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A comparison of three different stochastic population models with regard to persistence time

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Abstract

Results are summarized from the literature on three commonly used stochastic population models with regard to persistence time. In addition, several new results are introduced to clearly illustrate similarities between the models. Specifically, the relations between the mean persistence time and higher-order moments for discrete-time Markov chain models, continuous-time Markov chain models, and stochastic differential equation models are compared for populations experiencing demographic variability. Similarities between the models are demonstrated analytically, and computational results are provided to show that estimated persistence times for the three stochastic models are generally in good agreement when the models are consistently formulated. As an example, the three stochastic models are applied to a population satisfying logistic growth. Logistic growth is interesting as different birth and death rates can yield the same logistic differential equation. However, the persistence behavior of the population is strongly dependent on the explicit forms for the birth and death rates. Computational results demonstrate how dramatically the mean persistence time can vary for different populations that experience the same logistic growth.

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1. Introduction

Three types of stochastic models commonly used in population biology are: discrete-time Markov chain (DTMC) models, continuous-time Markov chain (CTMC) models, and stochastic differential equation (SDE) models. These stochastic models differ primarily in whether discrete or continuous variables are used for population size or time. However, comparisons have not been made among all three of these stochastic models with respect to persistence time. In biological applications, generally, SDEs or diffusion processes are used to approximate the CTMC or DTMC model when population sizes are large (e.g., Dennis, 2002; Dennis et al., 1991; Goel and Richter-Dyn, 1974; Nisbet and Gurney, 1982; Tier and Hanson, 1981) and sometimes the CTMC model is used to approximate the diffusion process (Wissel, 1989; Wissel and Schmitt, 1987; Wissel and Stöcker, 1991). In this paper, results are collected

from the mathematical, biological, and engineering literature regarding population persistence-time behavior as predicted by these three stochastic models. (In the mathematical and engineering literature, persistence time is generally referred to as first exit time or first passage time.) In addition, some interesting similarities are discovered in the three stochastic population models through comparison of the equations satisfied by the persistence time. Computational results show that the three stochastic models, when consistently formulated, yield similar results for the mean and variance in persistence time.

The three stochastic population models take into account the random nature of the individual birth and death processes-demographic variability. Environmental variability, where random fluctuations in the environment affect the entire population, is not considered in the present investigation. We do not estimate time to extinction using actual data as in Dennis et al. (1991), but compare analytical estimates for mean persistence time and higher-order moments of the persistence time and present some numerical comparisons.

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In the basic population model, it is assumed that the birth rate, $b(y)$, and the death rate, $d(y)$, are continuous and differentiable functions of the population size y . In addition, it is assumed that there exist numbers K and N such that $0 < K < N$ and

- (i) $b(0) = d(0) = 0$ and $b(y) = 0$ for $y \geq N$,
- (ii) $b(y) > 0$ for $y \in (0, N)$ and $d(y) > 0$ for $y \in (0, N]$,
- (iii) $b(y) > d(y)$ for $y \in (0, K)$,
- (iv) $b(y) < d(y)$ for $y \in (K, N)$.

Before describing the stochastic formulations, it is useful for comparison purposes to consider the analogous deterministic population growth model that satisfies assumptions (i)–(iv):

$$\frac{dy}{dt} = b(y) - d(y), \quad y(0) = y_0, \quad (1)$$

where $0 < y_0 < N$ and $y \equiv y(t)$ is the total population size at time t . There exists a unique solution $y(t)$ to (1) satisfying $y(t) \in (0, N)$ and

$$\lim_{t \rightarrow \infty} y(t) = K.$$

For this deterministic population model, the persistence time is always infinite. No matter how small the initial population size, extinction cannot occur. However, if the random nature of the birth and death process is taken into account, the persistence time for a stochastic model corresponding to (1) is likely to be finite. To determine the persistence time of a stochastic birth and death process, the per capita birth and death rates must be known. It is interesting that given only Eq. (1), the explicit forms for the birth and death rates are not known, only their difference $b(y) - d(y)$. As the following example illustrates many different birth and death rates can yield exactly the same deterministic equation.

An important and interesting example of (1) is the logistic equation, where $b(y) - d(y) = ry(1 - y/K)$, $r > 0$ and $K > 0$. Then (1) becomes

$$\frac{dy}{dt} = ry \left(1 - \frac{y}{K} \right). \quad (2)$$

Various stochastic formulations of the logistic model have been studied in the literature including SDEs or diffusion processes (see, e.g., Dennis and Costantino, 1988; Goel and Richter-Dyn, 1974; Golec and Sathanathan, 2003; Nisbet and Gurney, 1982; Tier and Hanson, 1981; Wissel and Schmitt, 1987; Wissel and Stöcker, 1991), CTMC models (see, e.g., Dushoff, 2000; Goel and Richter-Dyn, 1974; Keeling, 2000; Matis and Kiffe, 1999; Näsell, 2001, 2003; Nisbet and Gurney, 1982; Norden, 1982; Pielou, 1977; Renshaw, 1993; Tognetti and Winley, 1980; Tuckwell and Koziol, 1987; Wissel and Zschke, 1994), and DTMC models (Dennis and Taper, 1994; Allen, 2003). In a logistic model, it is reasonable to assume that the birth and

death rates satisfy

$$b(y) = b_1 y + b_2 y^2 \quad \text{and} \quad d(y) = d_1 y + d_2 y^2, \quad (3)$$

respectively, where b_i and d_i , $i = 1, 2$, are constants. It follows from Eqs. (2) and (3) that the constants b_i and d_i satisfy the following identities:

$$r = b_1 - d_1 \quad \text{and} \quad K = \frac{b_1 - d_1}{d_2 - b_2}. \quad (4)$$

Assumptions (i)–(iv) imply that $b_1 > d_1$, $d_2 > b_2$, $b_1 > 0$, $b_2 < 0$, and $d_1 \geq 0$. By inspecting (4), it is clear that given only the values for r and K , there are an infinite number of possibilities for b_1 , b_2 , d_1 , and d_2 . Because the probability of extinction and the persistence time depend on $b(y)$ and $d(y)$, there is a diversity of mean persistence times for the many possible stochastic birth and death processes that correspond to the single deterministic logistic growth model (2).

