ANALYSIS OF STEADY-STATE POPULATIONS WITH THE GAMMA ABUNDANCE MODEL: APPLICATION TO *TRIBOLIUM*[1]

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Abstract. We develop a stochastic model for the abundance of adult populations of the flour beetle *Tribolium*. The model is in the form of a stochastic differential equation containing adult recruitment and mortality rates perturbed by multiplicative noise. A deterministic version of the model (an ordinary differential equation) predicts a fixed, stable equilibrium; by contrast, the stochastic model predicts a stationary probability distribution for population size. The model can be approximated closely by a stochastic logistic equation having a gamma distribution as a stationary solution. We develop or clarify various practical aspects of making statistical inferences for the resulting gamma abundance model, including estimation of parameters, testing goodness of fit, obtaining confidence intervals for functions of parameters, and testing to compare two gamma distributions. Analyses of 11 data sets on *Tribolium* suggest that the gamma model deserves more widespread consideration as an equilibrium abundance model for other species.

Key words: gamma distribution; parameter estimation; stochastic differential equations; stochastic population model; Tribolium.

INTRODUCTION

The empirical observation that populations do not increase in abundance indefinitely prompted the Verhulst-Pearl logistic equation to become a part of ecological theory (Hutchinson 1978, Kingsland 1985). The logistic model forecasts that a population eventually reaches a fixed equilibrium abundance. Though this prediction was an alternative to the Malthusian argument of indefinite increase, the logistic model was still inadequate. Laboratory and field populations often did not attain a fixed point equilibrium, but rather appeared to fluctuate around some average value (Allee et al. 1949:319, Andrewartha and Birch 1954:358).

Leslie (1962) was among the first to study such data as a frequency distribution of abundances observed when a population was fluctuating in the region of its steady state. While Leslie's particular model for the flour beetle *Tribolium* did not describe the data very well, his call to view population equilibrium as a stationary probability distribution has proven to be a very useful idea (Leigh 1968, Goel and Richter-Dyn 1974, Ludwig 1974, May 1974*a*, Feldman and Roughgarden 1975, Ricciardi 1977, May et al. 1978, Roughgarden 1979, Costantino and Desharnais 1981, Nisbet and Gurney 1982, Dennis and Patil 1984).

One such stationary probability distribution, the gamma distribution, may have many applications as

a model of single-species population abundance (Costantino and Desharnais 1981, Dennis and Patil 1984). With just two parameters, the model is simple, yet it is flexible enough to describe a variety of data sets. The gamma is the stationary distribution arising from a stochastic version of the logistic equation (Leigh 1968). Just as the logistic equation is a mathematical approximation to many population growth curves, the gamma can be viewed as an approximate stationary solution to the stochastic versions of those growth curves (Dennis and Patil 1984).

In this paper, we propose a role for the gamma distribution as the stochastic population equilibrium of adult numbers in flour beetle populations. We show that the gamma has underlying biological justification as a population model, and we present a variety of statistical methods for explicit testing of hypotheses associated with the model. Our specific objectives in this paper are twofold.

First, we develop the biological theory behind the gamma model. In our theory, the deterministic "signal" is an ordinary differential equation for population size based on adult recruitment and mortality rate functions. The differential equation contains a fixed, stable equilibrium population size; we clear up some persisting confusion in the ecological literature on how such models can be approximated by the logistic equation. However, the model by itself does not account for the large amount of variation present in replicate flour beetle populations. We therefore incorporate stochastic "noise" into the model, arguing that the noise

should be scaled by a function proportional to population size. Such multiplicative noise obscures not only the location of the fixed equilibrium, but even the usefulness of the equilibrium as a concept. Using the approximation technique of Dennis and Patil (1984), we then approximate the stochastic flour beetle model with a stochastic logistic equation, and derive the gamma as the stationary distribution for population size. This stochastic differential equation model has many emergent and biologically important properties that are considerably different from the deterministic version.

Second, we develop or clarify various practical aspects of making statistical inferences for the gamma model from population data sets, including estimation of parameters, testing goodness of fit, obtaining confidence intervals for parameters, and testing to compare two gamma distributions. We advocate using a multinomial likelihood function for the inferences, since computing is easily accomplished with nonlinear least squares packages, and since chi-square goodness-of-fit tests are then valid. An assumption for this approach, when applied to time series observations on one population, is that the observations are far enough apart for autocorrelation to be small. We discuss some effects of the violation of this assumption on parameter estimation and goodness-of-fit testing; this multinomial approach appears to have some robust qualities. We illustrate the various statistical inferences using 11 data sets on the flour beetle *Tribolium*.

The results presented in this paper suggest that the gamma deserves more widespread consideration as an abundance model for other species. We regard the gamma as a parsimonious, easy to use, and fully testable hypothesis about single species population regulation. By presenting these results, we hope that the gamma, and the concept of stochastic equilibrium in general, will become useful alternatives to the more familiar notions of fixed equilibria, periodic oscillations due to time lags and other factors, and deterministic chaos.

STATIONARY DISTRIBUTION MODELS

Deterministic flour beetle population models

Let $X(t)$ be a positive, real-valued, continuous function of time representing a population's abundance at time t. Ecologists traditionally have modeled changes in population abundance, in the absence of other interacting species, with an ordinary differential equation (ODE) of the form

$$dX(t) = X(t)g[X(t)] \, dt. \qquad (1)$$

Here, $dX(t)$ represents an (approximate) increment in population abundance during a small time interval from t to $t + dt$, and $g[X(t)]$ is the per-unit-abundance growth rate when the population has size $X(t)$. The function g is typically a decreasing function, with a single, stable equilibrium population size, $X(\infty)$, given by $g[X(\infty)] = 0$. For many populations, Eq. 1 is somewhat simplistic

in neglecting age classes (though see Livdahl and Sugihara [1984] for an example of how such simple dynamic behavior can emerge from complex natality and mortality schedules). For flour beetles, however, such an ODE can usefully represent some important features in the dynamics of the adult age class.

In the species *T. castaneum* and *T. confusum,* an important life stage interaction is the cannibalism of pupae by adults. If we let C be the per capita rate at which adults cannibalize pupae and we assume that the adults act independently, then the proportion of pupae that survive to adulthood is $\exp[-CX(t)]$, where $X(t)$ is the total number of adults. Coupling this density-dependent function together with the density-independent rates of pupal production, B, and adult mortality, D, we have

$$dX(t) = X(t)[Be^{-CX(t)} - D] \, dt \qquad (2)$$

as an ODE of the form of Eq. 1 for the incremental change in adult numbers. The nonlinear recruitment rate function $X(t)B \exp[-CX(t)]$ has appeared throughout the *Tribolium* literature: Crombie (1946), Landahl (1955*a, b*), Rich (1956), Neyman et al. (1956), Taylor (1965, 1967, 1968, 1971), Lloyd (1968), and Sonleitner (1977) are examples of its early use. Furthermore, the population Eq. 2 has been discussed in fisheries biology by Ricker (1954, 1975*a, b*), Levin and Goodyear (1980), and May (1980), and in general population theoretical studies by Moran (1950), Cooke (1965), May (1974*b,* 1976), Smith (1968, 1974), and May and Oster (1976).

The dynamics of the deterministic model (Eq. 2) are straightforward. If $B > D$, the equilibrium number of adults given by $X(\infty) = [\log(B/D)]/C$ is globally stable. If $B \le D$, then the population will go extinct. In the neighborhood of $X(\infty)$, the rate of approach to equilibrium is given by the eigenvalue $\lambda = D \log(D/B)$.

The ordinary logistic model can serve as an approximation for deterministic models, such as Eq. 1, with a single stable equilibrium. The flour beetle model (Eq. 2) cannot be solved for $X(t)$ as an explicit function of time; consequently, the model is difficult to use for describing and analyzing data. The logistic becomes an approximation to Eq. 1 by expanding the per capita growth rate, $g[X(t)]$, in a Taylor series *around the stable equilibrium* $X(\infty)$, and discarding second-order or higher terms:

$$g[X(t)] = g[X(\infty)] + [X(t) - X(\infty)]g'[X(\infty)] + \ldots$$
$$\approx a - bX(t), \qquad (3)$$

where $a = -X(\infty)g'[X(\infty)]$, and $b = -g'[X(\infty)]$. Some derivations of the logistic in the ecological literature take the expansion *around zero* (e.g., Roughgarden 1979: 306), and thus produce an incorrect value for $X(\infty)$. Other derivations leave the expansion point unspecified (e.g., Lotka 1924, Pielou 1977, Hutchinson 1978); this may have helped foster an undeserved reputation for the logistic as a biologically vague model. For the flour beetle model (Eq. 2), the logistic approximation

produces $a = D \log(B/D)$ and $b = CD$. Note that $X(\infty)$ in this logistic is not a vaguely defined "carrying capacity," but rather an equilibrium balance of recruitment, cannibalism, and mortality.

