

LOGISTIC POPULATION GROWTH UNDER RANDOM DISPERSAL*

■ HENRY C. TUCKWELL
Department of Mathematics, Monash University,
Clayton, Victoria 3168, Australia

■ JAMES A. KOZIOL
Department of Basic and Clinical Research,
Research Institute of Scripps Clinic,
La Jolla, CA 92037, U.S.A.

Various diffusion processes employed for modelling logistic growth are briefly summarized. A discrete-time, discrete-state space stochastic process for population growth is proposed and analyzed with either Bose–Einstein or Maxwell–Boltzmann statistics for the distribution of offspring in available sites in a restricted region. A diffusion approximation is constructed, which differs from those previously employed. The logistic law is a natural deterministic analog of the diffusion process.

1. Introduction. The logistic growth law is described by the differential equation,

$$dN/dt = mN - nN^2, \quad t > 0, \quad N(0) = N_0 > 0 \quad (1)$$

where $N(t)$ is the population size at time t and m and n are constants. Although this law was first introduced by Verhulst (1838) as a mathematical model for negative feedback on population growth due to competition for and depletion of resources, it has never been derived from first principles. Lotka (1925), for example, obtained (1) by considering a general power series for the growth rate

$$dN/dt = a_1N + a_2N^2 + a_3N^3 + \dots$$

and simply truncating the series at the quadratic term.

The uniqueness of the logistic law was questioned by Feller (1939a), who found that population trajectories described by (1) could equally well be fitted by scaled normal distribution curves with time-dependent argument. Jensen (1975) has queried the meanings of the parameters which occur in the various forms of equation (1).

Typically, the representation of population growth by equation (1) is an assumption whose validity is tested by comparing the predictions of the theory

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and experience (Pearl and Reed, 1920; Pearl, 1924; Yule, 1925). Recently, Leach (1981) compared the relative merits of the logistic law and the component method for population projection, and determined that the logistic method can be quite useful in practice. [See also Koziol and Tuckwell (1986).]

The first study of a random logistic growth process seems to have been that of Feller (1939b). (In the sequel we will use the notation N_t to denote a random population size at time t . The various diffusions for growth can be succinctly described by stochastic differential equations. In these, W_t will represent a standard Wiener process and all integrals with respect to W_t will be taken in the Ito sense unless otherwise specified.) The stochastic equation describing that process is

$$dN_t = (aN_t - bN_t^2) dt + c(N_t)^{1/2} dW_t, \quad (2)$$

where a , b and c are constants. The corresponding Kolmogorov equation for the transition density has never been solved. It is not clear why randomness should enter a logistic growth process as in (2), though the random term, that involving W_t , was ascribed to "sampling variation" by Levins (1969). Note that the process described by (2) takes values in $(0, \infty)$, so there is no upper limit on the size of the population unless a barrier is introduced at the carrying capacity.

This property also holds for the class of models considered by Goel *et al.* (1971),

$$dN_t = f(N_t) dt + aN_t dW_t, \quad (3)$$

where solutions of $dN(t)/dt = f(N(t))$ asymptote to some fixed positive number, as $t \rightarrow \infty$, for positive net growth rates. May (1973) and Ludwig (1975) found the equilibrium distribution and conditions for its existence, for solutions of (3) when it is of the form

$$dN_t = aN_t(b - N_t) dt + cN_t dW_t; \quad (4)$$

Feldman and Roughgarden (1975) pointed out how the various definitions of stochastic integrals affected the conditions for an equilibrium to exist.

Levins (1969) and Tuckwell (1974) considered the effects of a random growth rate through the stochastic equation

$$dN_t = aN_t(b - N_t) dt + cN_t(b - N_t) dW_t. \quad (5)$$

If the integral is taken in the Stratonovich sense, then no equilibrium distribution exists and the population tends to zero or carrying capacity with probability one, according to whether $a < 0$ or $a > 0$.