In the next section, we describe the three different stochastic birth and death processes based on assumptions (i)–(iv). In Section 3, the persistence-time behavior for each model is summarized from the literature. Some new results demonstrate the similarities in the persistence time among the three models. In Section 4, numerical examples are given illustrating the persistence-time results for each model and the diversity of persistence times when different birth and death rates are assumed. The last section summarizes our findings and discusses the applicability of each of the three models.

2. Stochastic birth and death processes

Let $Y(t)$ denote the random variable for the total population size at time t and assume that the birth and death rates $b(y)$ and $d(y)$ satisfy assumptions (i)–(iv). Some well-known properties of three consistent stochastic formulations for model (1) are discussed in this section. In the first two formulations $Y(t)$ is a discrete random variable, $Y(t) \in \{0, 1, 2, \dots, N\}$, but in the third formulation $Y(t)$ is a continuous random variable, $Y(t) \in [0, N]$. In all cases, N represents the maximum population size.

2.1. Discrete-time Markov chain model

In the DTMC model, both time and population size are discrete-valued. Let Δt be a fixed time interval and $t \in \{0, \Delta t, 2\Delta t, \dots\}$. It is assumed that Δt is sufficiently small such that at most one change occurs during the time interval Δt , either a birth or a death. Given the population size is y , a birth occurs with probability $b(y)\Delta t$ and a death with probability $d(y)\Delta t$. It is assumed that $b(y)$ and $d(y)$ satisfy assumptions (i)–(iv) for the discrete set of points $y \in \{0, 1, \dots, N\}$.

Let the probabilities associated with $Y(t)$ be denoted as

$$p_y(t) = \text{Prob}\{Y(t) = y\}, \quad y = 0, 1, \dots, N,$$

and $p(t) = (p_0(t), p_1(t), \dots, p_N(t))^T$. Denote the transition probabilities as $p_{yx}(\Delta t) = \text{Prob}\{Y(t + \Delta t) = y | Y(t) = x\}$, where

$$p_{yx}(\Delta t) = \begin{cases} b(x)\Delta t, & x = y - 1, \quad y \in \{1, \dots, N\}, \\ d(x)\Delta t, & x = y + 1, \quad y \in \{0, 1, \dots, N - 1\}, \\ 1 - [b(x) + d(x)]\Delta t, & x = y, \quad y \in \{0, 1, \dots, N\}, \\ 0 & \text{otherwise.} \end{cases} \quad (5)$$

Then, $p_y(t + \Delta t)$ satisfies the following difference equations:

$$p_y(t + \Delta t) = b(y - 1)\Delta t p_{y-1}(t) + d(y + 1)\Delta t p_{y+1}(t) + (1 - [b(y) + d(y)]\Delta t)p_y(t) \quad (6)$$

for $y = 1, 2, \dots, N - 1$. For $y = 0$ and $y = N$,

$$p_0(t + \Delta t) = p_0(t) + d(1)\Delta t p_1(t)$$

and

$$p_N(t + \Delta t) = b(N - 1)\Delta t p_{N-1}(t) + (1 - d(N)\Delta t)p_N(t).$$

The difference equations project forward in time and can be expressed in matrix form as

$$p(t + \Delta t) = Pp(t), \quad p_{y_0}(0) = 1, \quad (7)$$

where matrix $P = (p_{yx}(\Delta t))$ is the transition matrix

$$P = \begin{pmatrix} 1 & d(1)\Delta t & 0 & 0 & \dots & 0 \\ 0 & 1 - [b(1) + d(1)]\Delta t & d(2)\Delta t & 0 & \dots & 0 \\ 0 & b(1)\Delta t & 1 - [b(2) + d(2)]\Delta t & d(3)\Delta t & \dots & 0 \\ 0 & 0 & b(2)\Delta t & 1 - [b(3) + d(3)]\Delta t & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & d(N)\Delta t \\ 0 & 0 & 0 & 0 & \dots & 1 - d(N)\Delta t \end{pmatrix} \quad (8)$$

(see e.g., Allen, 2003). To ensure that P is a stochastic matrix (nonnegative and the column elements sum to one), it is assumed that

$$\max_{y \in \{1, 2, \dots, N\}} \{[b(y) + d(y)]\Delta t\} \leq 1.$$

For this model, zero is the only absorbing state, $p_{00}(\Delta t) = 1$. Eventually, population extinction occurs with probability one, i.e., $\lim_{t \rightarrow \infty} p_0(t) = 1$.

2.2. Continuous-time Markov chain model

For the CTMC model, $t \in [0, \infty)$ and $Y(t) \in \{0, 1, 2, \dots, N\}$. For Δt sufficiently small, the infinitesimal transition probabilities $p_{yx}(\Delta t)$ are similar to those given in (5). The transition probabilities for the CTMC model assume

$$p_{yx}(\Delta t) = \begin{cases} b(x)\Delta t + o(\Delta t), & x = y - 1, \quad y \in \{1, \dots, N\}, \\ d(x)\Delta t + o(\Delta t), & x = y + 1, \quad y \in \{0, \dots, N - 1\}, \\ 1 - [b(x) + d(x)]\Delta t + o(\Delta t), & x = y, \quad y \in \{0, 1, \dots, N\}, \\ o(\Delta t) & \text{otherwise.} \end{cases}$$

Taking the limit as $\Delta t \rightarrow 0$, a system of differential equations for the probabilities $p_y(t) = \text{Prob}\{Y(t) = y\}$ can be shown to satisfy the forward Kolmogorov differential equations:

$$\frac{dp_y(t)}{dt} = b(y - 1)p_{y-1}(t) - [b(y) + d(y)]p_y(t) + d(y + 1)p_{y+1}(t), \quad y \in \{1, \dots, N\},$$

$$\frac{dp_0(t)}{dt} = d(1)p_1(t) \quad (9)$$

(e.g., Goel and Richter-Dyn, 1974; Karlin and Taylor, 1975; Nisbet and Gurney, 1982). This system can be

written in matrix form as

$$\frac{dp}{dt} = Qp, \quad p_{y_0}(0) = 1, \quad (10)$$

where matrix $Q = (q_{ij})$ is the infinitesimal generator matrix (Karlin and Taylor, 1975):

$$Q = \begin{pmatrix} 0 & d(1) & 0 & 0 & \dots & 0 \\ 0 & -[b(1) + d(1)] & d(2) & 0 & \dots & 0 \\ 0 & b(1) & -[b(2) + d(2)] & d(3) & \dots & 0 \\ 0 & 0 & b(2) & -[b(3) + d(3)] & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & d(N) \\ 0 & 0 & 0 & 0 & \dots & -d(N) \end{pmatrix}.$$

