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Moment closure and the stochastic logistic model

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Abstract

The quasi-stationary distribution of the stochastic logistic model is studied in the parameter region where its body is approximately normal. Improved asymptotic approximations of its first three cumulants are derived. It is shown that the same results can be derived with the aid of the moment closure method. This indicates that the moment closure method leads to expressions for the cumulants that are asymptotic approximations of the cumulants of the quasi-stationary distribution.

MSC: 60J27; 92D40

Keywords: Quasi-stationary distribution; Asymptotic approximation; Demographic stochasticity; Moment closure

1. Introduction

The stochastic logistic model takes the form of a birth-death process with finite state space, and with an absorbing state at the origin. The stationary distribution of this process is degenerate, with probability one at the origin, corresponding to extinction of the population studied. To study the long-term behaviour of a non-extinct population we use instead the so-called quasi-stationary distribution, which is a stationary distribution, conditional on non-extinction.

The mathematical analysis of this model is concerned with two entities, namely the time to extinction and the quasi-stationary distribution. A detailed analysis is given by Nåsell (2001a,b). One of the features of the model is that it contains a phase transition phenomenon. It is described in terms of three parameter regions in which both the quasi-stationary distribution and the time to extinction behave in qualitatively distinct ways. Thus, the time to extinction is long, and the quasi-stationary distribution is approximately normal, in one of the regions. This is the region that normally is studied with the deterministic logistic model, and also the region that we are concerned with in this paper. The time to extinction is short, and the quasi-stationary distribution is approximately geometric, in a second region. A third region is a transition region between these two. In this region, the time to extinction is moderately long, and the quasi-stationary distribution is more complicated than in the other two. The results in Nåsell (2001a) give explicit approximate expressions for both the quasi-stationary distribution and for the time to extinction in each of these three parameter regions. In the present paper we shall be concerned with the first three cumulants of the quasi-stationary distribution in one of the parameter regions, namely the one where the time to extinction is long, and where the quasi-stationary distribution is approximately normal. We shall, however, derive three terms (of different order in the maximum population size) in an approximation of the mean, two terms in an approximation of the variance, and one term in an approximation of the third cumulant. This represents an extension of earlier results, where only one term was derived for each of the first two cumulants.

The stochastic logistic model is of basic importance in mathematical population biology. It is useful for models in both ecology and epidemiology. Its transition rates depend nonlinearly on the population size. These nonlinearities lead to mathematical difficulties in the analysis of the stochastic model. Thus, the cumulants of the quasi-stationary distribution cannot be determined explicitly. Progress therefore rests on finding useful approximations. In this paper we shall use both

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the moment closure method first described in the classical paper by Whittle (1957) and the alternative method introduced by Nåsell (2001a), where asymptotic approximations play an important role. The latter method gives mathematically more satisfying results, but it requires considerably more work than the moment closure method. The two methods give essentially the same results. We can therefore conclude that the moment closure method leads to asymptotic approximations of the first several cumulants of the quasi-stationary distribution.

2. Model formulation

The stochastic logistic model that we are concerned with is a finite-state birth–death process. The model formulation requires us to define the birth rate λ_n and the death rate μ_n as functions of the population size n. We use the same notation as in Nåsell (2001a). Thus, we start out by introducing N to denote the maximum possible population size. This means that the state space is equal to $\{0, 1, 2, \ldots, N\}$. On the state space we allow the birth rate per individual λ_n/n to be a linearly decreasing function of n and the death rate per individual μ_n/n to be a linearly increasing function of n. Thus, we make the following specifications:

$$\lambda_n = \begin{cases} \mu R_0\left(1 - \alpha_1 \dfrac{n}{N}\right)n, & n = 0, 1, \ldots, N-1, \\ 0, & n = N, \end{cases}$$

and

$$\mu_n = \mu\left(1 + \alpha_2 \frac{n}{N}\right)n, \quad n = 0, 1, \ldots, N.$$

The parameters α_1 and α_2 are assumed to satisfy the inequalities $0 \leqslant \alpha_1 \leqslant 1$ and $\alpha_2 \geqslant 0$. In order to assure density dependence we assume that at least one of them is strictly positive.

The parameter R_0 serves to identify the three parameter regions discussed in the introduction. In the present study it is confined to values strictly larger than one. This is the region where the quasi-stationary distribution is approximately normal.

Our specification of the transition rates differs somewhat from the formulations used by most other authors, including Bartlett et al. (1960), Keeling (2000), Matis and Kiffe (1996, 1998), Renshaw (1991, 1998). These papers express λ_n and μ_n as some variation of $\lambda_n = a_1 n - b_1 n^2$ and $\mu_n = a_2 n + b_2 n^2$. The differences may appear minor, but they are indeed essential for the kind of results we present here. Our formulation is based on the concepts of dimensional analysis and scaling, which are known to be powerful ideas in many parts of applied mathematics. A general discussion is given by Lin and Segel (1974), while some specifics for population models, including the concept of quasi-dimension, are contained in Nåsell (1985).

