorithms such as the Nelder-Mead method (see Olsson and Nelson [45]).

#### CONCLUSIONS

A useful way of constructing stochastic models is by adding white noise to the specific growth rate in deterministic differential-equation models of population abundance. The noise is a statistical description of the random fluctuations in growth rate caused by unspecified environmental factors. If the deterministic model has a stable equilibrium, the approximate stationary distribution of population abundance for the stochastic version is a gamma distribution. Thus, the gamma is a general model of a population fluctuating around a steady state. The gamma model is consistent with the data of Costantino and Desharnais [13] and approximates quite well the exact pdfs for various population models popular in the ecological literature.

These findings provide a theoretical basis for certain descriptive uses of the gamma model in statistical ecology, including uses as: (1) a mixing

distribution in sampling models, (2) a species abundance distribution, and (3) a prior distribution in Bayesian statistics.

Some relationships between these deterministic and stochastic models have important implications for population dynamics. Modes, rather than means, of the stationary distributions from the stochastic models roughly correspond to the equilibria from the deterministic models. Also, adding stochastic forces to a deterministic population model is similar to adding constant-effort harvesting. These relationships provide a concise graphical summary of the interactions between density dependent and density independent population regulation.

Deterministic population models often contain a removal term describing the effects on growth rate of predation, harvesting, Allee effects, or other forces. The stationary distributions for the stochastic versions of such models are weighted gamma distributions. The deterministic models may possess multiple stable and unstable equilibria, whereas the corresponding stationary distributions may display multiple modes and antimodes. Several examples of deterministic models from the ecological literature display multimodal shapes in their stochastic versions. The whole framework of catastrophe theory, used for analyzing deterministic models with multiple steady states, may be applied to the multimodal stationary distributions. Data analysis using maximum-likelihood techniques would allow explicit tests of various hypotheses concerning the models, such as unimodality versus multimodality.

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