Note that by subtracting $Ip(t)$ from both sides of (7), dividing through by Δt , and taking the limit as $\Delta t \rightarrow 0$, it follows that

$$\lim_{\Delta t \rightarrow 0} \frac{P - I}{\Delta t} = Q.$$

The system of difference equations (7) may be considered a discrete-time approximation to the differential system (10). Approximation (7) will yield results close to the CTMC model (10) provided that Δt is sufficiently small. Because $q_{00} = 0$, it follows that zero is the unique absorbing state in (10), i.e. $\lim_{t \rightarrow \infty} p_0(t) = 1$.

2.3. Stochastic differential equation model

In the third stochastic formulation, both time and state are continuous variables, $t \in [0, \infty)$ and $Y(t) \in [0, N]$. Let $p(y, t)$ denote the probability density function (p.d.f.) for the continuous random variable $Y(t)$, i.e.,

$$\text{Prob}\{Y(t) \in [a, b]\} = \int_a^b p(y, t) dy.$$

Assume that the birth and death rates $b(y)$ and $d(y)$ satisfy conditions (i)–(iv) and, in addition, assume that $b(y)$ and $d(y)$ are $C^2([0, N])$. It is well known (Gardiner, 1985; Goel and Richter-Dyn, 1974; Karlin and Taylor, 1981; Nisbet and Gurney, 1982) that the probability density function for this birth and death process satisfies the following forward Kolmogorov differential equation:

$$\frac{\partial p(y, t)}{\partial t} = - \frac{\partial([b(y) - d(y)]p(y, t))}{\partial y} + \frac{1}{2} \frac{\partial^2([b(y) + d(y)]p(y, t))}{\partial y^2} \tag{11}$$

for $y \in (0, N)$, $t \in (0, \infty)$, and $p(y, 0) = \delta(y - y_0)$, where $b(y) - d(y)$ is the infinitesimal mean and $b(y) + d(y)$ is the infinitesimal variance. The forward Kolmogorov equation can be derived directly from the forward equations for the CTMC model (see, e.g., Goel and Richter-Dyn, 1974; Wissel and Schmitt, 1987; Wissel and Stöcker, 1991).

It follows from the forward Kolmogorov equation (11) that sample paths $Y(t)$ of the stochastic process satisfy the following Ito stochastic integral equation:

$$Y(t) = y_0 + \int_0^t [b(Y(u)) - d(Y(u))] du + \int_0^t \sqrt{b(Y(u)) + d(Y(u))} dW(u) \tag{12}$$

(see, e.g., Gardiner, 1985; Wissel and Schmitt, 1987; Wissel and Stöcker, 1991) or can be derived directly from the birth and death process (Allen, 1999). In (12), W is the standard Wiener process, where $\Delta W(t) = W(t + \Delta t) - W(t)$ has a normal distribution, $N(0, \Delta t)$.

The first integral in (12) is a Riemann integral, but the second integral is an Ito stochastic integral (Gard, 1988; Øksendal, 2000; Schurz, 2002). For notational convenience, the stochastic integral equation (12) is often expressed as the SDE:

$$\frac{dY(t)}{dt} = b(Y(t)) - d(Y(t)) + \sqrt{b(Y(t)) + d(Y(t))} \frac{dW(t)}{dt},$$

$$Y(0) = y_0 > 0. \tag{13}$$

Notice that the deterministic term in the SDE (13) is identical to the right-hand side of the deterministic equation (1). The stochastic term in (13) is due to demographic variations in the birth and death rates. For example, for a small time interval the mean and variance of changes in the population size using (13) have the correct terms to $O(\Delta t^2)$. In particular,

$$E(\Delta Y) = [b(Y) - d(Y)]\Delta t + O((\Delta t)^2),$$

$$E((\Delta Y)^2) = [b(Y) + d(Y)]\Delta t + O((\Delta t)^2).$$

For this model, zero is an absorbing state as $b(0) = d(0) = 0$, so the solution $Y(t)$ to (13) satisfies $Y(t + \Delta t) = 0$ provided that $Y(t) = 0$.

3. Persistence time

Let T be the random variable for the time until population extinction. Because the distribution of T depends on the initial population size, we shall denote this dependence by T_{y_0} . Let τ_{y_0} denote the expected time until extinction or the mean persistence time when the initial population size is y_0 , that is,

$$\tau_{y_0} = E(T_{y_0}).$$

Denote the r th moment, $r > 1$, as $\tau_{y_0}^r = E(T_{y_0}^r)$. Since zero is an absorbing state, $\tau_0 = 0$ and $\tau_0^r = 0$, for $r > 1$. Let the moment vectors for the persistence time for an initial population size $y_0 \in \{1, 2, \dots, N\}$ be denoted as $\tau = (\tau_1, \dots, \tau_N)^T$ and $\tau^r = (\tau_1^r, \dots, \tau_N^r)^T$ for $r > 1$. A well-known explicit formula for the mean persistence time is given for the two Markov chain models. We derive a linear recurrence relationship satisfied by the higher-order moments for the CTMC model and for the SDE model. These formulas are also well known. However, we discover some new relationships between the persistence time in the Markov chain models and the SDE model.

3.1. Persistence time in the Markov chain models

For the DTMC model (7), in a small period of time Δt , there can be either a birth or a death or no change in the population size. The mean persistence time for the

DTMC model satisfies the following difference equations:

$$\tau_y = b(y)\Delta t(\tau_{y+1} + \Delta t) + d(y)\Delta t(\tau_{y-1} + \Delta t) + (1 - [b(y) + d(y)]\Delta t)(\tau_y + \Delta t), \tag{14}$$

where $y = 1, 2, \dots, N$ and $b(N) = 0$. The difference equations (14) can be written in a simplified form as follows (see, for example, Leigh, 1981):

$$d(y)\tau_{y-1} - [b(y) + d(y)]\tau_y + b(y)\tau_{y+1} = -1, \tag{15}$$

where $y = 1, 2, \dots, N$. Relationship (15) follows from the backward difference equations as opposed to the forward difference equations given in (6).