Application of these ideas commonly leads to a reparametrization, where parameters are of two different types, "essential" and "innocent", as described in Nåsell (2002b). A parameter is called innocent if it can be eliminated by a rescaling of the state variables, or by time. If this is not possible, the parameter is called essential. Our formulation of the model identifies five parameters, namely μ, N, R_0, α_1, and α_2. Among these, μ is innocent, while the other four are essential. One notes that μ has the quasi-dimension inverse time, while the other four parameters are free of quasi-dimension. Note also that the parameter N, although essential for the stochastic model, is innocent for the deterministic version. The innocent parameter μ will not affect the results concerning the cumulants of the quasi-stationary distribution.

Our parametrization has the advantage that the maximum population size is explicitly represented by the parameter N. This will be important in our later development of asymptotic approximations as N becomes large.

The corresponding deterministic model leads to the differential equation

$$Y' = r\left(1 - \frac{Y}{K}\right)Y,$$

where the intrinsic growth rate per individual is

$$r = \mu(R_0 - 1),$$

and the carrying capacity is given by

$$K = \frac{R_0 - 1}{\alpha_1 R_0 + \alpha_2} N.$$

The stochastic model has a quasi-stationary distribution which in the present case with $R_0 > 1$ is approximately normal in its body with mean K and standard deviation

$$\sigma = \frac{\sqrt{(\alpha_1 + \alpha_2)R_0}}{\alpha_1 R_0 + \alpha_2}\sqrt{N}. \tag{1}$$

A derivation is given in Nåsell (2001a). An alternate derivation uses a diffusion approximation. It leads to the result that K is the solution of the equation $\lambda_n = \mu_n$, and that the variance can be determined from the expression

$$\sigma^2 = \frac{\lambda_K}{\mu'_K - \lambda'_K}, \tag{2}$$

where the primes are used to denote derivatives with respect to n. This expression for σ^2 can easily be derived from the following expression given already by Bartlett, et al. (1960):

$$\sigma^2 = -\left.\frac{1}{\frac{d(\lambda_n/\mu_n)}{dn}}\right|_{n=K}.$$

For the evaluations that follow it is useful to introduce the notation

$$f_1 = \frac{R_0+1}{R_0-1},$$

$$f_2 = \frac{\alpha_1 R_0 - \alpha_2}{\alpha_1 R_0 + \alpha_2},$$

and to note that σ^2 can be determined from f_1, f_2, and K via the relation

$$\sigma^2 = \tfrac{1}{2}(f_1 - f_2)K.$$

3. Model analysis

The method used in Nåsell (2001a,b) for analysis of the quasi-stationary distribution $\{q_n\}$ of the stochastic logistic model $\{X(t)\}$ can be adapted to the situation that we are concerned with here, namely analysis of the first few cumulants of the quasi-stationary distribution in case $R_0 > 1$ and N is large. The results in Nåsell (2001a) are based on the study of two auxiliary processes $\{X^{(0)}(t)\}$ and $\{X^{(1)}(t)\}$, as briefly described in Appendix A. The auxiliary processes have non-degenerate stationary distributions, $\left\{p_n^{(0)}\right\}$ and $\left\{p_n^{(1)}\right\}$, that can be determined explicitly. The explicit expressions for these stationary distributions are, however, complicated and uninformative. Progress rests on deriving asymptotic approximations of these two stationary distributions. The results in Nåsell (2001a) use the first term only in the asymptotic approximations of each of these two distributions. The adaptation here requires an extension to five such terms in the asymptotic approximation of one of these stationary distributions, namely $\{p_n^{(0)}\}$.

We recall that the first three cumulants κ_1, κ_2, and κ_3 of a distribution are equal to the expected value, the variance, and the centered third moment, respectively. The results concerning the first three cumulants $\kappa_i(X^{(0)}), i = 1,2,3,$ of the stationary distribution $\left\{p_n^{(0)}\right\}$ can be expressed in the following form:

$$\kappa_1(X^{(0)}) \sim K - \frac{\sigma^2}{K} - f_1\frac{\sigma^2}{K^2}, \quad N \to \infty, \tag{3}$$

$$\kappa_2(X^{(0)}) \sim \sigma^2 + \frac{1}{2}(f_1+f_2)\frac{\sigma^2}{K}, \quad N \to \infty, \tag{4}$$

$$\kappa_3(X^{(0)}) \sim -f_2\sigma^2, \quad N \to \infty. \tag{5}$$

The derivation of these results is lengthy. Some steps in the derivation are indicated in Appendix A, while additional details are given through a Maple worksheet in Nåsell (2002a).

