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Decoupling Moment Equations for Stochastic Population Models

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Abstract

Stochastic population models incorporating realistic transition probabilities may result in an open coupled system of differential equations for the moments which cannot be solved successively and must be decoupled in order to obtain estimates for the moments. Three existing general techniques are reviewed each of which reduces the coupled system to a set of nonlinear equations which may be solved using a numerical integration method. For the case where only estimates of the first 2 moments are required 2 existing techniques are presented and a new technique is developed and in each case the use of a numerical integration method is avoided. All of the techniques are compared for a stochastic model of a chemical process and the new technique performs favorably. A second example related to the logistic model of growth reveals a problem with one of the existing techniques and provides an insight into problems with stochastic models which have mean logistic behavior.

Keywords: coupled moment equations, logistic growth, stochastic population models.

1. Introduction

Early studies in the mathematics of population growth were mainly concerned with deterministic models represented by differential or difference equations where the population size is determined by solving a functional equation given some initial conditions. There are at least two objections to this approach: these models assume that

the population size is a real-valued continuous function of time; and they predict that at time t the population size will always be the same if the initial conditions are not altered, which ignores the large number of random or chance factors that may influence the population growth. Attempts to overcome these objections led to the development of stochastic models and the early work was done by Yule [1] and McKendrick [2]. Feller [3,4] was the first to treat systematically stochastic models of population growth within the framework of the theory of stochastic processes and significant contributions were made by Kendall [5,6]; Bartlett [7,8]; and Pollard [9,10].

May [11] refers to stochastic features arising from the fact that the population size is fundamentally discrete as demographic stochasticity and these features are incorporated into the model by considering the probabilities that an individual will give birth or die in the next time interval Δt. By considering the resulting birth and death process it is possible to either make a probability statement about the population size at time t or at least determine the mean population size and the variance at that time. In a different approach Levins [12] studied the effects of introducing stochasticity into model parameters in an attempt to incorporate stochastic elements related to a fluctuating environment. In this approach the analysis of the probability distribution of population size is often done using the Fokker-Planck (Kolmogroff) diffusion equation where it is assumed that variability in the environmental parameter is white noise [11]. A clear discussion of the use of diffusion models is given by Feller [4] and Bailey [13].

In this article the concern is not with the analysis of random fluctuations in environmental parameters which leads to the use of diffusion approximations. Instead, the concern is with demographic stochasticity involving a system of differential equations describing the transition probabilities associated with changes in the value of the random variable $N(t)$ which represents the population size at time t. From this system of equations it is possible to derive a system of differential equations for the moments of the process. However, in general this system for the moments is an open coupled system of equations where the equation for the j-th moment (M_j) involves higher order moments. The system cannot be solved successively and it must be decoupled in order to obtain estimates for the moments. This is referred to as the moment closure[1] problem and it arises in a wide range of stochastic modeling situations [14,15]. In population modeling the problem has been addressed mainly by expressing higher order moments in terms of

[1] A search of the ScienceDirect online database identified 570 articles up to year 2007 across diverse fields of study which refer to the problem of moment closure.

lower order moments based on, and assessed against, the results of simulations incorporating specific features of the type of population growth being modeled [16-22].

Following the mathematical representation of the problem this article describes 3 existing techniques for decoupling the system of moment equations to obtain estimates for the first *l* moments. For these techniques the (*l* + 1)-th moment is expressed in terms of lower order moments and the system reduces to a set of *l* nonlinear differential equations which is then solved by a numerical integration method. Next the article considers the common situation where estimates are required for only the first 2 moments. In this case 2 existing techniques are described and a new technique is developed. These techniques result in a pair of differential equations which may be solved without the need to use a numerical integration method. All of the techniques are compared for an example where the exact solutions for the first 2 moments are known. A second example of logistic population growth reveals a problem with one of the existing techniques and highlights concerns with stochastic models which have mean logistic behavior.