The CTMC model (10) satisfies the same relationships as in (14), where a term of $o(\Delta t)$ is added to the right-hand side of the equations. If $\Delta t \rightarrow 0$, then the mean persistence time satisfies the same relationship as the one for discrete time, that is, the equations given by (15). In the next section, (15) will be shown to follow from the backward Kolmogorov differential equations, where the connection to the SDE is also demonstrated.

The equations in (15) can be expressed as a single matrix equation, $D\tau = -\mathbf{1}$, where $\mathbf{1} = (1, \dots, 1)^T$ and

$$D = \begin{pmatrix} -b(1) - d(1) & b(1) & 0 & \dots & 0 & 0 \\ d(2) & -b(2) - d(2) & b(2) & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & d(N) & -d(N) \end{pmatrix}. \tag{16}$$

Matrix D is irreducibly diagonally dominant and therefore, nonsingular (Ortega, 1987). The solution for the mean persistence time is just $\tau = D^{-1}\mathbf{1}$.

An explicit solution for τ_y can be obtained because matrix D is tridiagonal (e.g., Goel and Richter-Dyn, 1974; Nisbet and Gurney, 1982; Richter-Dyn and Goel, 1972). Suppose $Y(0) = y$ for $y \in \{1, 2, \dots, N\}$. Then the mean persistence time satisfies

$$\tau_y = \begin{cases} \frac{1}{d(1)} + \sum_{i=2}^N \frac{b(1)\dots b(i-1)}{d(1)\dots d(i)}, & y = 1, \\ \tau_1 + \sum_{s=1}^{y-1} \left[\frac{d(1)\dots d(s)}{b(1)\dots b(s)} \sum_{i=s+1}^N \frac{b(1)\dots b(i-1)}{d(1)\dots d(i)} \right], & y = 2, \dots, N. \end{cases} \tag{17}$$

An expression for τ_y^r can be derived for the CTMC model. This expression was originally derived by Richter-Dyn and Goel (1972). The value for τ_y^r for $r > 1$ in the DTMC model is not the same as that for the CTMC model because terms of $o(\Delta t)$ do not disappear in the discrete-time model. However, the higher-order moments for the Markov chain models will be close provided Δt is small. The r th-order moment for the CTMC model can be expressed in terms of the $(r - 1)$ th-order moment:

$$d(y)\tau_{y-1}^r - [b(y) + d(y)]\tau_y^r + b(y)\tau_{y+1}^r = -r\tau_y^{r-1} \tag{18}$$

for $y = 1, 2, \dots, N$ (Goel and Richter-Dyn, 1974; Nisbet and Gurney, 1982; Norden, 1982). Relationship (18) will be shown to follow from the backward Kolmogorov differential equation in the next section. Note that for $r = 1$, the equations in (18) reduce to the equations derived for the mean persistence time in (15), where $\tau_y^1 = \tau_y$. The difference equations (18) can be expressed as the matrix equation $D\tau^r = -r\tau^{r-1}$, where matrix D is defined in (16). The solution is $\tau^r = -rD^{-1}\tau^{r-1}$. The r th-order moments can be found recursively, by applying the operator $-rD^{-1}$ to the $(r - 1)$ th-order moment. Using this procedure, an explicit solution for τ_y^r is derived here as

$$\tau_y^r = \begin{cases} r \frac{\tau_1^{r-1}}{d(1)} + r \sum_{i=2}^N \frac{b(1)\dots b(i-1)\tau_i^{r-1}}{d(1)\dots d(i)}, & y = 1, \\ \tau_1^r + r \sum_{s=1}^{y-1} \left[\frac{d(1)\dots d(s)}{b(1)\dots b(s)} \sum_{i=s+1}^N \frac{b(1)\dots b(i-1)\tau_i^{r-1}}{d(1)\dots d(i)} \right], & y = 2, \dots, N. \end{cases} \tag{19}$$

3.2. Persistence time in the SDE model

As in the other two formulations, the backward Kolmogorov differential equation is used to determine the moments of the persistence time for the SDE (13). The function $R(y, t)$, which is known as the reliability function in engineering applications, satisfies the backward Kolmogorov differential equation (Roberts, 1986; Sharp and Allen, 1998),

$$\frac{\partial R}{\partial t} = [b(y) - d(y)] \frac{\partial R}{\partial y} + \frac{[b(y) + d(y)]}{2} \frac{\partial^2 R}{\partial y^2} \tag{20}$$

for $y \in (0, N)$ and $t \in (0, \infty)$. The reliability function $R(y, t)$ satisfies $R(y, 0) = 1$, $y \in (0, N)$, $R(0, t) = 0$ and

$$\left. \frac{\partial R(y, t)}{\partial y} \right|_{y=N} = 0$$

for $t \in (0, \infty)$. The reliability function is the probability that the persistence time is greater than t assuming an initial population size of y (Roberts, 1986); that is,

$$R(y, t) = \text{Prob}\{T_y > t\}.$$

Denote the probability density function of T_y as $p_{T_y}(t)$, where y is the initial population size. Then the above relationship implies that

$$p_{T_y}(t) = -\frac{\partial R(y, t)}{\partial t}.$$

Thus, the mean persistence time, $\tau_y = E(T_y)$, satisfies

$$\tau_y = -\int_0^\infty t \frac{\partial R(y, t)}{\partial t} dt = \int_0^\infty R(y, t) dt,$$

where the last identity is obtained via integration by parts along with the assumption that $\lim_{t \rightarrow \infty} tR(y, t) = 0$.

Higher order moments satisfy

$$\tau_y^r = - \int_0^\infty t^r \frac{\partial R(y, t)}{\partial t} dt.$$

Again, application of integration by parts and the assumption that $\lim_{t \rightarrow \infty} t^r R(y, t) = 0$ implies that

$$\tau_y^r = r \int_0^\infty t^{r-1} R(y, t) dt. \tag{21}$$

In order to apply formula (21), the reliability function must be known.