We note that three terms are given in the approximation of the mean κ_1, while the number of terms is two for the variance κ_2 and one for the third cumulant κ_3. The three terms for κ_1 are of the orders $O(N), O(1)$, and $O(1/N)$, respectively, since K and σ^2 are both $O(N)$. Similarly, the two terms for κ_2 are of the orders $O(N)$ and $O(1)$, while the one term for κ_3 is of order $O(N)$. It follows that the measure of skewness $\gamma_1 = \kappa_3/\sigma^3 = -f_2/\sigma$, which is known to be equal to zero for the normal distribution, approaches zero as $N \to \infty$.

We conjecture that the right–hand sides in (3)–(5) are actually asymptotic approximations of the corresponding cumulants of the quasi-stationary distribution. Strong support for this conjecture is given by the numerical evaluations in Table 1. It indicates that the difference between the first cumulant κ_1 and its three-term approximation in (3) is $O(1/N^2)$, the difference between the second cumulant κ_2 and its two-term approximation in (4) is $O(1/N)$, and that the difference between the third cumulant κ_3 and its one-term approximation in (5) is $O(1)$, all as $N \to \infty$.

Numerical illustrations of the approximations in (3)–(5) are given in Figs. 1–3. The first term in each of the approximations of the three cumulants is seen to be of the order $O(N)$. One can therefore expect that each cumulant divided by N is approximately constant as a function of N. The three figures show the first three cumulants of the quasi-stationary distribution, divided by N, as a function of N for given values of the parameters R_0, α_1, and α_2. Furthermore, the three approximations of the first cumulant divided by N formed by including one, two, and three terms of the asymptotic approximation in (3) are included in Fig. 1. Similarly, Fig. 2 shows also the two approximations of the second cumulant divided by N formed by including one and two terms of the asymptotic approximation in (4). Finally, Fig. 3 includes the approximation of the third cumulant divided by N given by (5).

Table 1
Numerical evaluations of the first three cumulants of the quasi-stationary distribution of the stochastic logistic model are shown in the third column.

N	Cumulant	Value	Difference
10	κ_1	6.1	-1.7×10^{-2}
10	κ_2	3.4	1.3×10^{-1}
10	κ_3	−2.1	-2.8×10^{-1}
100	κ_1	66.2	-4.1×10^{-4}
100	κ_2	28.2	1.9×10^{-2}
100	κ_3	−19.1	-6.1×10^{-1}
1000	κ_1	666.2	-3.9×10^{-6}
1000	κ_2	278.2	1.8×10^{-3}
1000	κ_3	−185.8	-5.7×10^{-1}

The parameters are $R_0 = 5, \alpha_1 = 1$, and $\alpha_2 = 1$. The last column shows the difference between the third column values and the corresponding approximations from (3)–(5).

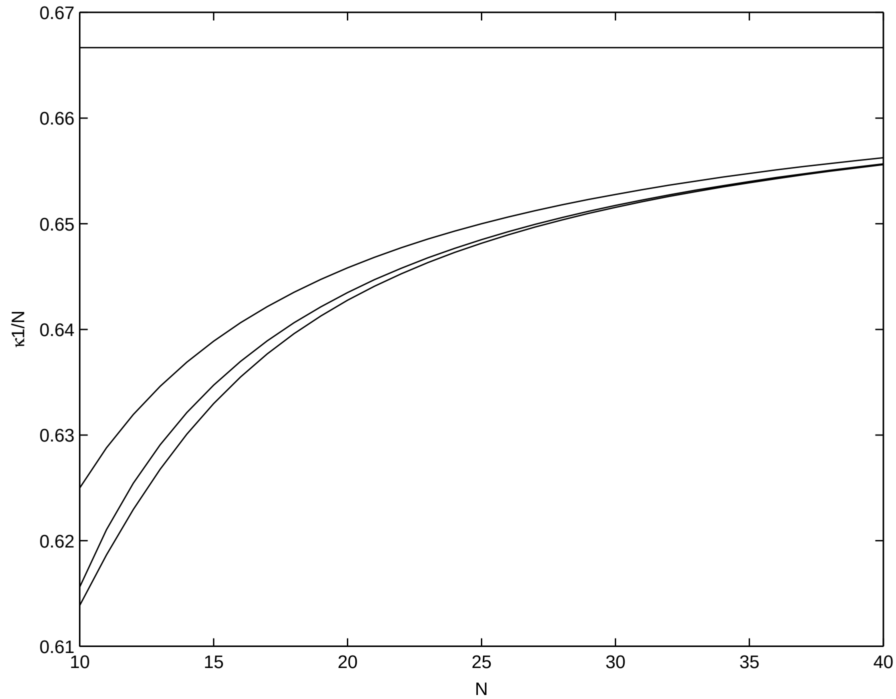

Fig. 1. Numerical illustration of κ_1/N with $R_0 = 5, \alpha_1 = 1$, and $\alpha_2 = 1$. The lowest curve shows κ_1/N for the quasi-stationary distribution, as a function of N. The three approximations of κ_1/N formed by including one, two, and three terms from the right-hand side of (3) are shown as the first, second, and third curves from above.