Levins (1969) considered the original logistic law with a random carrying capacity:

$$dN_t = aN_t(1 - bN_t) dt + cN_t^2 dW_t, \quad (6)$$

where again N_t may become infinite. This model was also investigated by Feldman and Roughgarden (1975). Prajneshu (1980) studied the logistic law with additive white noise,

$$dN_t = N_t(a - N_t) dt + b dW_t, \tag{7}$$

and found the eigenfunction expansion of the transition probability density. A modified version of (2),

$$dN_t = (a - b \log N_t)N_t dt + cN_t dW_t \tag{8}$$

(Stratonovich intergral) was introduced by Capocelli and Ricciardi (1974), who obtained the transition density of the process.

In all the above stochastic models, the logistic equation or a variation of it has been the starting point, with the randomness being inserted in a rather ad hoc manner. Ludwig (1976), commenting on this approach, suggested that diffusions, if approximating a random process, should instead be derived from discrete processes. He also obtained a diffusion model for logistic type growth,

$$dN_t = aN_t(b - N_t) dt + c(N_t + kN_t^2)^{1/2} dW_t, \tag{9}$$

deriving it from a discrete model in which it was necessarily assumed that offspring per individual are Poisson random variables with parameters that behave like $1 - N/K$, where K is the carrying capacity.

In this note, we will analyse a stochastic model for population growth, in which offspring disperse among a finite number of habitats or sites. From this model, we will obtain a diffusion approximation. A deterministic approximation will give rise to a general growth law with the classical logistic law as a special case.

2. Growth with Random Dispersal in a Limited Environment. We consider the following simple model for population growth in a limited environment which contains K viable sites. Suppose at time t there are $N(t)$ individuals (occupying different sites), where $N(t) \leq K$. We will assume uniform fecundity with each adult giving rise to μ offspring, and a uniform death rate, λ . Then, just subsequent to time t , there are $N(t) + (\mu - \lambda)N(t)$ individuals. We assume that the $N(t)(1 - \lambda)$ survivors retain their habitats, but each of the $\mu N(t)$ offspring must occupy one of the remaining $K - N(t)(1 - \lambda)$ available sites in order to survive to the next reproductive season, at $t + \Delta t$.

Bose-Einstein dispersal rule. Consider now the dispersal of the offspring among the vacant sites under a probability model that may be described with Bose-Einstein statistics (Feller, 1968, p. 41). Suppose r offspring are dispersed among n sites. Under our probability model this means there are only

$$\binom{n+r-1}{n-1}$$

distinguishable arrangements of the offspring among the sites, and each of these is assigned equal probability. The probability that exactly m habitats remain empty is then

$$p_m = \binom{n}{m} \binom{r-1}{n-m-1} / \binom{n+r-1}{r}. \tag{10}$$

Let the random variable U denote the number of unoccupied habitats. Then, if $r \geq n$,

$$\begin{aligned} E(U) &= \sum_{m=0}^{n-1} m \binom{n}{m} \binom{r-1}{n-m-1} / \binom{n+r-1}{r} \\ &= n \sum_{m=1}^{n-1} \binom{n-1}{m-1} \binom{r-1}{n-m-1} / \binom{n+r-1}{r} \\ &= n \sum_{k=0}^{n-2} \binom{n-1}{k} \binom{r-1}{n-1-k-1} / \binom{n+r-1}{r} \\ &= n(n-1)/(n+r-1). \end{aligned} \tag{11}$$

Similarly,

$$\begin{aligned} E[U(U-1)] &= \sum_{m=2}^{n-1} m(m-1) \binom{n}{m} \binom{r-1}{n-m-1} / \binom{n+r-1}{r} \\ &= n(n-1) \sum_{m=2}^{n-1} \binom{n-2}{m-2} \binom{r-1}{n-2-(m-2)-1} / \binom{n+r-1}{r} \\ &= n(n-1)(n-1)(n-2)/(n+r-1)(n+r-2). \end{aligned} \tag{12}$$

Note that expressions (11) and (12) for the first and second factorial moments of U remain valid if $r < n$. It follows that

$$\begin{aligned} \text{var}(U) &= E[U(U-1)] + E(U)[1 - E(U)] \\ &= n(n-1)r(r-1)/(n+r-1)^2(n+r-2). \end{aligned} \tag{13}$$