An alternate method to find the higher-order moments uses a differential equation for τ_y^r . For example, by multiplying (20) by 1 or t and integrating over t from 0 to ∞ , it is readily seen that τ_y and τ_y^2 satisfy the following boundary value problem:

$$[b(y) - d(y)] \frac{d\tau_y}{dy} + \frac{[b(y) + d(y)]}{2} \frac{d^2\tau_y}{dy^2} = -1,$$

$$[b(y) - d(y)] \frac{d\tau_y^2}{dy} + \frac{[b(y) + d(y)]}{2} \frac{d^2\tau_y^2}{dy^2} = -2\tau_y,$$

where $\tau_0 = 0 = \tau_0^2$ and

$$\left. \frac{d\tau_y}{dy} \right|_{y=N} = 0 = \left. \frac{d\tau_y^2}{dy} \right|_{y=N}.$$

Extending this method to higher-order moments, it can be easily shown (Gardiner, 1985; Langtangen, 1994) that

$$[b(y) - d(y)] \frac{d\tau_y^r}{dy} + \frac{[b(y) + d(y)]}{2} \frac{d^2\tau_y^r}{dy^2} = -r\tau_y^{r-1}, \tag{22}$$

$r \geq 1,$

where $\tau_0^r = 0$ and $d\tau_y^r/dy = 0$ when $y = N$.

We point out a new relationship between the differential equations in (22) and the difference equations in (18) for the Markov chain models. Consider approximating the derivatives using a central difference scheme, i.e.,

$$\frac{d\tau_y^r}{dy} \approx \frac{\tau_{y+1}^r - \tau_{y-1}^r}{2} \quad \text{and} \quad \frac{d^2\tau_y^r}{dy^2} \approx \tau_{y+1}^r - 2\tau_y^r + \tau_{y-1}^r.$$

Applying these relations to (22), the difference equations (18) are obtained. This result illustrates the close similarities between the three different stochastic models.

Another new relationship between the stochastic models can be seen with the derivation of (18) from the backward Kolmogorov differential equations. Denote the reliability function for the CTMC model as $R_y(t)$. This function is a solution of the backward Kolmogorov differential equation:

$$\frac{dR_y(t)}{dt} = d(y)R_{y-1}(t) - [b(y) + d(y)]R_y(t) + b(y)R_{y+1}(t). \tag{23}$$

Note that the backward equation (23) is a discrete version of the backward equation (20), where $\partial R(y, t)/\partial y$ and $\partial^2 R(y, t)/\partial y^2$ in (20) are approximated by central difference schemes in y . As noted previously, a similar comparison was made for the forward equations by Goel and Richter-Dyn (1974), Wissel and Schmitt (1987), and Wissel and Stöcker (1991). As was true for the SDE model, $R_y(0) = 1, \lim_{t \rightarrow \infty} t^r R_y(t) = 0,$

$$\tau_y = - \int_0^\infty t \frac{dR_y(t)}{dt} dt = \int_0^\infty R_y(t) dt,$$

and

$$\tau_y^r = r \int_0^\infty t^{r-1} R_y(t) dt.$$

Multiplying Eq. (23) by 1 or t , then integrating over t from 0 to ∞ yields Eq. (18) for $r = 1, 2,$ respectively.

Generally, a numerical scheme is required to solve (22). However, in the special case of linear birth and death rates, $b(y) = b_1 y = d(y)$, then τ_y and τ_y^2 can be solved exactly to obtain

$$\tau_y = \frac{y}{b_1} \left(1 + \ln \left(\frac{N}{y} \right) \right) \quad \text{and}$$

$$\tau_y^2 = \frac{4N}{b_1^2} y - \frac{2}{b_1^2} \left[(1 + \ln N) \frac{y^2}{2} + \frac{3y^2}{4} - \frac{y^2}{2} \ln(y) \right]. \tag{24}$$

For example, at $y = N$:

$$\tau_N = \frac{N}{b_1} \quad \text{and} \quad \tau_N^2 = \frac{3N^2}{2b_1^2}. \tag{25}$$

The variance at $y = N$ is $\tau_N^2 - (\tau_N)^2 = N^2/2b_1^2$. In addition, the mean persistence time for the Markov chain models can be calculated exactly for this example. Using formula (17),

$$\tau_y = \frac{y}{b_1} \left(1 + \sum_{k=y+1}^N \frac{1}{k} \right). \tag{26}$$

The formulas in (19) give an explicit formula for τ_y^2 also. The CTMC model satisfies

$$\tau_N = \frac{N}{b_1} \quad \text{and} \quad \tau_N^2 = \frac{3N^2 + N}{2b_1^2}. \tag{27}$$

The variance at $y = N$ is $(N^2 + 2N)/2b_1^2$. At $y = N$, the two formulas for the mean, (25) and (27), are the same. The second moments and variances in the two formulas differ by $O(N)$, but their ratio approaches unity as $N \rightarrow \infty$. Also, since $\ln \left(\frac{N+1}{y+1} \right) \leq \sum_{k=y+1}^N \frac{1}{k} \leq \ln \left(\frac{N}{y} \right)$, the summation in (26) can be approximated for large values of N by

$$\sum_{k=y+1}^N \frac{1}{k} \approx \ln \left(\frac{N}{y} \right).$$

Substituting this approximation into (26) yields the same formula for the mean persistence time that is given by (24).

4. Numerical examples

In this section, the three stochastic models are applied to estimate persistence times for populations satisfying logistic growth. It is seen that the three models generally agree very well even for small initial population sizes. In addition, it is shown that the same deterministic logistic growth model can result in more than one stochastic model and, furthermore, these stochastic models can experience much different persistence behavior.