The logistic approximation is nearly indistinguishable from the flour beetle model for many parameter values. The flour beetle model has an inflection point occurring at a value of $X(t) < X(\infty)/2$, while the inflection point of the logistic occurs exactly at $X(\infty)/2$. Population growth data sets tend to be scattered and seldom reveal such fine details of curvature. The logistic has only two parameters; in the authors' experience, the third parameter in the flour beetle model often causes estimation problems when fitting the model to scattered data sets.

Stochastic differential equations

We present evidence in this paper that a simple stochastic extension of Eq. 1 offers substantial improvement for describing real populations. The stochastic version of Eq. 1 we consider is the following stochastic differential equation (SDE):

$$dX(t) = X(t)g[X(t)] \, dt + \sigma X(t) \, dW(t). \quad (4)$$

Here $dW(t)$ has a normal distribution with a mean of zero and a variance of dt, and σ is a positive constant. Computationally, the SDE indicates how the trajectory of $X(t)$ might be simulated. For each small time interval of length dt, one would generate a normal random variable, $dW(t)$, independent of that of the previous interval. The new population size at time $t + dt$ would be computed as $X(t) + dX(t)$. Ecologically, the model arises from adding "white noise" to $g[X(t)]$ to represent the effects of unpredictable fluctuations in the per-unit-abundance growth rate of the population. Mathematically, the differential $dX(t)$ is formally defined in terms of either an Ito or a Stratonovich stochastic integral (see Soong 1973, Karlin and Taylor 1981, or Horsthemke and Lefever 1984). We will use the Ito interpretation of the SDE (Eq. 4), which corresponds to the above-mentioned simulation method (e.g., Turelli 1977). The Stratonovich interpretation can be obtained in what follows (and in the above simulation method) by replacing $g[X(t)]$ with $g[X(t)] + \sigma^2/2$. Dennis and Patil (1984) have shown that qualitative results about the stationary distribution for the SDE (Eq. 4) are unaffected by choice of Ito or Stratonovich interpretation.

If $\sigma = 0$ in Eq. 4, the deterministic model (Eq. 1) is recovered, and the trajectory of $X(t)$ levels off at the stable equilibrium, $X(\infty)$. However, with $\sigma > 0$ the probability distribution for $X(t)$ typically approaches a limiting, stationary distribution as t becomes large. The stationary distribution has a probability density function (pdf) of the form

$$f(x) = K \exp\{(2/\sigma^2) \int [g(x)/x] \, dx - 2 \log x\},$$
$$0 < x < \infty, \quad (5)$$

where K is a constant that is found by setting the area under $f(x)$ equal to 1. For some forms of $g(x)$, the area under $f(x)$ is infinite, and a stationary distribution in the form of Eq. 5 does not exist. (There may be a degenerate stationary distribution at $x = 0$, implying population extinction with probability 1.) When $f(x)$ is a legitimate pdf, the probability that $X(\infty)$ would take values below a certain population size, w, becomes the area under $f(x)$ between 0 and w. A rigorous mathematical derivation of Eq. 5 was presented by Tanaka (1957). Books by May (1974a), Roughgarden (1979), and Nisbet and Gurney (1982) also provide derivations of Eq. 5. Though the mathematics underlying SDEs such as Eq. 4 is formidable, many of the results are easy to apply in practice. Note, for instance, that finding the form of the stationary distribution (Eq. 5) for the stochastic version of any particular growth model (Eq. 1) requires just two integrations: an indefinite integral (antiderivative) given by $\int [g(x)/x] \, dx$ (with the integration constant simply absorbed into K), and a definite integral to find the value of K. Furthermore, various statistical inferences concerning the stationary distribution are easily performed with data using the methods outlined in this paper.

Alternate SDE versions of deterministic models of the form of Eq. 1 exist. The versions have a function of $X(t)$, rather than $X(t)$ itself, as a scale multiplier of $dW(t)$. For instance, an SDE constructed as an approximation to a linear stochastic birth–death process could have a noise term of $\sigma[X(t)]^{1/2} \, dW(t)$ (Nisbet and Gurney 1982:172). Or, an SDE approximation to a stochastic difference equation with additive noise might simply have $\sigma dW(t)$. In the SDE literature, models with $\sigma dW(t)$ are said to have "additive noise," while models with $\sigma X(t) \, dW(t)$ have "multiplicative noise" (e.g., Horsthemke and Lefever 1984:15).

The multiplicative noise term in Eq. 4 has advantages for representing fluctuations in flour beetle populations. First, notable fluctuations are present in large as well as small flour beetle populations (e.g., Costantino and Desharnais 1981). Demographic fluctuations, as represented in linear birth–death models such as those proposed by Desharnais and Costantino (1982), or as represented in some SDE models with noise terms scaled by $[X(t)]^{1/2}$, typically become negligible for large population sizes. Second, the stationary distributions (Eq. 5) resulting from multiplicative noise are defined for $0 < x < \infty$, a natural range for application to populations. The multiplicative fluctuations vanish as $X(t)$ approaches zero, producing an unattainable "natural" or "entrance" boundary at $X(t) = 0$ (Karlin and Taylor [1981:226] provide an excellent guide to the complicated topic of boundary classification). Additive noise models, by contrast, usually lead to a range of $-\infty < x < +\infty$, and thus may require inconvenient truncation at zero for population modeling.

Stochastic flour beetle population models

The stochastic version of Eq. 2 in the form of Eq. 4 becomes

$$dX(t) = X(t)[Be^{-CX(t)} - D] \, dt + \sigma X(t) \, dW(t). \quad (6)$$

The stationary distribution for $X(\infty)$ in this model has a pdf of the form

$$f(x) = Kx^{-(2D/\sigma^2)-2} \exp[-(2B/\sigma^2)E_1(Cx)], \quad (7)$$

with $0 < x < \infty$. This pdf exists (i.e., is integrable) only if $B - D > \sigma^2/2$ (or $B - D > 0$ for the Stratonovich version); otherwise the population becomes extinct with probability 1. The function E_1 is the exponential-integral function, which can be expressed as an integral, an infinite series, or an incomplete gamma function (Abramowitz and Stegun 1965):

$$
\begin{aligned}
E_1(z) &= \int_z^\infty v^{-1} e^{-v} \, dv \\
&= -\gamma - \log z - \sum_{i=1}^\infty (-z)^i/[i(i!)] = \Gamma(0, z). \quad (8)
\end{aligned}
$$

Here γ represents Euler's constant ($=0.5772156649 \ldots$). The constant K cannot be written down explicitly, but must be evaluated by numerical integration for every set of values of B, C, D, and σ^2. This feature becomes somewhat troublesome when computing parameter estimates from data, since the estimation algorithms require many iterations. The pdf (Eq. 7) has a mode at $(1/C)\{\log(B/D) - \log[1 + (\sigma^2/D)]\}$.

The gamma distribution arises as the stationary distribution to the stochastic version of the logistic model (Leigh 1968). The logistic model takes $g[X(t)]$ in Eq. 1 to be a linear decreasing function of $X(t)$, and so the stochastic version (Eq. 4) becomes

$$dX(t) = X(t)[a - bX(t)] \, dt + \sigma X(t) \, dW(t). \quad (9)$$

As t becomes large, the distribution for $X(t)$ approaches a gamma distribution. Specifically, the pdf for $X(\infty)$, given by Eq. 5, becomes

$$f(x) = [\beta^\alpha/\Gamma(\alpha)]x^{\alpha-1}e^{-\beta x}, \quad (10)$$

where $0 < x < \infty$, $\alpha = (2a/\sigma^2) - 1$, and $\beta = 2b/\sigma^2$. The parameters α and β are positive. (However, if $\sigma^2 \geq 2a$, then $\alpha \leq 0$ under the Ito interpretation of the SDE [Eq. 9], and the stationary distribution is no longer a gamma. Instead, the stationary distribution is degenerate at $x = 0$.)