2. Mathematical Representation of the Problem

If the random variable $N(t)$ represents the population level at time t and $P_k(t)$ is the probability that $N(t) = k$, given $N(0) = N_0$, then, using standard techniques for birth and death processes ([23]), the system of differential equations describing the transition probabilities is,

$$\frac{dP_k}{dt} = U_{k-1}P_{k-1} + D_{k+1}P_{k+1} - (U_k + D_k)P_k$$
$$\frac{dP_0}{dt} = D_1P_1 \qquad (1)$$

where: U_k and D_k are the infinitesimal birth and death rates, respectively; $U_k\Delta t + o(\Delta t)$ is the probability that in a population of size k there will be a single birth in the next time interval Δt; $D_k\Delta t + o(\Delta t)$ is the probability of a single death in the same time interval; and $o(y)$ is any function such that $o(y)/y$ approaches 0 as y approaches 0.

From (1), the j-th moment for the process $M_j(t) = E[N^j(t)]$ and satisfies the system of differential equations,

$$\frac{dM_j}{dt} = \sum_k k^j \frac{dP_k}{dt} = \sum_k [((k+1)^j - k^j)U_k - (k^j - (k-1)^j)D_k]P_k \text{ , for j = 1, 2, 3, ...} \qquad (2)$$

and if $U_k = \sum_{i=0}^{n} \alpha_i k^i$ and $D_k = \sum_{i=0}^{n} \beta_i k^i$ then the differential equation for M_j has the form $\frac{dM_j}{dt} = F(M_1, M_2, M_3, ..., M_{n+j-1})$. This equation will not involve moments of order higher than M_j if $\alpha_2 = \beta_2$ and $\alpha_i = \beta_i = 0$, for $3 \le i \le n$. Otherwise, (2) is an open coupled system of differential equations which cannot be solved successively.

In many population models it is assumed that $U_k = k(\alpha_1 + \alpha_2 k)$ and $D_k = k(\beta_1 + \beta_2 k)$ ([23]). This reflects the realistic assumption that at time t the probability of a single individual in the population producing a single birth in the next time interval Δt is dependent on the population size k at that time and is $(\alpha_1 + \alpha_2 k)\Delta t + o(\Delta t)$. Similarly, the probability of a single individual dying in the next time interval Δt is $(\beta_1 + \beta_2 k)\Delta t + o(\Delta t)$ and births and deaths of individuals are independent. Using these assumptions the differential equation for M_j, has the form,

$$\frac{dM_j}{dt} = G(M_1, M_2, M_3, ..., M_{j+1}) \qquad (3)$$

and although the coupling in (2) is now simplified it is still an open coupled system which cannot be solved successively and this is the form of coupling that is considered throughout this article.

3. Decoupling Techniques

This section first reviews 3 existing techniques for obtaining estimates for the first *l* moments. Next 2 existing techniques for obtaining estimates for only the first 2 moments are presented and for this situation a new technique is proposed.

3.1 Estimating the First *l* Moments

Goel and Richter-Dyn [24] suggest expressing all of the moments higher than the *l*-th moment, which appear in the first *l* equations in (2), in terms of the first *l* moments using $M_l = M_l M_{j-l}$, for $j > l$. For example, using this technique M_3 is replaced by $M_1 M_2$.

Wang [25] assumes that $M_j \equiv \xi_j^j$ is a smooth function of j and uses this to express ξ_j, for $j > l$, in terms of $\xi_1, \xi_2, \xi_3, \ldots, \xi_l$ by polynomial extrapolation where in general, $\xi_j = \sum_{i=1}^{l} (-1)^{l-i\ j-i-1} C_{l-1}{}^{j-1} C_{i-1} \xi_i$, for $j > l$. Using this technique M_3 is replaced by $(2\sqrt{(M_2)} - M_1)^3$.

Bailey [13] suggests setting the (I + 1)-th cumulant of the process to zero. If the third cumulant is set to zero then M_3 is replaced by $3M_1M_2 - 2M_1^3$ and this is equivalent to assuming that the coefficient of skewness is zero.