As a first example, consider birth and death rates given by

$$b(y) = 2y - \frac{y^2}{50} \quad \text{and} \quad d(y) = y + \frac{y^2}{50}, \quad N = 100. \quad (28)$$

The corresponding deterministic logistic model satisfies the differential equation,

$$\frac{dy}{dt} = y \left(1 - \frac{y}{25} \right), \quad (29)$$

where $r = 1$ and $K = 25$. Three individual sample paths or stochastic realizations are graphed for each of the three stochastic models and compared to the solution of the deterministic model when the initial population size is $y_0 = 3$. Fig. 1 presents the sample paths corresponding

to: (a) the DTMC model (7), (b) the CTMC model (10), and (c) the SDE model (13). The smooth curve in each figure is the solution of (29). The individual sample paths illustrate the differences between the stochastic and deterministic models. In addition, numerical simulation of a large number of sample paths is useful for approximating the probability distribution of the process over time. The sample paths for the Markov chain models are graphed as continuous functions, but they are discontinuous at the points where the process jumps to a new state. The sample paths of the SDE model are continuous functions of time.

The mean and variance of the probability distribution is computed for each of these three stochastic models at time $t = 10$ when $y_0 = 3$ and at time $t = 2$ when $y_0 = 25$. They are presented in Table 1. The mean and variance are computed directly from the discrete-time model by projecting forward in time until $t = 10$ using (7) with $\Delta t = 0.001$, but for the continuous-time models (10) and (13), the mean and variance are computed from 10,000 stochastic sample paths.

From this example, it can be seen that the dynamics of these three stochastic logistic models are in close agreement even for a small initial population size. Graphs of the probability distribution corresponding to

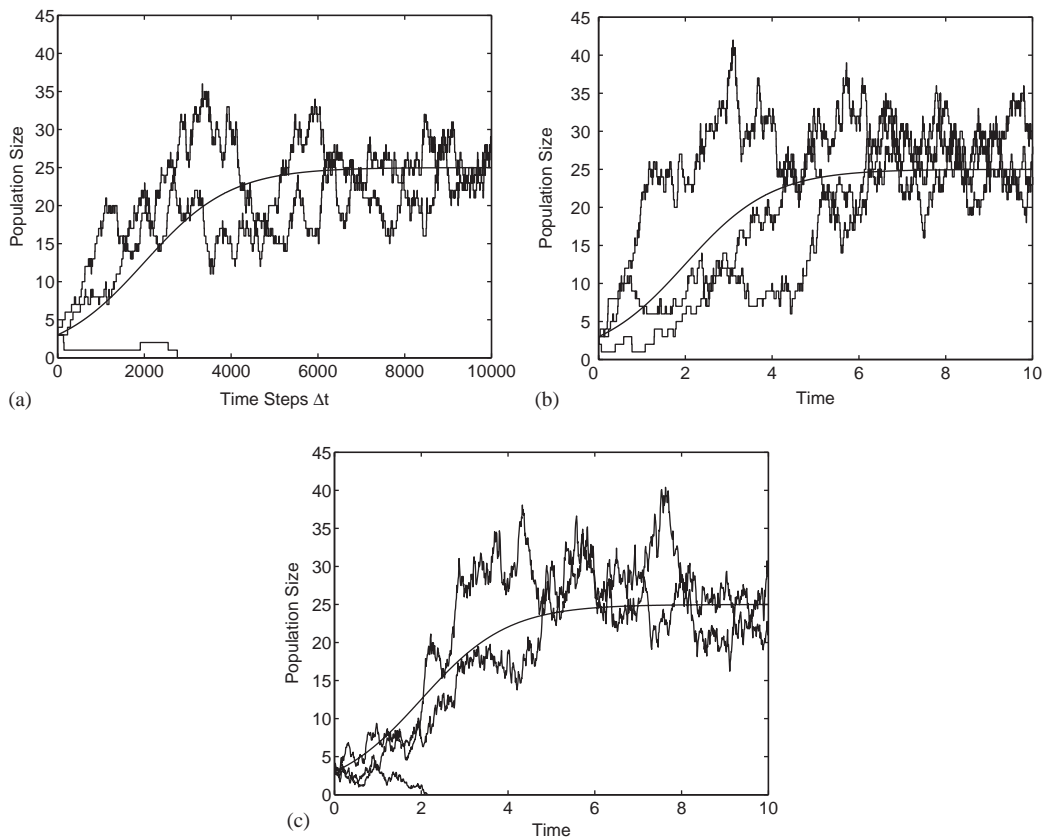


Fig. 1. Three sample paths for each of the stochastic logistic models corresponding to the birth and death rates given in (28), when $y_0 = 3$. In (a), the sample paths correspond to the DTMC model (7). In (b), the sample paths correspond to the CTMC model (10) and in (c), the sample paths correspond to the SDE model (13). The smooth curve in each figure is the deterministic solution.

the DTMC model (7) are straightforward to numerically simulate and can be used to approximate the probability distribution for all of the stochastic models. In Fig. 2, the probability distribution is numerically calculated based on the forward projection (7) for the birth and death rates given in (28) and for two different initial conditions, $y_0 = 3$ and 25, when $\Delta t = 0.001$. Note that when $y_0 = 3$, there is already a significant positive probability of population extinction at $t = 10$, i.e., $p_0(10) \approx 0.17$.

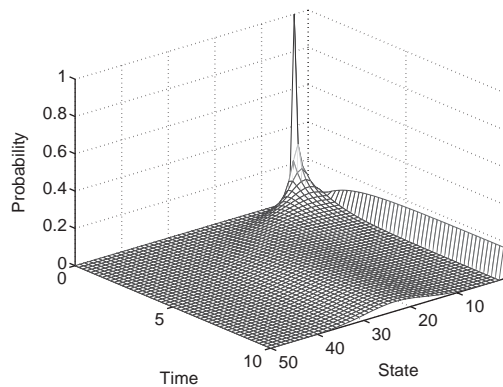
From the equations derived for the moments of the persistence time in (18) and (22) it can be seen that the difference in birth and death rates $[b(y) - d(y)]$ and the sum $[b(y) + d(y)]$ are important to the dynamics of the stochastic models. They represent the infinitesimal mean and infinitesimal variance, respectively, in the SDE model. We now present two examples of different birth and death rates, where the difference $[b(y) - d(y)]$ is the same, but where the sum $[b(y) + d(y)]$ differs. Each example corresponds to the same deterministic logistic model but it is shown that the mean persistence time differs significantly between the two examples. Assume that the deterministic population model satisfies the differential equation,

$$\frac{dy}{dt} = y \left(1 - \frac{y}{10} \right),$$

Table 1

The mean (m) and variance (v) of the probability distribution for the discrete-time Markov chain (DTMC) model, the continuous-time Markov chain (CTMC) model, and the stochastic differential equation (SDE) model for the birth and death rates given in (28)