Just as the logistic model can approximate the deterministic flour beetle model, the logistic SDE (Eq. 9) can approximate the flour beetle SDE (Eq. 6), and the gamma distribution can be used to approximate the stationary pdf (Eq. 7) of the flour beetle SDE (Dennis and Patil 1984). One simply uses the linear approximation to $g[X(t)]$, (Eq. 3), in the stochastic logistic model (Eq. 9). The resulting stationary gamma distri-

bution is in the form of Eq. 10, with $\alpha = [(2D/\sigma^2) \cdot \log(B/D)] - 1$, $\beta = 2CD/\sigma^2$. The mode of the gamma at $(\alpha - 1)/\beta = (1/C)[\log(B/D) - \sigma^2/D]$ approximates the location of the true mode when σ^2/D is small. The gamma essentially captures the right-skewed, unimodal shape of the true pdf (Eq. 7). The right tail of Eq. 7 is heavier than that of the gamma, however; the underlying convex shape of $g[X(t)]$ in Eq. 6 gives less restoring force toward $X(\infty)$ for large values of $X(t)$ than does the linearized version of $g[X(t)]$ in Eq. 9.

Emergent properties of SDE models

We cannot overemphasize the fact that SDE models may display dynamic behavior considerably different from their deterministic counterparts. The emergent system properties of stochastic forces are particularly marked for SDE models with multiplicative noise in the form of Eq. 4. In many cases, testable and sometimes striking biological predictions result from converting an ODE to an SDE. To illustrate, we summarize here some of the differences between the logistic SDE (Eq. 9) and the more familiar logistic ODE.

The logistic SDE has a stationary probability distribution for population abundance rather than a fixed point equilibrium. A population in stochastic equilibrium continues to fluctuate above and below the deterministic equilibrium; outbreaks and crashes are not uncommon.

The most likely stationary population abundance is indicated by the mode of the gamma pdf and is below the deterministic equilibrium. Since the stationary pdf represents the proportion of time the population spends at various abundance levels (see discussion of Eq. 31), and since the median of the gamma pdf is also below the deterministic equilibrium, the population spends in the long run more than half the time below the deterministic equilibrium.

A deterministic equilibrium is manifested in the SDE model (Eq. 4) as a mode, not mean or median, of the stationary pdf. This happens primarily when the intensity of the stochastic forces as measured by the constant σ is small. In the stochastic logistic, the mode of the gamma pdf is a visible sign of an underlying deterministic stable equilibrium. Some logistic-based ODE models proposed in the ecological literature have multiple stable and unstable equilibria; multiple modes and antimodes in the SDE versions may correspond to (though in general do not equal) these equilibria (see Dennis and Patil 1984). In particular, the example of a bimodal stationary pdf in the SDE version of a deterministic model with two stable equilibria (separated by an unstable equilibrium) shows how bad the mean population size can be in characterizing stochastic model behavior.

Stochastic forces as modeled by Eq. 4 have effects similar to harvesting in a deterministic model. The ODE (Eq. 1) has an equilibrium given by $g[X(\infty)] = 0$; if population members are removed at a rate $hX(t)$,

where h is a constant harvesting effort, the resulting equilibrium satisfying $g[X_h(\infty)] - h = 0$ is lower than that of an unexploited population. Interestingly, the mode, X_m, of the stationary pdf for the SDE (Eq. 4) satisfies $g(X_m) - \sigma^2 = 0$. Thus, the mode of the stochastic model equals the equilibrium of a deterministic harvesting model. The mode of the stationary gamma in the stochastic logistic, for instance, equals the equilibrium of a Schaefer (logistic-based) harvesting model having a harvest effort of σ^2 (Dennis and Patil 1984).

The mean population size in the stochastic logistic (Eq. 9), defined by $E[X(t)|X(0) = x_0]$, does not obey a logistic ODE. The lack of agreement between the mean of the SDE and the solution of the ODE is a rather general consequence of multiplicative noise. The mean for the stochastic logistic has been obtained by Hamada (1981) and is a complicated formula. However, the harmonic mean of $X(t)$ in Eq. 9 does obey a logistic equation. It can be shown than the harmonic mean defined by $H(t) = \{E[1/X(t)|X(0) = x_0]\}^{-1}$ is the solution to $dH(t)/dt = H(t)[(a - \sigma^2) - bH(t)]$. Thus $H(t)$ obeys a Schaefer harvesting version of the original logistic ODE. We mention that all of the nonequilibrium statistical properties of the logistic SDE are contained in the full time-dependent transition pdf for $X(t)$, a complicated expression obtained by Prajneshu (1980) and Schenzle and Brand (1979).

Changes in the intensity of the stochastic forces as measured by σ can fundamentally alter the dynamical behavior of SDE models of the form of Eq. 4. In the logistic SDE, for instance, an increase in σ can transform the stationary gamma pdf from a unimodal mound-shaped distribution ($\alpha > 1$) to a J-shaped distribution ($\alpha \leq 1$). Further increases in σ can (under the Ito interpretation of the SDE) eliminate the stationary gamma altogether; population extinction is the ultimate outcome. Such "noise-induced transitions," in which system behavior changes drastically in response to changes in noise level, have received much attention in the physics literature (see Horsthemke and Lefever 1984). A further example pertains to SDE models of the form of Eq. 4, in which there are two stable equilibria in the ODE version. An increase in σ can transform a bimodal stationary pdf into a unimodal one; such noise levels effectively mask the underlying deterministic dynamics (Dennis and Patil 1984).

The stationary distribution properties of the logistic SDE differ substantially from those of deterministic logistic-based "chaos" models. Since May and Oster's (1976) paper, it has become well known 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 and Kot [1986]; our discussion here is restricted to one-species systems.) In fact, the concept of a stationary distribution can be applied to the chaotic behavior of a difference equation model. The types of logistic-based difference equations listed by May and Oster (1976) possess so-called invariant measures; that is, the long run abundance frequencies of a chaotic population trajectory approach a limiting stationary distribution (see Lasota and Mackey 1985). For instance, the simple difference equation given by $X_{t+1} = 4X_t(1 - X_t)$ has a "stationary distribution" of $f(x) = [\pi\sqrt{x(1 - x)}]^{-1}$, $0 < x < 1$. Stationary distributions of other difference equations can seldom be obtained analytically, but it is straightforward to iterate any given model until limiting relative frequencies are obtained. To our knowledge, such exercises carried out to date almost always produce U-shaped (bimodal) or irregular stationary distributions for population abundance. By contrast, the logistic SDE predicts a unimodal mound-shaped or J-shaped distribution. Admittedly, much research remains to be done on distinguishing chaotic behavior from "conventional" stochastic behavior in population data; many directions for such analyses may be found in Holden (1986).

STATISTICAL INFERENCES

We present in this section details of various statistical procedures that can be used in conjunction with the gamma model or other stationary distribution models. The data considered here consist of observed sizes of a population presumed to be fluctuating around a steady state. More ideally, the data could represent an ensemble of populations fluctuating around the same equilibrium value, as in Figs. 1 and 2. The procedures are based on the use of a multinomial likelihood function and assume that the time intervals between observations are large enough so that autocorrelation is negligible. However, we presently regard the use of the multinomial as reasonable and practical even for time series with more closely spaced observations.

Maximum likelihood estimates

We compute maximum likelihood (ML) estimates for the parameters α and β in the gamma model (Eq. 10) using grouped data and a multinomial likelihood function. Use of a multinomial likelihood function has some practical advantages over the more conventional use of the raw, ungrouped (or "complete") data and a likelihood function involving a product of gamma pdf's. First, computing ML estimates for a multinomial likelihood is extremely easy with existing nonlinear regression packages. Computing ML estimates for the complete gamma likelihood requires some laborious (though not difficult) programming. Second, the familiar Pearson chi-square goodness-of-fit test, plus follow-up tests for deviations in individual cells, are based on a multinomial likelihood. When statistical distributions are fitted using the complete likelihood function, the Pearson statistic does not have a chi-square distribution (this fact does not seem to be widely disseminated in the ecological literature). Finally, there is some prelim-

inary justification for using a multinomial likelihood function even when the observations form an auto-correlated time series. These points are discussed in detail below. We do recommend using the complete likelihood function when the only goal of the analysis is parameter estimation, since the standard errors of the estimates will be smaller. However, we have here chosen to develop the grouped multinomial approach with the view that ecologists would likely have model evaluation as an additional goal. This factor, plus ease of computing and robustness of the analysis, compensate for the small loss of information when using grouped data.