Each of these techniques reduces (2) to a set of I nonlinear differential equations which may be solved by numerical integration methods. For these techniques truncation of the system (2) at a higher order results in an improvement in the estimates for the moments but this is achieved at the expense of more difficult computation.

3.2 Estimating only the First 2 Moments

If estimates for only M_1 and M_2 are required and the open coupling is of the form represented by (3) then the open coupled system in (2) reduces to,

$$\begin{aligned}\frac{dM_1}{dt} &= c_0 + c_1M_1 + c_2M_2 \\ \frac{dM_2}{dt} &= d_0 + (2c_0 + d_1)M_1 + (2c_1 + d_2)M_2 + 2c_2M_3\end{aligned} \tag{4}$$

where, $c_i = \alpha_i - \beta_i$, $d_i = \alpha_i + \beta_i$, for i = 0, 1, 2.

Two existing techniques due to McQuarrie [26] are presented first. The presentation is more general than that given by McQuarrie who proposed these techniques in discussing a particular stochastic model of an irreversible bimolecular chemical reaction (see § 4.1). This is followed by the presentation of a new technique. In each case these techniques avoid the solution of a pair of nonlinear differential equations using numerical integration which would be required if any of the 3 general techniques described in §3.1 were used.

3.2.1 Two Existing Techniques (McQuarrie [26])

Technique 1: In (4) replace M_2 by M_1^2 in the first equation and solve for M_1. Then, using the solution for M_1, replace M_3 by M_2M_1 in the second equation which will then have the form $\frac{dM_2}{dt} + P(t)M_2 = Q(t)$ and may be solved using the integrating factor $\exp[\int P(t)dt]$. As an illustration, the solution for M_1 has been included in Appendix §A.1.

Assuming $M_2 = M_1^2$ is equivalent to assuming the variance of the stochastic process is zero. This means that the solution for M_1 is the same as that obtained from the deterministic model of the process and this appears to be a reasonable assumption. The second assumption that $M_3 = M_2M_1$ is a particular case of the more general approach described above due to Goel and Richter-Dyn [24].

Technique 2: In (4) replace M_2 by $M_1^2\exp(pt)$, where p = $\dfrac{d_0 + d_1 N_0 + d_2 N_0^2}{N_0^2}$,

and solve for M_1. This results in a Riccati differential equation for M_1 and in general a solution in closed form may not be possible ([27]) and a series solution for M_1 is given in Appendix §A.2. Finally, M_2 is estimated by $M_1^2\exp(pt)$ and effectively no use appears to be made of the second equation in (4).

However, although not presented by McQuarrie [26], the rationale for using $M_2 = M_1^2\exp(pt)$ does involve consideration of the second equation in (4) as follows:
Let $M_2 = f(t)M_1^2$. Differentiating with respect to t and using the first equation in (4) gives, $\dfrac{dM_2}{dt} = \dfrac{df}{dt}M_1^2 + 2f(t)M_1[c_0 + c_1M_1 + c_2M_2]$. If, at t = 0, this equation is identical to the second equation in (4) then $f(0) = 1$ and $\dfrac{df}{dt}\Big|_{t=0} = \dfrac{d_0 + d_1N_0 + d_2N_0^2}{N_0^2}$. Consequently, $f(t) = \exp(pt)$ is suggested.

3.2.2 A New Technique

The rationale for this new technique was motivated by the good performance of McQuarrie's first technique in estimating M_1 and Bailey's technique for estimating M_2 when estimates for these moments were produced for the process considered in §4.1. The technique assumes that the mean for the stochastic process is approximated by the corresponding deterministic model of the process and, as for McQuarrie's first technique, M_2 is replaced by M_1^2 in the first equation in (4) and a solution is obtained for M_1. This solution is then used in the second equation in (4) together with the assumption used by Bailey that $M_3 = 3M_1M_2 - 2M_1^3$, which means that the coefficient of skewness is zero. Then the second equation in (4) has the form $\dfrac{dM_2}{dt} + R(t)M_2 = S(t)$ where, R(t) = $-(2c_1 + d_2 + 6c_2M_1)$ and S(t) = $d_0 + (2c_0 + d_1)M_1 - 4c_2M_1^3$ and this equation may be solved using the integrating factor $\exp[\int R(t)dt]$.