	DTMC	CTMC	SDE
$y_0 = 3$	$m = 19.187$	$m = 19.232$	$m = 19.098$
$t = 10$	$v = 110.14$	$v = 107.96$	$v = 114.30$
$y_0 = 25$	$m = 23.852$	$m = 23.853$	$m = 23.831$
$t = 2$	$v = 37.55$	$v = 37.72$	$v = 36.921$



where $r = 1$ and $K = 10$. There are two different birth and death rates assumed which are labelled (a) and (b):

$$(a) \quad b(y) = 1.35y - \frac{y^2}{20}, \quad d(y) = 0.35y + \frac{y^2}{20}, \quad N = 27,$$

$$(b) \quad b(y) = 2y - \frac{y^2}{20}, \quad d(y) = y + \frac{y^2}{20}, \quad N = 40.$$

The mean persistence times for examples (a) and (b) are calculated using formulas (18) and (22) for the Markov chain models and the SDE model, respectively. Graphs of the mean persistence time as a function of initial population size for these examples are presented in Fig. 3. The mean persistence time differs by a factor of 10 in these two examples, from a maximum of about 400 in example (a) to about 40 in example (b).

In Fig. 4, the standard deviation for the stochastic models is graphed. The standard deviation is calculated using formulas (18) and (22) for $r = 2$, $\sqrt{\tau_y^2 - (\tau_y)^2}$. Again, there is an order of magnitude difference between the standard deviations in the two examples (a) and (b).

Notice that for example (a), $b(y)/d(y)$ varies from 3.25 to 0.26 as y increases from 1 to 20. However, in example (b), $b(y)/d(y)$ varies from 1.86 to 0.50 as y increases from 1 to 20. The low death rate in example (a) for small values of y accounts for the rapid increase in the persistence time τ_y for low initial population sizes. The SDE model underestimates the persistence time in this situation. However, for the more realistic situation of example (b), the three stochastic models agree very well even for small initial population sizes.

The results using the stochastic logistic models illustrate the diversity of persistence times that can be obtained from simple population models, but where the dynamics of the underlying deterministic model remains unchanged. Such diversity in behavior can be exhibited in many other problems. For example, consider an epidemic model, where the population size is variable and the disease is vertically transmitted (Busenberg and Cooke, 1993). Suppose a deterministic epidemic model

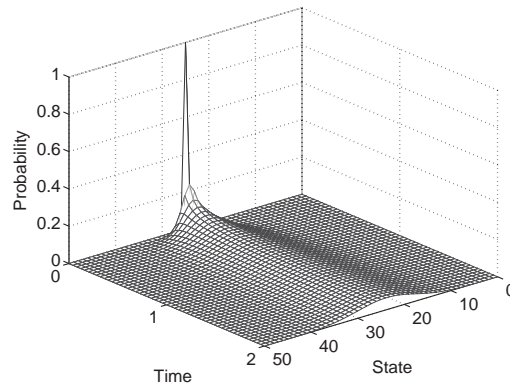


Fig. 2. The distribution of probabilities for the discrete-time Markov chain model for the birth and death rates given in (28) and initial conditions $y_0 = 3$ or $y_0 = 25$.

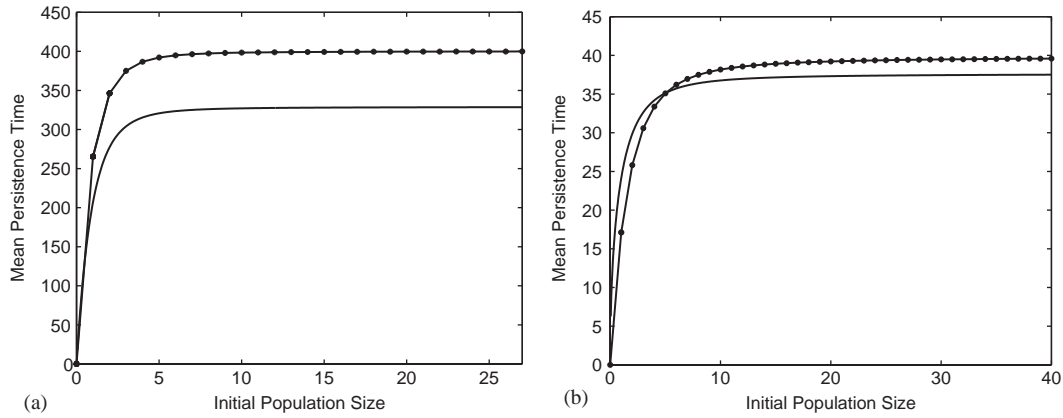


Fig. 3. The mean persistence time for the Markov chain models (curve with dots) and the SDE model for examples (a) and (b).

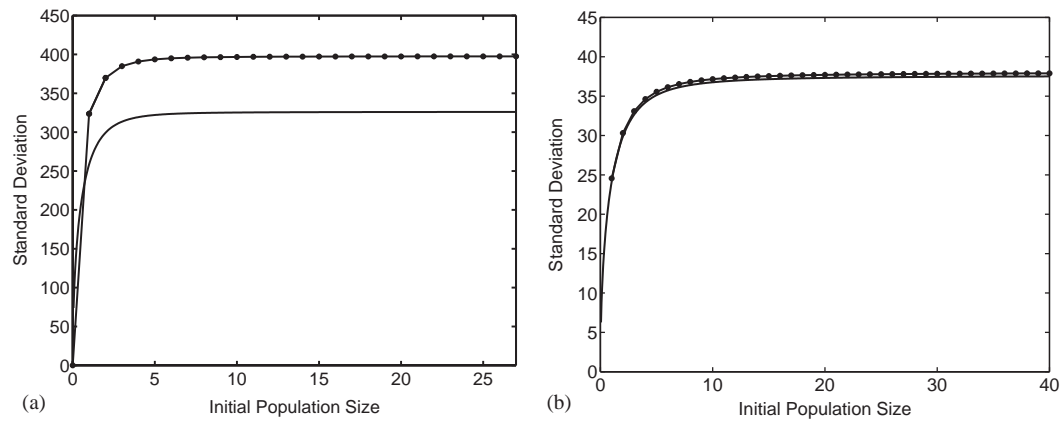


Fig. 4. The standard deviation of the persistence time for the CTMC model (curve with dots) and the SDE model for examples (a) and (b).