The ML estimates require the quantities $y_1, y_2, \ldots , y_m$, representing the frequency counts of the n observations grouped into m interval classes. As with any frequency histogram, the interval classes are selected by the investigator; the main consideration is insuring that the expected frequencies are large enough to conduct goodness-of-fit testing (see Goodness-of-fit Testing). The class intervals selected should partition the entire (positive real) sample space. Thus, the class intervals would be in the form $(0, s_1], (s_1, s_2], \ldots , (s_{m-2}, s_{m-1}], (s_{m-1}, \infty)$; then y_1 is the number of observations >0 but $\leq s_1$, etc. Under this setup, the values $y_1, \ldots , y_m$ can be described with a multinomial distribution, with $\sum y_i = n$. The probabilities for the interval categories are given by the corresponding areas under the gamma pdf (Eq. 10), or if preferred, some other stationary pdf.

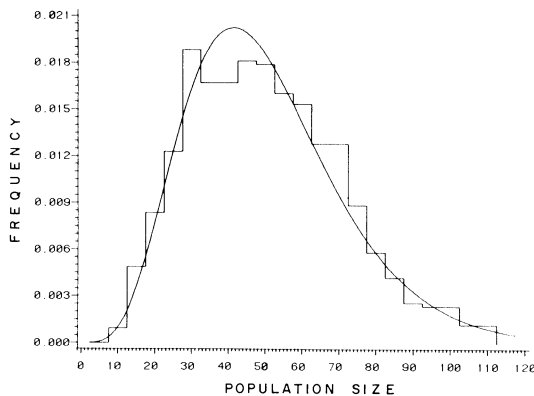The cumulative distribution function (cdf) for the

FIG. 1. Relative frequency histogram of numbers of *Tribolium castaneum* adults fluctuating around equilibrium, plus fitted gamma probability density function (pdf) given by $f(x; \hat{\alpha}, \hat{\beta})$, where $f(x; \alpha, \beta) = [\beta^\alpha/\Gamma(\alpha)]x^{\alpha-1}e^{-\beta x}$, x = population size, and $\hat{\alpha}$ and $\hat{\beta}$ are ML estimates ($n = 861$, $X^2 = 21.25$, $P = .27$, df = 18, $\hat{\alpha} = 5.57047$, $\hat{\beta} = 1.10435 \times 10^{-1}$, $\hat{\sigma}_1^2 =$ ML estimate of var($\hat{\alpha}$) = 7.30330×10^{-2}, $\hat{\sigma}_2^2 =$ ML estimate of var($\hat{\beta}$) = 3.10806×10^{-5}, $\hat{\sigma}_{12} =$ ML estimate of cov($\hat{\alpha}, \hat{\beta}$) = 1.44386×10^{-3}). Note: first and last histogram bars in this and subsequent figures indicate relative frequencies of observations in population size intervals $(0, s_1]$ and (s_{m-1}, ∞), respectively. Data are from Moffa and Costantino (1977).
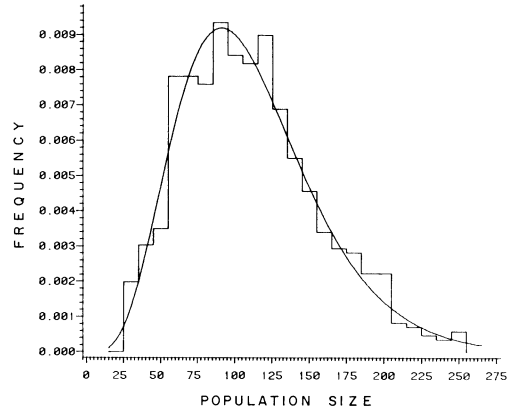

FIG. 2. Equilibrium frequency of *T. castaneum* cultured at 24°C, plus fitted gamma pdf ($n = 857$, $X^2 = 18.70$, $P = .48$, df = 19, $\hat{\alpha} = 5.52220$, $\hat{\beta} = 4.98460 \times 10^{-2}$, $\hat{\sigma}_1^2 = 7.05185 \times 10^{-2}$, $\hat{\sigma}_2^2 = 6.30151 \times 10^{-6}$, $\hat{\sigma}_{12} = 6.38465 \times 10^{-4}$, classes 21 and 22 were pooled during estimation). Data are from Park (1954) as listed in Leslie (1962).

gamma distribution is defined as the area under the pdf between 0 and x:

$$F(x) = \Pr[X(\infty) \leq x] = \int_0^x f(u)\, du$$

$$= \int_0^x [\beta^\alpha/\Gamma(\alpha)]u^{\alpha-1}e^{-\beta u}\, du. \quad (11)$$

The function $F(x)$ is an integral that has no simple form. Computing the ML estimates requires a subroutine to evaluate $F(x)$ for various values of x, α, and β. The gamma cdf is a library function (PROBGAM) in SAS (SAS 1985) and is available in IMSL (IMSL 1979) as well. Press et al. (1986:160) provide an easily programmed algorithm for computing the gamma cdf. Note that these routines typically compute the cdf, $P(\alpha, x)$, of a standardized gamma, defined as the integral from 0 to x of $u^{\alpha-1}e^{-u}/\Gamma(\alpha)$. Then $F(x)$ above is obtained as $P(\alpha, \beta x)$.

The probabilities in the multinomial distribution are defined in terms of the gamma cdf:

$$p_1(\alpha, \beta) = F(s_1),$$
$$p_2(\alpha, \beta) = F(s_2) - F(s_1),$$
$$\vdots$$
$$p_{m-1}(\alpha, \beta) = F(s_{m-1}) - F(s_{m-2}),$$
$$p_m(\alpha, \beta) = 1 - F(s_{m-1}). \quad (12)$$

Clearly, $\sum p_j = 1$. The multinomial likelihood function for $y_1, \ldots , y_m$ is then

$$l(\alpha, \beta) = Q \prod_{j=1}^m [p_j(\alpha, \beta)]^{y_j}, \quad (13)$$

where $Q = (n!)/[(y_1!)(y_2!) \ldots (y_m!)]$. The ML estimates are the values of α and β which maximize $l(\alpha, \beta)$ or log $l(\alpha, \beta)$. The values are roots to the following equations:

$$\partial \log l/\partial \alpha = \sum_{j=1}^{m} (y_j/p_j)(\partial p_j/\partial \alpha) = 0, \qquad (14)$$

$$\partial \log l/\partial \beta = \sum_{j=1}^{m} (y_j/p_j)(\partial p_j/\partial \beta) = 0. \qquad (15)$$

These equations may be solved by performing a non-linear least squares regression (Jennrich and Moore 1975). The regression uses the values $y_1, y_2, \ldots, y_m$ as observations on the dependent variable, and the values $np_1(\alpha, \beta), np_2(\alpha, \beta), \ldots, np_m(\alpha, \beta)$ (the expected values of the y_j's) become the model to be fit. The regression must be "iteratively reweighted"; that is, weights of $[np_j(\alpha, \beta)]^{-1}$ must be computed at every iteration. In other words, the standard nonlinear regression algorithms are designed to iterate toward the values of α and β minimizing $\sum w_j[y_j - np_j(\alpha, \beta)]^2$, where the w_j values are fixed weights provided by the investigator. If these weights are assigned as $w_j = 1/[np_j(\alpha, \beta)]$, they are recomputed each iteration with updated values of α and β and hence are no longer fixed. The resulting iterations converge to the values of α and β, maximizing the multinomial likelihood (Eq. 13) (proof given by Jennrich and Moore 1975); the nonlinear least squares package is "tricked" into computing multinomial ML estimates of α and β. We have found the moment estimates given by $\tilde{\alpha} = \bar{x}^2/s^2$ and $\tilde{\beta} = \bar{x}/s^2$, where $\bar{x}$ is the sample mean and s^2 is the sample variance of the ungrouped observations, to be convenient starter values for the ML calculations.

Nonlinear regression packages, such as PROC NLIN of SAS (SAS 1985) or AR of BMDP (Dixon 1985), are widely available. These two packages are particularly convenient because they do not require derivatives. Also, options are available in both packages (SIGSQ = 1 in SAS; MEANSQUARE IS 1 in BMDP) which produce properly scaled standard errors. SAS has the additional convenience of the library gamma cdf; the function must be coded as a subroutine (possibly through IMSL) when using current versions of BMDP.