4. Examples

The first example is taken from McQuarrie [26] and concerns an irreversible bimolecular chemical reaction. McQuarrie provides the exact solutions for the first 2 moments and these are used for comparing the estimates for M_1 and M_2 obtained using:
(i) each of the 3 general techniques due to Goel and Richter-Dyn [24], Wang [25], and Bailey [13] where in each case a fourth order Runge-Kutta method was used to solve the truncated system of 2 nonlinear differential equations.
(ii) the 2 techniques proposed by McQuarrie and the new technique all of which avoid the need to use a numerical integration method.

The second example concerns logistic population growth and reveals a problem with the use of McQuarrie's second technique. Also, the example provides important insights into to problems associated with stochastic models which have mean logistic behavior.

4.1 An Irreversible Bimolecular Chemical Reaction

The differential equations for the moments of the stochastic process are:

$$\frac{dM_1}{dt} = rM_1 - rM_2 \ , \qquad \frac{dM_2}{dt} = -2rM_1 + 4rM_2 - 2rM_3 \tag{5}$$

which is a particular case of (4) and corresponds to infinitesimal birth and death rates U_k = k(-r/2 + rk/2) and D_k = k(-3r/2 + 3rk/2), respectively, where r > 0.

Table 1 shows the estimates for M_1 and M_2 as well as the exact solutions for these moments using each of the general techniques described in §3.1 in conjunction with a fourth order Runge-Kutta numerical integration method. For each estimate the one closest to the exact value is highlighted.

From Table 1 it appears that each of these general techniques provides reasonable estimates for the first 2 moments. However, Wang's and Bailey's techniques both provide closer estimates than those obtained using the technique due to Goel and Richter-Dyn. Bailey's technique appears to be better than either of the others for estimates of both of the moments.

Table 1: A comparison of exact solutions and estimates of M_1 and M_2 using 3 general techniques.

N_0 r	t	Exact Solutions		Goel and Richter-Dyn		Wang		Bailey	
		M_1	M_2	M_1	M_2	M_1	M_2	M_1	M_2
10 0.025	1	8.15	68.97	8.14	70.08	**8.15**	68.85	**8.15**	**68.87**
	2	6.86	50.19	6.80	52.99	**6.87**	**50.15**	**6.87**	50.27
	3	5.93	38.33	5.77	42.50	**5.93**	38.08	**5.93**	**38.27**
	4	5.21	30.14	4.93	35.71	5.23	**30.10**	**5.22**	30.23
	6	4.21	20.31	3.57	28.22	4.23	20.20	**4.21**	**20.35**
50 0.005	1	40.15	1625.37	**40.15**	1631.88	**40.15**	**1625.37**	**40.15**	1624.79
	2	33.50	1138.14	**33.45**	1152.39	**33.55**	**1141.01**	**33.55**	1141.28
	3	28.80	845.01	28.65	864.24	**28.80**	844.78	**28.80**	**845.01**
	4	25.20	649.71	24.95	673.78	**25.20**	649.52	**25.20**	**649.71**
	6	20.20	420.68	19.70	451.12	**20.20**	420.25	**20.20**	**420.68**
100 0.0025	1	80.10	6438.34	**80.10**	6456.05	**80.10**	**6441.48**	**80.10**	**6441.48**
	2	66.90	4501.70	66.80	4528.66	**66.90**	**4506.44**	**66.90**	4507.19
	3	57.40	3325.76	57.20	3357.71	**57.30**	**3314.18**	**57.30**	**3314.18**
	4	50.20	2549.98	50.00	2601.00	**50.20**	2548.89	**50.20**	**2549.43**
	6	40.20	1641.29	39.70	1698.77	**40.20**	1640.89	**40.20**	**1641.29**

Note: Goel and Richter-Dyn [24] use $M_3 = M_1M_2$; Wang [25] uses $M_3 = (2\sqrt{M_2} - M_1)^3$; Bailey [13] uses $M_3 = 3M_1M_2 - 2M_1^3$.