satisfies the following differential equation:

$$\frac{dI}{dt} = \beta \frac{I}{N} \left(1 - \frac{I}{N}\right) + I(\tilde{b}(N) - \tilde{d}(N)) \quad \text{and}$$

$$\frac{dN}{dt} = b(N) - d(N),$$

where $I(t)$ is the number of infected individuals at time t , β is the contact rate and $S(t) = N(t) - I(t)$ is the number of susceptible individuals. The total population size is $N(t) = S(t) + I(t)$, the functions $\tilde{b}(N)$ and $\tilde{d}(N)$ are the per capita birth and death rates, respectively, and $b(N) = N\tilde{b}(N)$ and $d(N) = N\tilde{d}(N)$. The term $I\tilde{b}(N)$ implies all individuals are born infected (vertical transmission of the disease to newborns). For this epidemic model, as for the logistic model, a variety of different birth and death rates correspond to the same deterministic model.

5. Discussion

Over 25 years ago, Pielou (1977) listed the flaws inherent in the logistic model; these flaws are inherent in

many other simple deterministic population models. Stochastic models such as Markov chain models and SDE models provide alternatives to deterministic models and alleviate some of the problems with the deterministic formulation. Knowledge of the similarities and differences in these models is useful in selecting the correct formulation or a formulation that is consistent among the different stochastic models; that is, if properly formulated, the results obtained using a SDE model should be similar to those of a Markov chain model.

In the present investigation, results were collected from the biological, mathematical, and engineering literature and compared for three different types of stochastic model formulations common in population biology. CTMC and DTMC models were compared with consistently formulated SDE models, where in the latter case both time and population size are continuous variables. In addition, the persistence time behavior was compared in all three models. It was seen that the equations satisfied by moments of the persistence time are very similar. For example, for the Markov chain models, the mean persistence time τ_y for an initial

population of size y satisfies

$$d(y)\tau_{y-1} - [b(y) + d(y)]\tau_y + b(y)\tau_{y+1} = -1, \quad (30)$$

where $y = 1, 2, \dots, N$ and $\tau_0 = 0$. For the SDE model, τ_y satisfies:

$$[b(y) - d(y)] \frac{d\tau_y}{dy} + \frac{[b(y) + d(y)]}{2} \frac{d^2\tau_y}{dy^2} = -1, \quad (31)$$

where $\tau_0 = 0$ and $\frac{d\tau_y}{dy}|_{y=N} = 0$. If a central difference approximation is applied to (31), then (30) is obtained which verifies the similarity between the three different stochastic models.

Furthermore, it was shown how the same deterministic population model can correspond to a wide range of stochastic models if the birth and death rates are not explicitly known. An important example of this is logistic population growth for which only the difference $b(y) - d(y)$ is known. Indeed, there are an infinite number of stochastic models that reduce to the same deterministic logistic growth model when the stochastic terms are removed. Computational results show that without explicit knowledge of the birth and death rates, it is impossible to accurately estimate the persistence time behavior of a population.

The SDE model follows from a diffusion approximation of a CTMC model when population sizes are large (e.g., Dennis, 2002; Dennis et al., 1991; Goel and Richter-Dyn, 1974; Nisbet and Gurney, 1982; Tier and Hanson, 1981). However, we have seen in examples that even when the population sizes are relatively small, the SDE provides a good approximation. The use of the diffusion approximation must be tested for accuracy before it is used in an application, particularly if the population size is small. At small population sizes, there are additional biological forces (e.g., an Allee effect) which may be significant and need further consideration (Dennis, 2002).

In biological applications, the majority of the stochastic population models are continuous in time, SDE models and CTMC models (e.g., Allen and Victory, 2003; Goel and Richter-Dyn, 1974; Matis and Kiffe, 2000; Nisbet and Gurney, 1982; Pielou, 1977; Renshaw, 1993; and references cited previously). However, some recent population modeling efforts have employed DTMC models (e.g., Caswell, 2001; Cushing et al., 2003; Dennis and Taper, 1994), where the populations have nonoverlapping generations. In these models, the DTMC formulations are more biologically realistic. There are some advantages of the DTMC model over the continuous-time formulations. For example, the DTMC model is often simpler to formulate from first principles and is more readily understood than the continuous-time models.

In determining model behavior, computational ease may be an important consideration. There are some numerical advantages in using DTMC or SDE models

instead of CTMC models. In a DTMC model, by projecting forward in time using the transition matrix, calculation of the probability distribution is straightforward. The probability distribution in the case of the continuous-time stochastic models can be estimated via simulation of a large number of sample paths. However, to attain a good estimation of the probability distribution in the continuous cases may require a very large number of sample paths and many more numerical computations than in the discrete case. When there are several interacting populations, the advantages of a DTMC may disappear. Setting up the transition matrix in a DTMC model can be very complicated when there are several random variables. In this case, it may be computationally simpler to use the SDE approximation. In a SDE model, Euler's method and other more efficient numerical methods can be used to compute sample paths (Kloeden and Platen, 1992; Kloeden et al., 1997; Schurz, 2002). Of course, in any stochastic modeling formulation, a model should be chosen for its biological realism. Then, for ease in computation or analysis, it may be possible to approximate the original model using a different stochastic formulation.

The application of more realistic models (e.g., structured, individual-based, and metapopulation models) and the development of techniques to evaluate them have and will continue to improve model predictability and reliability (Cushing, 1998; DeAngelis and Gross, 1992; Hanski and Gilpin, 1997). It is through the use of both deterministic and stochastic modeling techniques that a more thorough understanding of the underlying processes will be obtained (Renshaw, 1993).

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