Maxwell-Boltzmann dispersal rule. The use of Bose-Einstein statistics implies a uniform probability for distinguishable arrangements of the offspring among the sites, which is appropriate in the absence of any prior information or assumptions about the geometry of niches or dispersal mechanisms. Suppose instead that prior information is indeed available. In this regard, perhaps the most common circumstances would be adoption of the standard random

dispersal model, entailing uniform independent assignment of offspring to sites. Starting with the Maxwell–Boltzmann formula for the number $N_m(r, n)$ of distinguishable distributions of r offspring into n sites leaving exactly m sites empty,

$$N_m(r, n) = \binom{n}{m} \sum_{k=0}^{n-m} (-1)^k \binom{n-m}{k} (n-m-k)^r,$$

we may show that

$$E(U) = \sum_{m=0}^{n-1} mn^{-r} N_m(r, n) = \left(\frac{n-1}{n}\right)^{r-1} (n-1), \tag{14}$$

$$E[U(U-1)] = \left(\frac{n-2}{n}\right)^{r-1} (n-1)(n-2), \tag{15}$$

and finally

$$\text{var}(U) = \frac{n-1}{n^{r-1}} \{ (n-2)^r + (n-1)^{r-1} [1 - \left(\frac{n-1}{n}\right)^{r-1} (n-1)] \}. \tag{16}$$

Application to the model. The application of the formulas to our growth model proceeds directly. At time t , there are N occupied sites and $K-N$ available sites. At $t + \Delta t$, deterministically μN offspring compete for the $K - N(1 - \lambda)$ available sites. Let us set $1 - \lambda = \rho$, and let p denote the common probability that any offspring encounters a site (regardless of availability of sites). The parameter p reflects initial survival of offspring and $p(1 - \rho N/K)$ is thus the probability that an offspring encounters an available site. We let the random variable R denote the number of offspring encountering available sites, taken to be binomially distributed with parameters μN and $p(1 - \rho N/K)$. We lastly impose a dispersal mechanism. Under the general Bose–Einstein statistics, the expected number M of empty sites, conditioned on R offspring finding available sites, is from (11),

$$E(M|R) = (K - \rho N)(K - \rho N - 1)/(K - \rho N + R - 1). \tag{17}$$

Therefore,

$$\begin{aligned} E(M) &= E[E(M|R)] \\ &= \sum_{r=0}^{\mu N} \left(\frac{(K - \rho N)(K - \rho N - 1)}{(K - \rho N + r - 1)} \right) b[r; \mu N, p(1 - \rho N/K)], \end{aligned} \tag{18}$$

where $b(r; n, q)$ denotes the binomial probability $\binom{n}{r} q^r (1-q)^{n-r}$. The expectation of the increase in population size can thus be found from

$$E[\Delta N|N(t) = N] = (K - N) - E(M). \tag{19}$$

The variance of the increase in population size in time Δt is merely the variance of the change in the number of available sites. Hence, from (12) and (13),

$$\begin{aligned} \text{var}[\Delta N|N(t) = N] &= \text{var}(M) \\ &= E[\text{var}(M|R)] + \text{var}[E(M|R)] \\ &= E\left[\frac{(K - \rho N)(K - \rho N - 1)R(R - 1)}{(K - \rho N + R - 1)^2(K - \rho N + R - 2)}\right] \\ &\quad + \text{var}\left[\frac{(K - \rho N)(K - \rho N - 1)}{(K - \rho N + R - 1)}\right]. \end{aligned} \tag{20}$$

Exact series expressions similar to (18) can thus be obtained for the variance of ΔN .