Table 2 compares the estimates obtained for the first 2 moments using McQuarrie's 2 techniques and the new technique. For these 3 techniques the solutions for M_1 and M_2 are provided in Appendix §A.3. Again, the estimates closest to the exact solutions are highlighted.

From Table 2 it appears that each of these 3 techniques provides reasonable estimates for the first 2 moments. For the first moment McQuarrie's second technique appears to be only slightly better than the other 2 techniques which produce the same estimates. However, the new technique appears to be much better than either of McQuarrie's techniques for estimating the second moment.

Table 2: A comparison of exact solutions and estimates of M_1 and M_2 using McQuarrie's techniques and the new technique.

N_0 r	t	Exact Solutions		McQuarrie's Technique 1		McQuarrie's Technique 2		New Technique	
		M_1	M_2	M_1	M_2	M_1	M_2	M_1	M_2
10 0.025	1	8.15	68.97	**8.18**	69.95	8.02	67.27	**8.18**	**68.94**
	2	6.86	50.19	6.95	52.77	**6.84**	51.17	6.95	**50.54**
	3	5.93	38.33	6.06	41.89	**5.92**	40.03	6.06	**38.84**
	4	5.21	30.14	5.39	34.55	**5.13**	31.50	5.39	**30.99**
	6	4.21	20.31	4.44	25.50	**4.11**	21.96	4.44	**21.31**
50 0.005	1	40.15	1625.37	**40.15**	**1627.82**	40.05	1620.36	**40.15**	1622.86
	2	33.50	1138.14	33.60	1151.40	**33.50**	1144.56	33.60	**1140.48**
	3	28.80	845.01	**28.85**	856.95	**28.75**	851.02	**28.85**	**842.95**
	4	25.20	649.71	25.40	670.71	**25.10**	655.21	25.40	**654.92**
	6	20.20	420.68	20.40	440.94	**20.05**	426.33	20.40	**424.09**
100 0.0025	1	80.10	6438.34	**80.10**	**6447.45**	**80.10**	**6447.45**	**80.10**	6452.10
	2	66.90	4501.70	**67.00**	4533.89	**66.80**	**4506.86**	**67.00**	4517.02
	3	57.40	3325.76	**57.40**	3343.80	57.30	**3332.16**	**57.40**	3316.38
	4	50.20	2549.98	**50.30**	2580.39	**50.10**	2559.91	**50.30**	**2549.24**
	6	40.20	1641.29	**40.20**	1664.41	40.10	1656.14	**40.20**	**1631.88**

Note: McQuarrie's technique 1 uses $M_2 = M_1^2$, $M_3 = M_1M_2$; McQuarrie's technique 2 uses $M_2 = M_1^2\exp(pt)$; The new technique uses $M_2 = M_1^2$, $M_3 = 3M_1M_2 - 2M_1^3$.

Comparing the estimates in Tables 1 and 2 it appears that Wang's and Bailey's general techniques are providing better estimates for both of the moments than any of the other techniques and Bailey's technique appears to be better than Wang's. However, the techniques in Table 1 required the use of a numerical integration method and considering the much less amount of computation required by the techniques in Table 2 there is encouraging evidence to support the use of the new technique. Of course, this claim requires further evidence based on other stochastic processes.