The ML estimates have an asymptotic multivariate normal distribution (see, for example, Bishop et al. 1975: 509). The mean vector of the multivariate normal distribution is $[\alpha, \beta]'$, and the variance–covariance matrix is

$$\Sigma = \begin{bmatrix} \lambda_1/(\lambda_1\lambda_3-\lambda_2{}^2) & -\lambda_2/(\lambda_1\lambda_3-\lambda_2{}^2) \\ -\lambda_2/(\lambda_1\lambda_3-\lambda_2{}^2) & \lambda_3/(\lambda_1\lambda_3-\lambda'{}_2{}^2) \end{bmatrix},$$

$$(16)$$

where

$$\lambda_1 = n \sum_{j=1}^{m} (\partial p_j/\partial \beta)^2/p_j,$$

$$\lambda_2 = n \sum_{j=1}^{m} (\partial p_j/\partial \alpha)(\partial p_j/\partial \beta)/p_j,$$

$$\lambda_3 = n \sum_{j=1}^{m} (\partial p_j/\partial \alpha)^2/p_j, \qquad (17)$$

with $p_j = p_j(\alpha, \beta)$ defined by Eq. 12. The elements in Σ would be estimated by substituting the ML estimates $\hat{\alpha}$ and $\hat{\beta}$; the expressions in Eq. 17 could be computed with numerical derivatives. As an alternative, the options in SAS and BMDP mentioned above automatically produce the large sample correlation matrix (evaluated at $\hat{\alpha}$ and $\hat{\beta}$), along with asymptotic standard deviations (square roots of the diagonal elements of $\hat{\Sigma}$). The estimated variance–covariance matrix, $\hat{\Sigma}$, is then easily recovered from the computer output as follows. Let $\hat{\sigma}_1$ and $\hat{\sigma}_2$ be the printed estimates of the standard deviations of $\hat{\alpha}$ and $\hat{\beta}$, let $\hat{Q}$ be a 2×2 matrix containing $\hat{\sigma}_1$ and $\hat{\sigma}_2$ on the main diagonal and zeros elsewhere, and let $\hat{R}$ be the printed estimate of the correlation matrix. Then

$$\hat{\Sigma} = \hat{Q}\hat{R}\hat{Q}. \qquad (18)$$

Goodness-of-fit testing

Goodness-of-fit testing is easily accomplished when the ML estimates are computed using a nonlinear regression package. After convergence of the parameter estimates is achieved, the final value of the weighted residual sum of squares is

$$X^2 = \sum_{j=1}^{m} [y_j - np_j(\hat{\alpha}, \hat{\beta})]^2/[np_j(\hat{\alpha}, \hat{\beta})], \qquad (19)$$

which is just the Pearson chi-square statistic. Under the null hypothesis that the gamma model fits, X^2 has a large sample chi-square distribution with $m - 3$ (m − number of parameters estimated − 1) degrees of freedom (Bishop et al. 1975:516). The abundance classes should be chosen so that $np_j(\alpha, \beta) \geq 5$ for most classes in order that the chi-square approximation remain valid.

An alternative test statistic is the likelihood ratio (LR) statistic given by

$$G^2 = 2 \sum_{j=1}^{m} y_j \log(y_j/[np_j(\hat{\alpha}, \hat{\beta})]). \qquad (20)$$

The jth term in this sum is understood to be zero if $y_j = 0$. The LR statistic has the same large sample chi-square distribution as the Pearson statistic under the null hypothesis (Bishop et al. 1975:513). If the model fits, the values of X^2 and G^2 are usually very similar. We note that the ML estimates $\hat{\alpha}$ and $\hat{\beta}$ that maximize Eq. 13 also minimize G^2. The LR statistic can be computed in the SAS and BMDP nonlinear regression packages through use of the loss function option provided in each package.

A significant overall goodness-of-fit test may be followed up with tests for significant deviations of the model in individual abundance classes. The following quantity can be regarded as a generalized residual for the jth class:

$$\hat{u}_j = [y_j - np_j(\hat{\alpha}, \hat{\beta})]/[np_j(\hat{\alpha}, \hat{\beta})]^{1/2}. \qquad (21)$$

The Pearson chi-square statistic (Eq. 19) is the sum of the squared values of $\hat{u}_j$. A result from statistical theory is that $\hat{u}_j$ has a large sample normal distribution, under the null hypothesis that the model fits, with a mean of 0 and a variance of

$$v_j(\alpha, \beta) = 1 - p_j - (n/p_j)\boldsymbol{b_j}'\boldsymbol{\Sigma}\boldsymbol{b_j} \qquad (22)$$

(e.g., Rao 1973:394). Here $p_j = p_j(\alpha, \beta)$, $\boldsymbol{\Sigma}$ is the variance–covariance matrix for the ML estimates, and $\boldsymbol{b_j}$ is a vector of partial derivatives given by $\boldsymbol{b_j}' = [\partial p_j/\partial \alpha, \partial p_j/\partial \beta]$. This variance may be estimated by substituting the ML estimates of α and β: $\hat{v}_j = v_j(\hat{\alpha}, \hat{\beta})$. The partial derivatives in $\boldsymbol{b_j}$ can be computed numerically. The test statistic for the jth class is then

$$Z_j = \hat{u}_j/(\hat{v}_j)^{1/2}. \qquad (23)$$

Z_j has a large sample standard normal distribution under the null hypothesis that the model fits the jth class.

Asymptotic confidence intervals

The large sample multivariate normal distribution of the ML estimates may be used to construct asymptotic confidence intervals for the parameters. Let $\hat{\sigma}_1^2$ and $\hat{\sigma}_2^2$ be, respectively, the estimated variances of the ML estimates $\hat{\alpha}$ and $\hat{\beta}$, computed as diagonal elements of the estimated variance–covariance matrix. The following are 95% confidence intervals (large samples) of α and β:

$$\hat{\alpha} \pm 1.96 \, \hat{\sigma}_1, \qquad (24)$$
$$\hat{\beta} \pm 1.96 \, \hat{\sigma}_2. \qquad (25)$$

The multivariate normal distribution of ML estimates may also be used to obtain asymptotic confidence intervals for functions of the parameters. Let $h(\alpha, \beta)$ be a function differentiable with respect to α and β, and let $\boldsymbol{\pi} = [\partial h/\partial \alpha, \partial h/\partial \beta]'$. A standard result from statistical theory is that $h(\hat{\alpha}, \hat{\beta})$ has an asymptotic normal distribution with a mean of $h(\alpha, \beta)$ and a variance of $\boldsymbol{\pi}'\boldsymbol{\Sigma}\boldsymbol{\pi}$ (e.g., Rao 1973:388). A large sample 95% confidence interval for $h(\alpha, \beta)$ becomes $h(\hat{\alpha}, \hat{\beta}) \pm 1.96[\hat{\boldsymbol{\pi}}'\hat{\boldsymbol{\Sigma}}\hat{\boldsymbol{\pi}}]^{1/2}$. Here $\hat{\boldsymbol{\pi}}$ represents the vector $\boldsymbol{\pi}$ evaluated at the ML estimates $\hat{\alpha}$ and $\hat{\beta}$.

Large sample confidence intervals can be obtained, for example, for the mean and the mode of the gamma distribution. The mean and the mode are functions of the parameters:

$$\text{mean} = E[X(\infty)] = \alpha/\beta; \qquad (26)$$
$$\text{mode} = (\alpha - 1)/\beta. \qquad (27)$$

Thus, we have the following 95% confidence intervals:

$$(\hat{\alpha}/\hat{\beta}) \pm 1.96[(\hat{\sigma}_1^2/\hat{\beta}^2) + (\hat{\alpha}^2\hat{\sigma}_2^2/\hat{\beta}^4)$$
$$- (2\hat{\alpha}\hat{\sigma}_{12}/\hat{\beta}^3)]^{1/2}, \qquad (28)$$
$$(\hat{\alpha} - 1)/\hat{\beta} \pm 1.96\{(\hat{\sigma}_1^2/\hat{\beta}^2) + [(1 - \hat{\alpha})^2\hat{\sigma}_2^2/\hat{\beta}^4]$$
$$+ [2(1 - \hat{\alpha})\hat{\sigma}_{12}/\hat{\beta}^3]\}^{1/2}. \qquad (29)$$

Here $\hat{\sigma}_{12}$ is the estimated covariance of $\hat{\alpha}$ and $\hat{\beta}$ obtained from the matrix $\hat{\boldsymbol{\Sigma}}$.

Comparing two gamma distributions

The multivariate normal distribution of ML estimates may be used for comparing parameters from two separate data sets. Comparisons can be made, for example, between gamma distributions from two different populations or between distributions fit to the same population at two different times. The following multivariate statistical test allows formal comparison of the parameters from two gamma distributions.