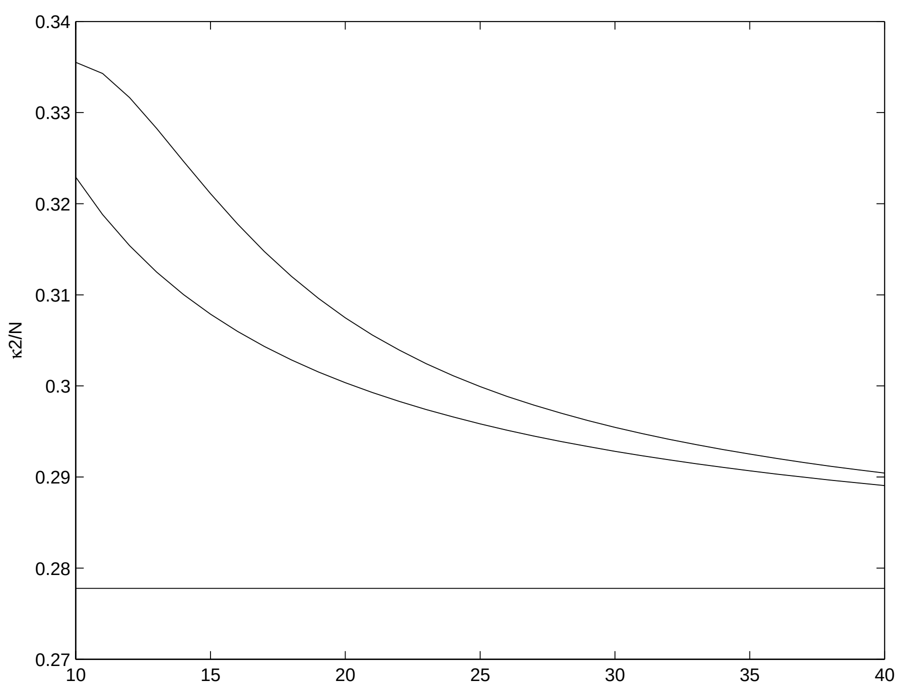

Fig. 2. Numerical illustration of κ_2/N with $R_0 = 5, \alpha_1 = 1$, and $\alpha_2 = 1$. The uppermost curve shows κ_2/N for the quasi-stationary distribution, as a function of N. The two approximations of κ_2/N formed by including one and two terms from the right-hand side of (4) are shown as the first and second curves from below.

The first term in each of approximations (3)–(5) was given as an approximation of the corresponding cumulant already in the insightful paper by Bartlett et al. (1960). They also give the second term in the asymptotic approximation of the mean κ_1. However, they did not claim that the approximations are asymptotic.

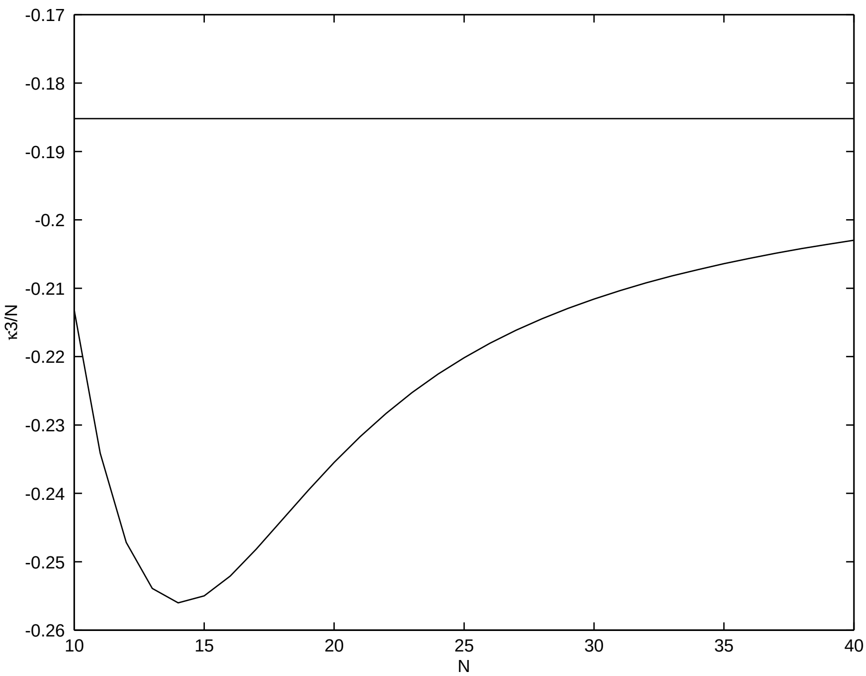

Fig. 3. Numerical illustration of κ_3/N with $R_0 = 5, \alpha_1 = 1$, and $\alpha_2 = 1$. The lowest curve shows κ_3/N for the quasi-stationary distribution, as a function of N. The approximation of κ_3/N formed from the right-hand side of (5) is shown as the uppermost (constant) curve.