4.2 Logistic Population Growth

Consider a stochastic population process where: at low population level b and m are the mean birth and death rates per individual, respectively; $r = b - m > 0$; and K (the saturation level) $> N_0 \geq 1$. For this process it is required that the population level should approach K asymptotically and that the infinitesimal birth and death rates (U_k, D_k) should depend on the current population level k and decrease and increase, respectively, to the same limiting value as k approaches K. These conditions are satisfied if,

$U_k = k(b - \frac{r\gamma_1 k}{K}), D_k = k(m + \frac{r\gamma_2 k}{K})$, where $\gamma_1 + \gamma_2 = 1$, and $0 \le \gamma_1 \le 1$. (6)

Thus from (4) the moment equations for M_1 and M_2 are,

$$\frac{dM_1}{dt} = rM_1 - \left(\frac{r}{K}\right)M_2, \ \frac{dM_2}{dt} = d_1 M_1 + (2r + d_2)M_2 - \left(\frac{2r}{K}\right)M_3, where \ d_1 = b + m,$$

$$d_2 = \frac{r}{K}(1 - 2\gamma_1).$$

Decoupling these moment equations using McQuarrie's first technique and the new technique the estimate for the first moment is given by $M_1 = \frac{K}{1 + \left(\frac{K - N_0}{N_0}\right)\exp(-rt)}$,

which is recognized as the familiar logistic equation. Since it was obtained by using $M_2 = M_1^2$ (i.e. the variance is zero) it is concluded that the stochastic population models defined in (6) have mean behavior that is approximated by the deterministic logistic relationship $\frac{dN}{dt} = r\left(1 - \frac{N}{K}\right)N$ and may be regarded as analogues of the deterministic logistic relationship ([28]). The estimates for M_2 using McQuarrie's first technique and the new technique are presented in Appendix §A.4.

If McQuarrie's second technique using $M_2 = M_1^2\exp(pt)$ is applied to the moment equations then the estimate for the first moment is given by,

$M_1 = \frac{N_0 K(r + p)}{(K(r + p) - rN_0)\exp(-rt) + rN_0 \exp(pt)}$, where $p = d_1 + d_2 N_0 > 0$. As t increases M_1 increases to a maximum value of $K\left(\frac{pN_0}{K(r + p) - rN_0}\right)^{\frac{p}{r+p}}$ at

$$t = \frac{1}{(r + p)}\ln\left(\frac{K(r + p) - rN_0}{pN_0}\right)$$

and then it decreases asymptotically to zero. In view of the assumptions about the transition probabilities in (6) the estimate for M_1, using this technique, seems quite unrealistic and this indicates that care will be need to taken in using McQuarrie's second technique as a basis for decoupling moment equations of the type in (4). On the other hand, both the new technique and McQuarrie's first technique provide plausible estimates.

This example also provides an important insight into the question as to whether or not it is possible to develop stochastic population models which have mean behavior that corresponds exactly to the deterministic logistic relationship. The stochastic models defined by (6) only approximate this behavior since for these models, $\frac{dM_1}{dt} = r\left(1 - \frac{M_2}{KM_1}\right)M_1 \prec r\left(1 - \frac{M_1}{K}\right)M_1$. If the infinitesimal birth and death rates in (6) are changed to, $U_k = k(b - \frac{r\gamma_1 M_1}{K}), D_k = k(m + \frac{r\gamma_2 M_1}{K})$, where $\gamma_1 + \gamma_2 = 1$, and $0 \le \gamma_1 \le 1$ then $\frac{dM_1}{dt} = r\left(1 - \frac{M_1}{K}\right)M_1$ which is the desired logistic differential equation. These are not the only choices for U_k and D_k that result in M_1 having logistic behavior but in all such cases the probability of a single individual producing a single birth, or dying, in the next time interval Δt will depend on the mean population size M_1 and not on the actual population size k. Superficially these appear to be reasonable models since they require that the individual birth rate is initially greater than the death rate and that the birth rate decreases while the death rate increases with time to the same limiting value. At that stage the process becomes a symmetric random walk.