Let $[\alpha_1, \beta_1]'$ be the column vector of parameters from the first gamma distribution, and let $[\alpha_2, \beta_2]'$ be the parameter vector from the second distribution. Since $[\hat{\alpha}_1, \hat{\beta}_1]'$ and $[\hat{\alpha}_2, \hat{\beta}_2]'$ both converge in distribution to multivariate normal distributions, the difference $[\hat{\alpha}_1, \hat{\beta}_1]' - [\hat{\alpha}_2, \hat{\beta}_2]'$ converges to a multivariate normal with a mean vector $[\alpha_1 - \alpha_2, \beta_1 - \beta_2]'$ and a variance–covariance matrix of, say, $\boldsymbol{\Sigma}_1 + \boldsymbol{\Sigma}_2$. The null hypothesis is H_0: $[\alpha_1 - \alpha_2, \beta_1 - \beta_2]' = [0, 0]'$, that is, both gammas have identical parameters. The alternate hypothesis is H_1: $[\alpha_1 - \alpha_2, \beta_1 - \beta_2]' \neq [0, 0]'$. The test statistic is a type of Wald statistic (e.g., Rao 1973:417):

$$D^2 = [\hat{\alpha}_1 - \hat{\alpha}_2, \hat{\beta}_1 - \hat{\beta}_2] [\hat{\boldsymbol{\Sigma}}_1 + \hat{\boldsymbol{\Sigma}}_2]^{-1} \cdot$$
$$[\hat{\alpha}_1 - \hat{\alpha}_2, \hat{\beta}_1 - \hat{\beta}_2]'. \qquad (30)$$

Under the null hypothesis, D^2 has a (large sample) chi-square distribution with two degrees of freedom.

As an alternative, we mention that the testing for differences between two gammas can be done with the likelihood ratio approach. One first finds pooled ML estimates of α and β by pooling the two data sets together. Denote by $\hat{l}_0 = l(\hat{\alpha}_0, \hat{\beta}_0)$ the likelihood (Eq. 13) evaluated at the pooled ML estimates $\hat{\alpha}_0$ and $\hat{\beta}_0$. One then obtains the ML estimates $[\hat{\alpha}_1, \hat{\beta}_1]$ and $[\hat{\alpha}_2, \hat{\beta}_2]$ separately for each data set. Denote by $\hat{l}_1$ and $\hat{l}_2$ the corresponding maximized likelihoods. Then $-2[\log \hat{l}_0 - \log(\hat{l}_1\hat{l}_2)]$ has a large sample chi-square distribution with two degrees of freedom under the null hypothesis. Additional computing effort is required for this test, though experience seems to indicate that it has better properties for smaller sample sizes.

Time-dependent observations

An underlying assumption for such ML estimates is that the frequency counts $y_1, \ldots, y_m$ form a sample from a multinomial distribution. The assumption is not strictly valid if the underlying observed population sizes are time series data. For time series data, Eq. 13

is not the true likelihood function for the frequency counts. However, as the time interval between observations becomes large, the likelihood function for the counts approaches Eq. 13 asymptotically. Thus, the question becomes whether the observations are far enough apart to justify using Eq. 13 as a likelihood function.

This question can be partly addressed by examining the empirical autocorrelation structure of the data using standard time series methods. If the autocorrelation between observations is small, then it is reasonable to compute ML estimates for the stationary gamma with the methods described in this paper.

These ML estimates may possibly remain reasonable even when the interval between observations is small, due to the ergodic nature of the process $X(t)$. As t becomes large, the proportion of time that the process spends in the abundance interval $(s_{j-1}, s_j]$ approaches the proportion $p_j(\alpha, \beta)$ given by Eq. 12. If the process was sampled at equal time intervals, the proportion y_j/n of samples found in the abundance interval $(s_{j-1}, s_j]$ should approach $p_j(\alpha, \beta)$. Specifically, the ergodic theorem states that

$$\lim_{t \to \infty} (1/t) \int_0^t I_{(a,b)}[X(\tau)] \, d\tau = F(b) - F(a), \quad (31)$$

where $I_{(a,b)}(x)$ is the indicator function of the interval $(a, b]$ (=1 if $a < x \le b$; 0 otherwise), and $F(x)$ is the cdf of the stationary distribution of $X(t)$ (e.g., Horsthemke and Lefever 1984:114). Thus, estimating α and β by maximizing Eq. 13 (i.e., minimizing the "discrepancy" between y_j/n and $p_j(\alpha, \beta)$ as measured by G^2 [Eq. 20]) appears to be a reasonable procedure, even when the observations of the process $X(t)$ are closely spaced. Two qualifications are: (a) the process must be observed for a long time, and (b) the process should be observed at equally spaced intervals. It is worth mentioning that if the observation times are selected at random from a uniform distribution on $(0, t)$, then the actual distribution of the interval counts $y_1, \ldots, y_m$ will be approximately multinomial for large t, with the likelihood function given by Eq. 13.

Recent results by Gleser and Moore (1985) indicate that the chi-square goodness-of-fit test (Eq. 19) will reject the null hypothesis too often when the observations are closely spaced. Thus, if the hypothesis of goodness of fit is not rejected by the chi-square test, one can be fairly confident that H_0 would also not be rejected using the true distribution of the test statistic. The effects of autocorrelation on the other statistical inferences described here, unfortunately, remain unknown at this time.

We note finally that these stationary distribution models are inappropriate for time series with significant periodic components. Spectral analysis can help determine if such components are present.

ILLUSTRATIVE EXAMPLES

In this section, we analyze 11 data sets on observed stationary distributions of the flour beetle *Tribolium*. The analyses of the data sets demonstrate the overall usefulness of the gamma model and illustrate several statistical procedures, including: the estimation of parameters, testing goodness of fit, obtaining confidence intervals for parameters, and the comparison of two gamma distributions. These examples serve to emphasize that flour beetle equilibria are stochastic, that data on stationary distributions of populations are sometimes available, and that the development of statistical procedures is important for evaluating stochastic models.

The observed distributions were obtained from several different laboratories, and the original experiments had differing objectives. Our descriptions of these experiments are necessarily brief due to space limitations; consequently, readers should consult the original sources for more details.

In general, the experiments had many common features. At the outset, a group of beetles (sometimes adults only, or perhaps a combination of all life stages) were placed in a vial containing a standard wheat flour medium. The cultures were maintained for many months and, in several experiments, for a period of 3 yr in incubators with temperature, relative humidity, light, and other environmental factors tightly controlled. At regular intervals (often 7, 14, or 30 d) the cultures were removed from the incubator and censused. All of the life stages (except eggs, usually) were counted and then all living life stages were returned to fresh medium. We should note that for one genetic stock the medium renewal schedule was, itself, an important environmental factor. Strain bI of *T. confusum* had such a low rate of cannibalism that self-destruction was avoided only by the intervention of the experimenter (Park et al. 1964).

The data considered here are the number of adults observed in many independent, replicate *Tribolium* cultures maintained in the region of their steady states. Arranged in m class intervals, the adult numbers recorded for the ensemble of replicates in each experiment were used to establish the grouped frequency counts $y_1, y_2, \ldots, y_m$, where the total number of observations $n = \sum y_i$. These y_i values constitute the observed grouped frequency distribution for a particular data set.

In these examples, we conduct goodness-of-fit tests at the 0.01 significance level. This more conservative level helps compensate for possible time series effects, which too often cause rejection of the null hypothesis as discussed earlier.

Convergence to a genetic polymorphism

One concern of population genetic research is the association between the genetic structure of a popu-

lation and its demographic behavior. Moffa and Costantino (1977) showed that 37 cultures of *T. castaneum* initially segregating for the corn oil sensitive, *cos*, allele converged to a stable polymorphic genetic equilibrium with an equilibrium *cos* allele frequency in the vicinity of 0.30. What was the corresponding size of the population? The frequency counts of adult beetles, y_1, y_2, ..., y_m taken in the region of the steady state (week 20 to week 68) on the 37 cultures grouped into $m = 21$ class intervals are given in Table 1. As mentioned in a previous section, the likelihood function is given by Eq. 13 and the ML estimates of $\hat{\alpha} = 5.57047$ and $\hat{\beta} = 0.110435$ were obtained as the roots of Eqs. 14 and 15. An ≈95% confidence interval for the mean abundance is obtained from Eq. 28 as 50.43888 ± 1.42544. Goodness-of-fit testing was accomplished using the chi-square statistic (Eq. 19) with $m - 3 = 18$ degrees of freedom. The computed chi-square value of 21.25 allowed us to accept the null hypothesis that the gamma model fits these data, which seems reasonable from the sketch of the observed and gamma expected distributions given in Fig. 1.

SDE models can be constructed to yield other skewed distributions, such as the lognormal, as stationary solutions (e.g., Dennis and Patil 1984, 1988). Also, SDE models can be approximated by a Gaussian (time-dependent Ornstein-Uhlenbeck) process through singular perturbation methods, yielding a normal stationary distribution (see Gardiner 1985:177). Do these distributions fit the data as well as a gamma? Readers are invited to confirm that a lognormal distribution does not fit these data as well due to the heavy right tail of the lognormal, and that a normal distribution does not fit due to the skewness of the data.