On the other hand, had we assumed in particular random dispersal with attendant Maxwell–Boltzmann statistics, we would have, from (14),

$$E(M|R) = \left(\frac{K - \rho N - 1}{K - \rho N}\right)^{R-1} (K - \rho N - 1); \tag{21}$$

and, in analogy to (18),

$$E(M) = \sum_{r=0}^{\mu N} \left(\frac{K - \rho N - 1}{K - \rho N}\right)^{r-1} (K - \rho N - 1) b\left[r; \mu N; p\left(1 - \frac{\rho N}{K}\right)\right]. \tag{22}$$

Hence

$$E[\Delta N|N(t) = N] = K - N - E(M), \tag{23}$$

and

$$\begin{aligned} \text{var}[\Delta N|N(t) = N] &= E[\text{var}(M|R)] \\ &\quad + \text{var}[E(M|R)] = E\left[\frac{K - \rho N - 1}{(K - \rho N)^{R-1}} \left\{ (K - \rho N - 2)^R \right. \right. \\ &\quad \left. \left. + (K - \rho N - 1)^{R-1} \left[1 - \left(\frac{K - \rho N - 1}{K - \rho N}\right)^{R-1} (K - \rho N - 1) \right] \right\}\right] \\ &\quad + \text{var}\left\{\left(\frac{K - \rho N - 1}{K - \rho N}\right)^{R-1} (K - \rho N - 1)\right\}. \end{aligned} \tag{24}$$

3. Diffusion Approximations and Logistic Growth. In this section we describe diffusion and deterministic approximations for populations which evolve according to the model considered in the preceding section. Since the exact

expressions for the mean and variance of N are rather unwieldy, we first obtain analytic approximations to them, using the delta method (Rao, 1973). The expected value of the change in the number of unoccupied habitats per unit time (i.e. setting $\Delta t = 1$) can be obtained approximately by replacing r in the coefficient of b in (18) by its mean. Thus, from our general dispersal model with *Bose-Einstein statistics*,

$$E[\Delta N|N(t) = N] \simeq K - N - \left[\frac{(K - \rho N)(K - \rho N - 1)}{K - \rho N - 1 + \mu N p(1 - \rho N/K)} \right]. \tag{25}$$

Again from the delta method, we obtain

$$\begin{aligned} \text{var}[\Delta N|N(t) = N] \simeq & \frac{(K - \rho N)(K - \rho N - 1)\mu N p(1 - \rho N/K)(\mu N p(1 - \rho N/K) - 1)}{(K - \rho N + \mu N p(1 - \rho N/K) - 1)^2(K - \rho N + \mu N p(1 - \rho N/K) - 2)} \\ & + \frac{(K - \rho N)^2(K - \rho N - 1)^2\mu N p(1 - \rho N/K)(1 - p(1 - \rho N/K))}{(K - \rho N - 1 + \mu N p(1 - \rho N/K))^4}. \end{aligned} \tag{26}$$

We now obtain more tractable approximations by assuming that the population size is large and that μp is less than one. Then

$$E[\Delta N|N(t) = N] \simeq (\mu p - \lambda)N \left[1 - \frac{\mu N p \rho}{(\mu p - \lambda)K} \right], \tag{27}$$

which can be written in more suggestive notation as

$$E[\Delta N|N(t) = N] \simeq rN \left[1 - \frac{N}{\kappa} \right], \tag{28}$$

where $r = \mu p - \lambda$ and $\kappa = (\mu p - \lambda)K/\mu p \rho$.

Similarly,

$$\begin{aligned} \text{var}[\Delta N|N(t) = N] \simeq & \frac{\mu^2 N^2 p^2 (K - \rho N)}{K^2 (1 + \mu N p/K)^3} + \frac{\mu N p (K - \rho N) (1 - p(K - \rho N)/K)}{K (1 + \mu N p/K)^4} \\ \simeq & \frac{(K - \rho N)\mu N p}{K} \left[1 - p(1 - N(\rho - 3\mu)/K) + \frac{4\mu N}{K} p^2 (1 - \rho N/K) + \dots \right]. \end{aligned} \tag{29}$$