However, there is a serious defect in these models which makes their use for simulation suspect. The models assume that the density dependent effect is based on the mean population size rather than the actual population size. Unfortunately, any attempt to take account of the actual population size in determining the transition probabilities results in the introduction of higher moments in the differential equation for M_1 and the loss of the logistic relationship. This means that one cannot simulate these processes on a computer relying only on information contained in the simulated population level; one must also evaluate independently the expression for the mean value.

Consider the following experiment to illustrate this. We place 100 people in a closed environment with food. After 20 years we single out a person and try to guess the probability of this person dying during the next small time interval. We are able to observe the number of people at this time. The most demographically plausible assumption would be that this probability should be proportional to the actual number of people. Thus, if there were 1,000 people present there would be a higher probability of any individual dying than if there were only 3 people. Unfortunately, insisting that the mean behavior must be logistic casts out this plausible assumption and denies that the

actual number of people is significant. In its place it assumes that the mean number in the population determines the probability. In other words, the logistic behavior tells us that instead of counting the number of people present, we must ignore this information and look at a clock to see how long it is since the beginning of our experiment, this time then allows us to compute the mean number of people from the logistic equation and only on this basis are we to calculate our probability. So whether we have 3 or 1,000 people present, logistic behavior tells us that the probability of one of these dying is exactly the same and the same implication applies for births.

The conclusion is that the logistic equation requires individual behavior that is not demographically acceptable.

5. Conclusions

This article examined techniques which may be applied to the open coupled system of differential equations for the moments of stochastic population models where the equation for the j-th moment involves higher order moments and the system of moment equations cannot be solved successively and must be decoupled in order to obtain estimates for the moments. Three general techniques which reduce the system to a set of nonlinear differential equations which may then be solved by a numerical integration method are considered. Two existing techniques and a new technique are described for the situation where only estimates for the first 2 moments are required and in each case the need for a numerical integration method is avoided.

Using all of these techniques estimates of the first 2 moments are found and compared to the exact solutions for a stochastic model of a bimolecular chemical process. In comparison to the other techniques the new technique is shown to perform favorably, especially considering that a numerical integration method is not needed, but these encouraging results need to be confirmed for other stochastic models.

A second example concerning stochastic models which approximate the popular deterministic logistic growth model reveals a problem with one of the existing techniques (McQuarrie's second technique) for estimating the first moment and indicates that caution should be used in applying this technique for such models. For this example the new technique provided plausible estimates for the first 2 moments.

In the second example it is shown that it is possible to construct stochastic models with mean logistic behavior. However, in all such models it is necessary to have the birth and death rates for individuals in the population dependent on the mean size of the population. This requirement is demographically unacceptable and poses problems for

simulating the process. On the other hand, if these rates are dependent on the actual population size, which is more realistic, then the mean size of the population does not satisfy the logistic equation and its differential equation is the first in an open coupled system. Thus the plausibility of a stochastic model having mean logistic behavior disappears when realistic assumptions are used for the birth and death rates of individuals in the population. These results indicate that although the logistic model is appealing its appeal is based more on its simplicity than its realism.

Appendix

A1. McQuarrie's Technique 1: Solution for M_1 in Equation (4)

M_1 is given by:

$$\frac{(a+c_1)(2c_2N_0 - a + c_1)\exp(at/c_2) + (a-c_1)(2c_2N_0 + a + c_1)}{2c_2[2c_2N_0 + a + c_1 - (2c_2N_0 - a + c_1)\exp(at/c_2)]}, \quad a \succ 0,$$

and

$$\frac{2c_2N_0 + (N_0c_1 + 2c_0)t}{2c_2 - (2N_0c_2 + c_1)t}, \quad a = 0,$$

where $a = \sqrt{(c_1^2 - 4c_0c_2)}.$

A2. McQuarrie's Technique 2: Series Solution for M_1 in Equation (4)

$$M_1 = \frac{N_o c_2 - \sum_{n=2}^{\infty} n u_n t^{n-1}}{c_2[1 - c_2N_0t + \sum_{n=0}^{\infty} u_n t^n]\exp(pt)}$$, where $n(n-1)u_n - (c+p)(n-1)u_{n-1} + c_0c_2 \sum_{m=0}^{n-2} \frac{u_m p^{n-2-m}}{(n-2-m)!} = 0$, for $n \geq 2$, and $u_0 = 1$, $u_1 = -c_2N_0$.