4. Differential equations for the cumulants

The starting point for the moment closure method is a set of differential equations for the first three cumulants $\kappa_1(t)$, $\kappa_2(t)$, and $\kappa_3(t)$ of the original process $\{X(t)\}$. A derivation is given by Matis and Kiffe (1996). Using our notation, the three equations can be written as follows:

$$\kappa_1' = \frac{r}{K}[(K - \kappa_1)\kappa_1 - \kappa_2], \tag{6}$$

$$\kappa_2' = \frac{r}{K}[(f_1 K - f_2\kappa_1)\kappa_1 + (2K - f_2)\kappa_2 - 4\kappa_1\kappa_2 - 2\kappa_3], \tag{7}$$

$$\kappa_3' = \frac{r}{K}[(K - \kappa_1)\kappa_1 - 6f_2\kappa_1\kappa_2 - 6\kappa_1\kappa_3 + (3f_1K - 1)\kappa_2 - 6\kappa_2^2 + 3(K - f_2)\kappa_3 - 3\kappa_4]. \tag{8}$$

These equations cannot be solved, since the number of unknowns exceeds the number of equations. The moment closure method is based on the assumption that the distribution of states is approximately normal. One consequence of this assumption is that the cumulants of order higher than 2 are small. Accordingly, we put $\kappa_3 = 0$ and study the steady-state solution of the two Eqs. (6) and (7) in Section 5, while Section 6 is concerned with the steady-state solution of the three Eqs. (6)–(8) with $\kappa_4 = 0$.

Two other consequences of the assumption that the distribution of states is approximately normal are that the variance $\kappa_2(t)$ is positive, and that the mean $\kappa_1(t)$ divided by the standard deviation $\sqrt{\kappa_2(t)}$ is large, since the state variable that measures the number of individuals is nonnegative. These two consequencies will be used below to reject spurious solutions.

The moment closure method can be used both for processes that have a non-degenerate stationary distribution, and for processes with an absorbing state, where the long-term behaviour of the non-absorbed process is described by a quasi-stationary distribution. The limiting values of the cumulants of the original process as $t \to \infty$ are equal to the cumulants of the stationary distribution in the first case, while they are equal to zero in the second case. In contrast, we find that the limiting values of the solutions of the moment closure equations above are equal to the cumulants of the stationary distribution in the first case, as expected, while they deviate strongly from the true cumulants, and will be used to derive approximations of the cumulants of the quasi-stationary distribution in the second case. It is the second case that holds for the stochastic logistic model that we consider in this paper.

5. Approximations of steady-state solutions for the first two cumulants

The steady-state solutions of the two differential equations (6) and (7) with $\kappa_3 = 0$ are denoted $\kappa_1^{(1)}$ and

$\kappa_2^{(1)}$. We find that the two approximations of the cumulants are related by

$$\kappa_2^{(1)} = (K - \kappa_1^{(1)})\kappa_1^{(1)}, \tag{9}$$

and that $\kappa_1^{(1)} = x$ satisfies the third-degree equation

$$4x^3 - 6Kx^2 + 2(K^2 + \sigma^2)x = 0. \tag{10}$$

This equation has one root equal to zero, while the other two roots are given by

$$x = \frac{3}{4}K \pm \frac{1}{4}K\sqrt{1 - \frac{8\sigma^2}{K^2}}. \tag{11}$$

Observe that the ratio σ^2/K^2 appearing in the square root is of the order of $1/N$. We can use this fact to determine an arbitrary number of terms in an asymptotic approximation of the square root as $N \to \infty$. Clearly, the one-term expansion is equal to one. This implies that the one-term approximations of the two roots in (11) are equal to K and $K/2$, respectively.

The assumption that $\kappa_3 = 0$ made above is inconsistent with the model. The inconsistency leads to spurious critical points of the system of differential equations. Only one of the three critical points is consistent with the stronger assumption that the distribution is approximately normal. The point for which the one-term approximation of $x = \kappa_1^{(1)}$ is equal to $K/2$ is rejected, since the ratio of mean to standard deviation, $\kappa_1^{(1)}/\sqrt{\kappa_2^{(1)}}$, is by (9) asymptotically equal to one, which is not sufficiently large. The point for which $x = 0$ is also rejected, since $\kappa_1^{(1)}/\sqrt{\kappa_2^{(1)}} = \sqrt{x/(K-x)}$ is an increasing function of $x = \kappa_1^{(1)}$ for $0 \leqslant x < K$. We conclude that only the critical point whose one-term asymptotic approximation is $x = K$ remains.