T. castaneum *cultured at 24°C*

Park (1954) studied 20 replicates of *T. castaneum* cultured at 24° and 70% relative humidity. The observed grouped frequency distribution was based on adult numbers recorded at 30-d intervals beginning at day 360 onward to day 720 (Leslie 1962: Table N) for a total of 857 observations (Fig. 2). An ≈95% confidence interval for the mean abundance is 110.78522 ± 3.14428. The hypothesis that a gamma distribution fits the data was accepted. Again, a lognormal distribution does not fit, suggesting that not just any right-skewed distribution will adequately describe the data. Also, a normal distribution does not fit, suggesting that normal approximations to stationary pdf's of the form of Eq. 5 might not be adequate in some circumstances.

Population outbreaks

Mertz (1969) investigated the effects of different initial conditions using a new strain, cIV-a, of *T. castaneum*. He set up nine sets of initial conditions representing different initial densities and ages of adult beetles. Ten cultures were started in each of the nine treatments and sampled every 30 d, though three of

TABLE 1. Observed frequency counts (y_j) of *Tribolium castaneum* adults, estimated expected counts [$np_j(\hat{\alpha}, \hat{\beta})$] under the gamma model, and left and right class interval boundaries (s_j), corresponding to Fig. 1.

Left s_{j-1}	Right s_j	Observed y_j	Expected $np_j(\hat{\alpha}, \hat{\beta})$
0	12.5	4	5.01
12.5	17.5	21	15.81
17.5	22.5	36	33.38
22.5	27.5	53	53.03
27.5	32.5	81	70.16
32.5	37.5	72	81.70
37.5	42.5	72	86.63
42.5	47.5	78	85.50
47.5	52.5	77	79.73
52.5	57.5	69	71.01
57.5	62.5	66	60.88
62.5	67.5	55	50.57
67.5	72.5	55	40.87
72.5	77.5	38	32.27
77.5	82.5	25	24.96
82.5	87.5	18	18.97
87.5	92.5	11	14.19
92.5	97.5	10	10.46
97.5	102.5	10	7.62
102.5	107.5	5	5.48
107.5	∞	5	12.77

the cultures were lost at the outset. By day 360, most of the transient effects of initial conditions, such as age structure imbalances, had damped out in the cultures. The 87 populations sampled from day 360 through day 600 provided a total of 783 observations on equilibrium adult numbers.

The equilibrium frequency distribution appears unimodal and positively skewed (Fig. 3). A gamma distribution does not fit very well, due to significant deviations in the 1st, 2nd, 4th, and 14th cells. The gamma does, however, describe the essential features of the equilibrium far better than a deterministic model with a fixed point equilibrium.

Mertz labeled certain observations as representing "outbreaks" in population levels. An outbreak was defined as a surge in population size of 25% or more within two sample periods. A stationary pdf such as the gamma provides a different definition of outbreak which may be useful in biological monitoring. An outbreak can be defined as the population exceeding some specified level, x. For the gamma model, the probability of that event is $1 - F(x)$, where $F(x)$ is the gamma cdf (Eq. 11). An estimate of the outbreak probability is obtained by substituting the ML estimates $\hat{\alpha}$ and $\hat{\beta}$ in $F(x)$ (and using a computer routine to evaluate the integral in Eq. 11). For instance, using a threshold level of $x = 132.5$, the estimated chance of outbreak is about 0.04, roughly in accord with the observed frequency of ≈0.05 (Fig. 3).

Interestingly, a lognormal distribution fits this data set somewhat better than the gamma (though still not acceptably at the .01 level). An SDE model that predicts a lognormal stationary distribution has a convex
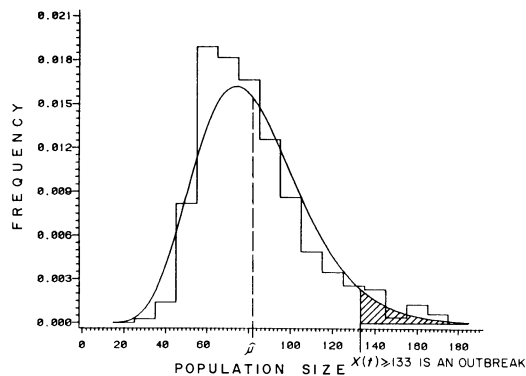
per-unit-abundance growth rate, $g[X(t)]$ (Dennis and Patil 1984, 1988). The original SDE flour beetle model also has a convex form for $g[X(t)]$; perhaps the linear approximation to $g[X(t)]$ implicit in the gamma model has some shortcomings for this data set. The possibility that details of curvature in $g[X(t)]$ might be detected through statistical analysis of stationary distributions deserves further study.

Comparison of two strains

Lloyd (1965, 1968) examined the growth pattern of two strains of *T. castaneum*. Twelve individual replicates of each strain, Brazil and Chicago, were initiated with 32 small larvae, 7 large larvae nearing pupation, and 8 adults. Thereafter each culture was censused each week for 35 wk. The observed stationary distributions (Fig. 4) were generated in the usual way beginning with the adult counts at week 19. The region of the steady state extended over 17 wk and gave a total of 204 observations on each strain.

The gamma hypothesis was accepted for the Chicago strain as well as for the Brazil strain. However, these strains have statistically different parameter estimates according to the D^2 test. Interestingly, Lloyd (1968) used the Mann-Whitney U test to evaluate the average number of adults in these two strains and concluded that the levels were essentially the same. Clearly, the differences were not large, but the use of the gamma does allow a fuller characterization of the steady state.

Polymorphism vs. homozygosity at the cos locus

An analysis of the stability of a dynamic system involves imposing a perturbation in the neighborhood of an equilibrium and then characterizing the subsequent response of the system. This approach was used by Desharnais and Costantino (1980, 1985) to study further the genetic polymorphism at the *cos* locus (Mof-

fa and Costantino 1977). Populations of *T. castaneum* homozygous for the corn oil sensitive allele were established. The question of stability was addressed by observing both the genetic and the age structure changes following the introduction of genetically different (+/+) individuals into the homozygous *cos* populations.

The data set consisted of 29 consecutive adult censuses on 11 *cos* homozygous populations (319 observations) and 6 polymorphic populations (174 observations) obtained while the adult numbers were fluctuating in the region of their steady states (week 62 to week 128). The hypotheses that these observed distributions (Fig. 5) were gamma was accepted for both populations. The null hypothesis that these gammas have identical parameters was rejected using the D^2 test statistic.

Several evolutionary models predict that natural selection will maximize the equilibrium size of a population (see Desharnais and Costantino 1983). Was that the situation in this experiment? As we have seen (Fig. 5), adult numbers in the experimental cultures did not converge to a fixed equilibrium point. Instead, the populations were found to fluctuate around a mean value. The stationary distribution concept has provided a way to characterize these genetically different populations so that we can begin to test experimentally this maximization hypothesis.