A3. Solutions for Equation (5) using McQuarrie's Techniques 1, 2 and the New Technique

McQuarrie's Technique 1:

$$M_1 = \frac{N_0}{N_0 + (1 - N_0)\exp(-rt)}, \quad M_2 = M_1^2[\frac{2(N_0 - 1)}{3N_0}(\exp(2rt) - \exp(-rt)) + 1].$$

McQuarrie's Technique 2:

$$M_1 = \frac{N_0(p+r)}{N_0 r\exp(pt) - (rN_0 - p - r)\exp(-rt)}\ , M_2 = M_1^2\exp(pt)\ ,$$

where $p = \frac{2r(N_0 - 1)}{N_0}$.

New Technique:

M_1 is the same as for McQuarrie's technique 1,

$$M_2 = \frac{\sum_{n=1}^{6} Q_n \exp(nrt)}{(A+\exp(rt))^6},\quad where\ \ A = \frac{1-N_0}{N_0}, Q_1 = \frac{2A^5}{3}, Q_2 = 5A^4, Q_3 = 16A^3,$$

$$Q_4 = \frac{1}{N_0^4} - 1 - 2A - 16A^3 - 5A^4 - \frac{2A^5}{3} - 8A^2 rt, Q_5 = 2A, Q_6 = 1.$$

A4. Estimates for M_2 for the Logistic Model Defined in (6) using McQuarrie's Technique 1 and the New Technique

McQuarrie's Technique 1:
M_2 is given by:

$$\frac{M_1^2}{K^2}\left[(K^2 + \frac{d_1 K}{d_2} + \frac{K(K-N_0)d_1}{N_0(r+d_2)})\exp(d_2 t) - (\frac{d_1 K}{d_2} + \frac{K(K-N_0)d_1\exp(-rt)}{N_0(r+d_2)})\right],\quad for\ \ d_2 \neq 0$$

and

$$M_1^2\left[1 + \frac{d_1 t}{K} + \frac{d_1(K-N_0)}{N_0 Kr}(1-\exp(-rt))\right],\quad for\ \ d_2 = 0\ .$$

New Technique:
M_2 is given by:

$$\frac{M_1^2}{K(\exp(rt)+A)^4}\left[\sum_{n=-1}^{4} Q_n \exp(nrt) + (K^5 N_0^{-4} - \sum_{n=-1}^{4} Q_n)\exp(d_2 t)\right], \quad for \ d_2 \neq 0$$

and

$$\frac{M_1^2}{K(\exp(rt)+A)^4}\left[\sum_{n=-1}^{4} R_n \exp(nrt) + K^5 N_0^{-4} - \sum_{n=1}^{4} R_n - \frac{A^5 d_1}{r}\right], \quad for \ d_2 = 0,$$

where , $A = \frac{K - N_0}{N_0}, Q_{-1} = \frac{-A^5 d_1}{r + d_2}, Q_0 = \frac{-5A^4 d_1}{d_2}, Q_1 = \frac{2A^3(5d_1 + 2rK)}{r - d_2}, Q_2 = \frac{2A^2(5d_1 + 6rK)}{2r - d_2},$

$Q_3 = \frac{A(5d_1 + 12rK)}{3r - d_2}, Q_4 = \frac{d_1 + 4rK}{4r - d_2}, R_n = Q_n$ *with* $d_2 = 0$ *for* $n = -1,\ 1,\ 2,\ 3,\ 4,$ *and* $R_0 = 5A^4 d_1 t.$

It is noted that the estimate for M_2 using the new technique is smaller than the estimate obtained using McQuarrie's technique 1.

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