The rejection of spurious critical points can also be based on showing that they are locally unstable. This basis for rejection was introduced by Whittle (1957). Keeling (2000) replaces the assumption of approximate normality of the quasi-stationary distribution by the assumption of approximate log-normality. This excludes spurious critical points in this case.

The remaining critical point with $x \sim K$ corresponds to the positive square root in (11). Inclusion of two terms in the asymptotic approximation of the square root in (11) as $N \to \infty$ leads to the following result:

$$\kappa_1^{(1)} \sim K - \frac{\sigma^2}{K}, \quad N \to \infty, \tag{12}$$

$$\kappa_2^{(1)} \sim \sigma^2, \quad N \to \infty. \tag{13}$$

These terms agree with the corresponding terms in (3) and (4). Thus, they give asymptotic approximations of the cumulants of the quasi-stationary distribution. Inclusion of one additional term in the asymptotic approximation of the square root in (11) will lead to an improved approximation of the root of (11). However, a comparison with (3) shows that the additional term does not agree with the corresponding term in the asymptotic approximation of κ_1 in (3). Therefore, additional terms in the expansion of the square root do not improve our approximations of the first two cumulants of the quasi-stationary distribution.

We note, incidentally, that the ratio of mean to standard deviation is asymptotically equal to K/σ, which is of the order of $\sqrt{N}$. This ratio grows arbitrarily large as $N \to \infty$, as required for acceptability of the normal approximation.

6. Approximations of steady-state solutions for the first three cumulants

We set $\kappa_4 = 0$ and denote the steady-state solution of the resulting three differential equations (6)–(8) by $\kappa_1^{(2)}, \kappa_2^{(2)}, \kappa_3^{(2)}$. We find then from the first two equations that $\kappa_2^{(2)}$ and $\kappa_3^{(2)}$ can be determined from $\kappa_1^{(2)}$ by the two relations

$$\kappa_2^{(2)} = (K - \kappa_1^{(2)})\kappa_1^{(2)}$$

and

$$\kappa_3^{(2)} = \tfrac{1}{2}\left[(f_1 K - f_2\kappa_1^{(2)})\kappa_1^{(2)} + (2K - f_2)\kappa_2^{(2)} - 4\kappa_1^{(2)}\kappa_2^{(2)}\right].$$

Insertion into the third equation shows that $\kappa_1^{(2)} = x$ satisfies the fourth-degree equation

$$6x^4 - 12Kx^3 + (7K^2 + 4\sigma^2)x^2 - [K^3 + (3K - f_2)\sigma^2]x = 0. \tag{14}$$

Clearly, one root of this equation is $x = 0$. The remaining roots satisfy a third-degree equation. Explicit solutions are too complicated to be useful, as already remarked in Matis and Kiffe (1996). We determine instead asymptotic approximations for large values of N. To do this, we search for solutions of the form $x = AN + B + C/N$. In doing this, the N-dependencies of the two parameters K and σ are made explicit by writing $K = a_1 N$ and $\sigma^2 = a_2 N$. After insertion of these expressions for x, K, and σ^2 into the third-degree equation, we determine three equations by setting the coefficients of N raised to the powers 3, 2, and 1 equal to zero. One of these equations contains A as the only unknown. The equation has three roots. Arguments similar to those of the preceding section show that two of them must be rejected as corresponding to spurious solutions. The value retained is $A = a_1$. This is consistent with the result of the preceding section. The remaining two equations for B and C are easily solved. The resulting asymptotic approximations for the three cumulants agree with the results in (3)–(5). Thus, we conclude that the moment closure approximations of the cumulants derived in this section agree with the actual cumulants of the quasi-stationary distribution to a higher order than the approximations of the preceding section.

We note that these results are noticeably easier to derive than those reported in Section 3.

7. Concluding comments

We have dealt here with two competing methods for deriving approximations of the three lowest cumulants of the quasi-stationary distribution of the stochastic logistic model in the case when $R_0 > 1$ and N is large. The moment closure method has the definite advantage over its competitor that the mathematical work required for applying it is reasonably brief. The alternative method allows us to derive asymptotic approximations of the first few cumulants of the stationary distribution of the auxiliary process $\{X^{(0)}(t)\}$. We combine this with the conjecture, strongly supported by numerical evaluations, that these are asymptotic approximations of the corresponding cumulants of the quasi-stationary distribution, to conclude that the cumulant approximations derived from the moment closure method are indeed asymptotic approximations of the true cumulants. This is a desirable property of the moment closure method which has not been known previously.