If we retain only terms of order p , we obtain the quadratic expression

$$\text{var}[\Delta N|N(t) = N] \simeq \mu p N (1 - \rho N/K). \tag{30}$$

We thus obtain the following diffusion approximation, N_t , $t \geq 0$, for the population size (Kimura, 1964):

$$dN_t = E[\Delta N|N_t = N] dt + (\text{var}[\Delta N|N_t = N])^{1/2} dW_t \quad (\text{Ito}); \tag{31}$$

if we adopt the approximations given by (28) and (30), this leads to the stochastic equation

$$dN_t = rN_t(1 - N_t/\kappa) dt + (\mu p N_t(1 - \rho N_t/K))^{1/2} dW_t. \tag{32}$$

In the case where the *death rate is zero*, we have the simpler equation

$$dN_t = rN_t(1 - N_t/K) dt + (rN_t(1 - N_t/K))^{1/2} dW_t. \tag{33}$$

Note that this diffusion approximation is of a different form from any of the diffusion processes summarized in Section 1.

We turn now to the more specialized random dispersal model, with *Maxwell–Boltzmann statistics*. Here we have

$$E[\Delta N|N(t) = N] \simeq K - N - \left(\frac{K - \rho N - 1}{K - \rho N}\right)^{\mu N p(1 - \rho N/K)} (K - \rho N), \tag{34}$$

and

$$\begin{aligned} \text{var}[\Delta N|N(t) = N] &\simeq \frac{K - \rho N - 1}{(K - \rho N)^{\mu N p(1 - \rho N/K) - 1}} \\ &\quad \left\{ (K - \rho N - 2)^{\mu N p(1 - \rho N/K)} + (K - \rho N - 1)^{\mu N p(1 - \rho N/K) - 1} \right. \\ &\quad \left. \left[1 - \left(\frac{K - \rho N - 1}{K - \rho N}\right)^{\mu N p(1 - \rho N/K) - 1} (K - \rho N - 1) \right] \right\} \tag{35} \\ &\quad + \left(\frac{K - \rho N - 1}{K - \rho N}\right)^{2\mu N p(1 - \rho N/K) - 2} \left[\mu N p \left(1 - \frac{\rho N}{K}\right) - 1 \right]^{-2} \\ &\quad \times (K - \rho N - 1)^2 \mu N p \left(1 - \frac{\rho N}{K}\right) \left[1 - p \left(1 - \frac{\rho N}{K}\right) \right]. \end{aligned}$$

Though (25) and (34) differ, we nevertheless obtain from (34) the approximation

$$E[\Delta N|N(t) = N] \simeq (\mu p - \lambda) N \left[1 - \frac{\mu N p \rho}{(\mu p - \lambda) K} \right],$$

so that (28) continues to hold under the random dispersal model. This again leads, via (31), to a logistic diffusion approximation, though there is no simplification analogous to (30).

We point out that the manner in which we have obtained an approximation, by means of (31), leads to what is called the standard or usual diffusion approximation. This was employed in the pioneering work of Sewall Wright [see Kimura (1964)] in studies of random genetic drift, and has also been employed in neural modelling (Johannesma, 1968). It has been investigated numerically in the neural case by Tuckwell and Cope (1980) who found such an

approximation valid when the increments in the original process in small time intervals are relatively small. More recently, such an approach has been found to give excellent agreements to voltage and current fluctuations due to the opening and closing of ion channels in nerve membrane (Tuckwell, 1987). Thus we expect the diffusion approximation in the present work to be accurate when the population size is moderate or large and the number of surviving offspring per parent is relatively small. As technical references we mention Kurtz (1981a,b) where such matters as weak convergence of a sequence of approximating processes to a diffusion are discussed clearly and in depth.