Same population at two different times

T. castaneum strain cIV was studied in 1964 and again in 1968 (Park et al. 1964, Leslie et al. 1968). For the 1964 data set the gamma was accepted but for the 1968 data this was not the case (Fig. 6). The gamma significantly overpredicts the 1st cell and significantly underpredicts the 4th cell of the 1968 data, though it
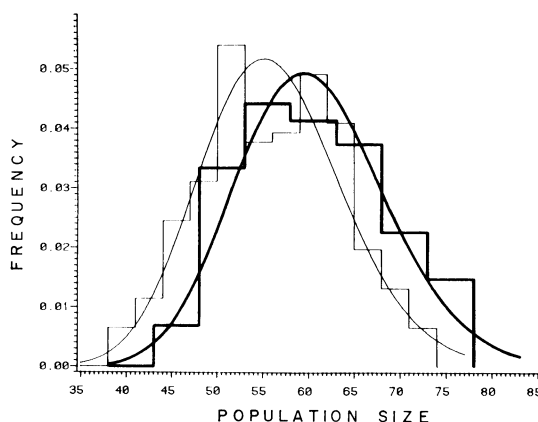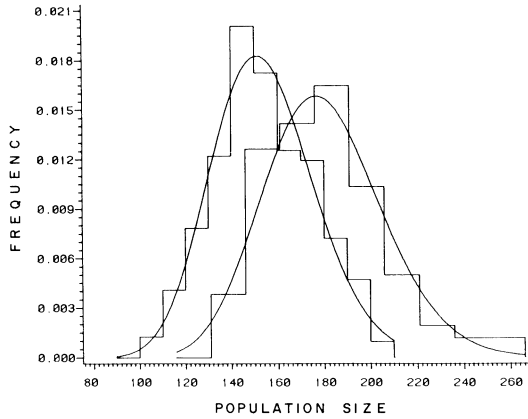
FIG. 5. Equilibrium frequencies of two groups of *T. castaneum* populations, one group homozygous for the *cos* (corn oil *s*ensitive) allele and the other group polymorphic, plus fitted gamma pdf's (homozygous: $n = 319$, $X^2 = 9.13$, $P = .33$, df $= 8$, $\hat{\alpha} = 49.08821$, $\hat{\beta} = 3.18271 \times 10^{-1}$, $\hat{\sigma}_1{}^2 = 16.59789$, $\hat{\sigma}_2{}^2 = 7.06359 \times 10^{-4}$, $\hat{\sigma}_{12} = 1.07790 \times 10^{-1}$; polymorphic: $n = 174$, $X^2 = 9.29$, $P = .16$, df $= 6$, $\hat{\alpha} = 50.34501$, $\hat{\beta} = 2.79550 \times 10^{-1}$, $\hat{\sigma}_1{}^2 = 37.95802$, $\hat{\sigma}_2{}^2 = 1.16405 \times 10^{-3}$, $\hat{\sigma}_{12} = 2.09354 \times 10^{-1}$). Data are from Desharnais and Costantino (1985). Homozygous: left; Polymorphic: right.
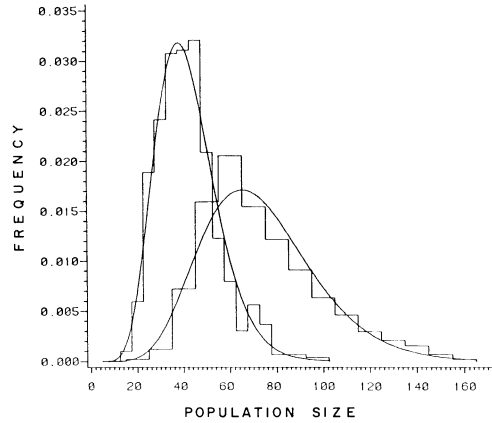

FIG. 6. Equilibrium frequencies of *T. castaneum* strain cIV in 1964 and 1968, plus fitted gamma pdf's (1964: $n = 604$, $X^2 = 21.99$, $P = .02$, df $= 11$, $\hat{\alpha} = 10.25296$, $\hat{\beta} = 2.44945 \times 10^{-1}$, $\hat{\sigma}_1{}^2 = 3.60986 \times 10^{-1}$, $\hat{\sigma}_2{}^2 = 2.19487 \times 10^{-4}$, $\hat{\sigma}_{12} = 8.70851 \times 10^{-3}$, classes 14–18 pooled during estimation; 1968: $n = 584$, $X^2 = 24.91$, $P < .01$, df $= 10$, $\hat{\alpha} = 8.95566$, $\hat{\beta} = 1.22223 \times 10^{-1}$, $\hat{\sigma}_1{}^2 = 1.98421 \times 10^{-1}$, $\hat{\sigma}_2{}^2 = 3.54295 \times 10^{-5}$, $\hat{\sigma}_{12} = 2.54135 \times 10^{-3}$, classes 13 and 14 pooled during estimation). Data are from Park et al. (1964) and Leslie et al. (1968). 1964: left; 1968: right.

captures the essential shape of the histogram. Comparing these two populations using the D^2 test is not appropriate, since the gamma does not fit one of them. However, it is clear that the distributions are not the same. Are the predictions of the stochastic model consistent with the biological information on this strain? In their analysis of strain cIV-1968, Leslie et al. (1968:15) discussed three changes in this stock: first, the average death rate per head of adult population per 30 d was reduced from 0.1982 in 1964 to 0.1571 in 1968; second, the average fertility of eggs was increased from 66.5 to 85.4%; and third, the average duration of the immature life stages was shortened from 31.09 to 27.81 d. As noted in Fig. 6, both the mean and variance of the stationary distribution increased in 1968 as compared with 1964, which is entirely consistent with the predictions of the gamma density function.

In a similar manner, strain bI of *T. confusum* was studied by these same authors in 1964 and again in 1968. The gamma model fits the 1968 data, but not the 1964 data (the 1964 data deviate significantly from the model in the 1st, 4th, and 9th cells of the 1964 data pooled for estimation as in the caption of Fig. 7). The observed distributions for these two years (Fig. 7) indicated a reduction in both the mean and variance of the stationary density. What had happened? Leslie et al. (1968:15) wrote, "the principal change in this strain appears to lie in an increase of its cannibalistic powers." Our prediction is in agreement with their statement: an increase in the rate of cannibalism C would reduce both the mean and variance of the gamma distribution.

CONCLUSIONS

In their excellent text, *Modelling Fluctuating Populations,* Nisbet and Gurney (1982:186) stated, "Calculation of a population's probability distribution is normally a means to an end rather than the end itself if for no other reason than that it is a virtually unmeasurable quantity, . . .". Though their statement is
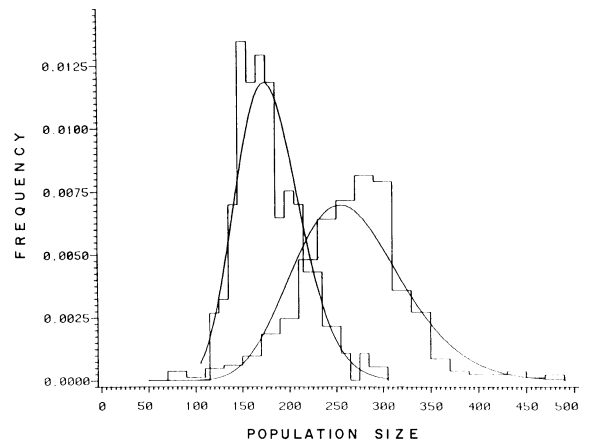

FIG. 7. Equilibrium frequencies of *T. confusum* strain bI in 1964 and 1968, plus fitted gamma pdf's (1964: $n = 406$, $X^2 = 54.20$, $P < .01$, df $= 12$, $\hat{\alpha} = 20.88335$, $\hat{\beta} = 7.82071 \times 10^{-2}$, $\hat{\sigma}_1{}^2 = 2.38350$, $\hat{\sigma}_2{}^2 = 3.40828 \times 10^{-5}$, $\hat{\sigma}_{12} = 8.91789 \times 10^{-3}$, classes 1–4 pooled and classes 18–21 pooled during estimation; 1968: $n = 186$, $X^2 = 10.52$, $P = .48$, df $= 11$, $\alpha = 27.56627$, $\hat{\beta} = 1.53157 \times 10^{-1}$, $\hat{\sigma}_1{}^2 = 7.92021$, $\hat{\sigma}_2{}^2 = 2.48806 \times 10^{-4}$, $\hat{\sigma}_{12} = 4.39736 \times 10^{-2}$, classes 15–19 pooled during estimation). Data are from Park et al. (1964) and Leslie et al. (1968). 1968: left; 1964: right.

quite correct for many populations, we believe there could be numerous situations in ecology for which the distribution is indeed observationally or experimentally accessible.

For instance, such data are available for adult populations of the flour beetle *Tribolium*. The flour beetle populations do not converge to a fixed, stable point equilibrium, but rather fluctuate irregularly around some mean value. A deterministic (ordinary differential equation) growth model can only describe the average forces of adult recruitment and mortality in these populations. A simple stochastic extension (stochastic differential equation), however, can capture the variability of these forces, producing emergent, testable predictions about the dynamic behavior of the populations. The stochastic flour beetle model presented in this paper predicts a positively skewed, stationary distribution for population size rather than a fixed point equilibrium. The model can be approximated reasonably well by a stochastic logistic model which yields a stationary gamma distribution for population size. Example data sets presented in this paper are consistent with this prediction.

Careful attention to statistical methods is important in assessing agreement of population dynamics models and data. Much research on statistical inference for dynamic models remains to be done, and much existing research in the mathematical statistics literature remains to be implemented in ecological work. The methods presented in this paper for estimation and testing with stationary distributions are simple, straightforward to compute, and easy to understand. With these methods, the concept of stochastic equilibrium becomes a parsimonious hypothesis about population regulation that is vulnerable to empirical testing.

In particular, our results with flour beetle data described in this paper suggest that the gamma distribution deserves more widespread consideration as a stochastic equilibrium abundance model for other species.

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