The distinction between the processes $\{X(t)\}$ and $\{X^{(0)}(t)\}$ is subtle. The reason is that these two processes have the same transition rates as long as the first one has not gone extinct. It is mentioned in Nåsell (2001a) that several authors use the stationary distribution $\left\{p_n^{(0)}\right\}$ to represent the quasi-stationary distribution that we denote by $\{q_n\}$, without noting that the first one is actually an approximation of the second one. The same is true also for Bartlett et al. (1960), Keeling (2000), Matis and Kiffe (1996, 1998), Renshaw (1991, 1998). This conceptual mis-hap is not expected to lead to any serious errors in the case considered here. It is, however, important to distinguish between $\{q_n\}$ and $\left\{p_n^{(0)}\right\}$ if one wants to study the left tail of the quasi-stationary distribution when $R_0 > 1$, which is important for the estimation of the time to extinction, or if one is concerned with the transition region near $R_0 = 1$ or the region where $R_0 < 1$.

Three closely related moment closure problems are studied by Matis and Kiffe (1996). In fact, the first and third of their problems concide with the problems we have studied in Sections 5 and 6, respectively. In addition, the second problem they study is to determine an approximation of the admissible critical point for the two differential equations (6) and (7), after inserting the expression in (5) for κ_3. As mentioned above, this result for κ_3 was found already by Bartlett et al. (1960).

Matis and Kiffe (1996) give explicit expressions for their approximations of the first two cumulants in the first two of their problems. With regard to their third problem, they report that closed form solutions are available, but that they are too complex to be useful. Therefore, they refrain from giving them. One may comment that the closed form solutions given for the first two of the problems are also rather complicated and difficult to interpret. In contrast, we note that our results in (3)–(5) contain a small number of terms that are easy to understand.

It is straightforward to show that asymptotic approximations of the approximations given in Matis and Kiffe (1996) for the mean and variance of their first problem coincide with our results in (12), (13), and that asymptotic approximations of the solutions of their second and third problems are found in our (3)–(5). This means in particular that problems 2 and 3 have the same asymptotic approximations.

Matis and Kiffe (1996) make numerical comparisons of their approximations for a number of test cases as a basis for recommendations for the choice of approximation. With the availability of asymptotic approximations, the need for such comparisons disappears.

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Appendix A. Approximations of the cumulants of the stationary distribution $p_n^{(0)}$

A brief summary is given here of the main steps in the derivation of the asymptotic approximations for the three cumulants reported in Section 3. The theoretical background for this work is given in Nåsell (2001a,b), while the Maple commands needed for the analysis are contained in Nåsell (2002a).

Two auxiliary processes $\{X^{(0)}(t)\}$ and $\{X^{(1)}(t)\}$ play an important role in this work. They are both birth-death processes that are close to the original process $\{X(t)\}$, but lack absorbing states. The state space of each of the two auxiliary processes coincides with the set of transient states $\{1, 2, \ldots, N\}$ for the original process. The process $\{X^{(0)}(t)\}$ can be described as the original process with the origin removed. Its death rate $\mu_1^{(0)}$ is equal to 0, while all other transition rates are the same as in the original process. The process $\{X^{(1)}(t)\}$ is found from the original process by allowing for one immortal individual. Here, the death rate μ_n is replaced by $\mu_n^{(1)} = \mu_{n-1}$, while the birth rates are unchanged.

The stationary distributions of the two auxiliary processes can be determined explicitly from knowledge of the transition rates λ_n and μ_n. In order to describe them we introduce two sequencies ρ_n and π_n as follows:

$$\rho_1 = 1, \quad \rho_n = \frac{\lambda_1\lambda_2\cdots\lambda_{n-1}}{\mu_1\mu_2\cdots\mu_{n-1}}, \quad n = 2, 3, \ldots, N,$$

$$\pi_n = \frac{\mu_1}{\mu_n}\rho_n, \quad n = 1, 2, \ldots, N.$$

The stationary distributions of the two auxiliary processes can be simply expressed in terms of these sequencies. The stationary distribution of the process $\{X^{(1)}(t)\}$ is given by

$$p_n^{(1)} = \rho_n p_1^{(1)}, \; n = 1, 2, \ldots, N, \text{ where } \quad p_1^{(1)} = \frac{1}{\sum_{n=1}^N \rho_n},$$

while the stationary distribution of $\{X^{(0)}(t)\}$ equals

$$p_n^{(0)} = \pi_n p_1^{(0)}, \; n = 1, 2, \ldots, N, \text{ where } \quad p_1^{(0)} = \frac{1}{\sum_{n=1}^N \pi_n}.$$