We turn next to the matter of *classification of boundaries*. According to the scheme of Feller (1952), a boundary for a diffusion process may be regular, natural, exit or entrance. The nature of the boundaries determines whether boundary conditions can be imposed on the forward and backward Kolmogorov equations and also relates to the uniqueness of their solutions. When N_t is close to zero, the stochastic equation (33) becomes

$$dN_t \simeq rN_t dt + (rN_t)^{1/2} dW_t, N_t \simeq 0^+. \tag{36}$$

This is the equation satisfied by a well-known diffusion approximation for the classical branching process. The boundary $N=0$ is an exit boundary for (36); we may therefore conclude that $N=0$ is also an exit boundary for the process satisfying (33). Consider now the boundary $N=K$. Setting $L=K-N$ for N near K , we find that L satisfies

$$dL_t \simeq -rL_t dt + (rL_t)^{1/2} dW_t, L_t \simeq 0^+. \tag{37}$$

Although this differs from (36) only in the sign of the drift, L_t is not the diffusion approximation to the branching process. Nevertheless, an examination of the relevant integrals shows that $L=0$ is an exit boundary.

This makes for good qualitative agreement with the behaviour of the original discrete model. Clearly, if N_t were to achieve the value zero, it would be absorbed (no population, no offspring). Similarly then, if all viable sites are occupied and no deaths occur, it is impossible that the population ever decreases below the carrying capacity. Note that this would not be the case if $\lambda \neq 0$; were this the case, then, if at any time N_t reached K , it could retreat inside the interval $(0, K)$ in the next small time interval with nonzero probability.

Lastly, we consider moment approximations. For the general Ito equation

$$dN_t = f(N_t) dt + g(N_t) dW_t, \tag{38}$$

the mean $M(t)$ and variance $V(t)$, given N_0 , can be found approximately under suitable conditions by solving coupled differential equations, the first of which is (Jazwinski, 1970, p. 139)

$$\frac{dM}{dt} = f(M) + \frac{V}{2} f_{xx}(M). \tag{39}$$

Applying this to equation (32), we find that since

$$f_{xx} = \frac{-2r}{\kappa}, \tag{40}$$

then providing $\kappa \gg r\lambda$ and $V(t)$ is small or moderate, the expected population size satisfies the differential equation

$$\frac{dM}{dt} = (\mu p - \lambda)M \left[1 - \frac{\mu p(1 - \lambda)M}{(\mu p - \lambda)K} \right], t > 0, M(0) = N_0. \tag{41}$$

This is the logistic differential equation where, moreover, all the parameters have well-defined meanings [cf. Jensen (1975)]. However, some remarks are in order. The positive equilibrium population level according to (41) is given by

$$K^* = \frac{\tilde{\mu} - \lambda}{\tilde{\mu}(1 - \lambda)} K, \tag{42}$$

where $\tilde{\mu} = \mu p$. Thus $0 < K^* < K$ if $\lambda < \tilde{\mu} < 1$ and $K^* \in (K, K/(1 - \lambda))$ if $\tilde{\mu} > 1$. Since a population greater than K could not arise in the original model we see that the continuous approximation is appropriate when $\lambda < \tilde{\mu} < 1$ and will have a larger domain of applicability with respect to variations in $\tilde{\mu}$ when λ is small.

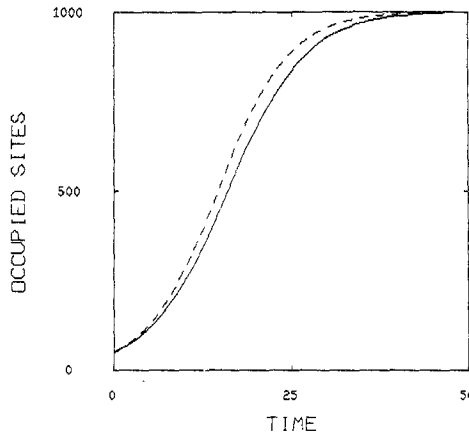


Figure 1. Expected population size for the discrete-time model (solid line) and the continuous time logistic approximation. For parameter values see text.

In Fig. 1 (solid line) we show the evolution of the expected population size using the same method of approximation (Jazwinski, 1970, p. 91) on the discrete-time process as calculated for equation (25) for $N_0 = 50, \mu = 2, p = 0.1, K = 1000, \lambda = 0$. The dashed line denotes the solution of the corresponding logistic differential equation (41) with the same values for the parameters. Clearly, the agreement is good.

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