The quantities ρ_n can be expressed in terms of gamma functions as follows:

$$\rho_n = \frac{1}{R_0}\frac{1}{1-\alpha_1 n/N}\frac{\Gamma(N/\alpha_1)\Gamma(N/\alpha_2)}{\Gamma(N/\alpha_1 - n)\Gamma(N/\alpha_2 + n)}\left(\frac{\alpha_1 R_0}{\alpha_2}\right)^n, \quad 0<\alpha_1\leqslant 1, \quad 0<\alpha_2.$$

(The treatment if either α_1 or α_2 equals zero follows that in Nåsell, 2001b). An asymptotic approximation for ρ_n can then be derived by applying asymptotic approximations of the gamma functions. Only the first term of this approximation (the Stirling formula) is used in Nåsell (2001b), while we require three terms here. Thus, we use the following asymptotic approximation of the gamma function:

$$\Gamma(x) \sim \left(\frac{x}{e}\right)^x \sqrt{\frac{2\pi}{x}} S(x), \quad x \to \infty,$$

where

$$S(x) = 1 + \frac{1}{12x} + \frac{1}{288x^2}.$$

The expression for π_n can be expressed in the following form

$$\pi_n \sim s(n)f(n)g(n)\exp(h(n)), \quad N \to \infty, \quad N - n \to \infty.$$

Here, the functions g and h are given in Nåsell (2001b). They are equal to

$$g(n) = \frac{1}{R_0}\frac{\sqrt{1+\alpha_2 n/N}}{\sqrt{1-\alpha_1 n/N}}$$

and

$$h(n) = n\log R_0 - \left(\frac{N}{\alpha_1} - n\right)\log\left(1 - \frac{\alpha_1}{N}\right) - \left(\frac{N}{\alpha_2} + n\right)\log\left(1 + \frac{\alpha_2 n}{N}\right).$$

Furthermore, the ratio π_n/ρ_n is given by

$$f(n) = \frac{\mu_1}{\mu_n} = f_{0a} f_a(n),$$

where

$$f_{0a} = 1 + \frac{\alpha_2}{N}$$

and

$$f_a(n) = \frac{1}{(1+\alpha_2 n/N)n}.$$

Finally, the extra terms in the asymptotic approximation of the gamma functions give rise to the factor $s(n)$. It can be expressed as follows:

$$s(n) = s_{0a}s_1(n)s_2(n),$$

where

$$s_{0a} = S(N/\alpha_1)S(N/\alpha_2),$$

$$s_1(n) = \frac{1}{S(N/\alpha_1 - n)},$$

and

$$s_2(n) = \frac{1}{S(N/\alpha_2 + n)}.$$

We start out with expanding all the functions of n above as Taylor series about $n = K$, which is the value of n for which $h(n)$ has a maximum. By including seven terms in the series expansion of $h(n)$ we find that $h(n)$ can be approximated as follows:

$$h(n) \approx \gamma_1 N - \frac{y_1(n)^2}{2} + h_a(n),$$

where

$$h_a(n) = h_3 y_1^3(n) + h_4 y_1^4(n) + h_5 y_1^5(n) + h_6 y_1^6(n),$$

and where we have introduced the notations

$$\gamma_1 = \frac{1}{\alpha_1}\left(\log R_0 - \frac{\alpha_1+\alpha_2}{\alpha_2}\log\frac{(\alpha_1+\alpha_2)R_0}{\alpha_1 R_0 + \alpha_2}\right)$$

and

$$y_1(n) = \frac{n-K}{\sigma}.$$

It is straightforward to determine the coefficients $h_3 - h_6$. Here, h_3 is of order $O(1/\sqrt{N})$, h_4 is of order $O(1/N)$, and generally h_k is of order $O(1/N^{k/2-1})$. It follows that the approximation of $h(n)$ above is actually asymptotic if $y_1(n) = O(1)$ as $N \to \infty$. This is the condition that characterizes the body of the distribution we are concerned with.

We introduce $\mathscr{A}_2(F(n))$ to denote a specific asymptotic approximation of $F(n)$ as $N \to \infty$, namely the one that includes terms up to the order of $1/N^2$. (We assume, of course, that $F(n)$ depends on N, although this is not apparent from the notation.) We assume throughout that $y_1(n) = O(1)$ as $N \to \infty$.

The asymptotic approximation of $\exp(h_a(n))$, up to terms of order $1/N^2$, and under the assumption that $y_1(n) = O(1)$ as $N \to \infty$, is denoted $h_b(n)$:

$$h_b(n) = \mathscr{A}_2(\exp(h_a(n))).$$

We conclude that

$$\exp(h(n)) \sim \sqrt{2\pi} h_0 \varphi(y_1(n)) h_b(n), \quad y_1(n) = O(1), \quad N \to \infty,$$

where

$$h_0 = \exp(\gamma_1 N),$$

and where

$$\varphi(x) = \frac{1}{\sqrt{2\pi}} \exp(-x^2/2)$$

denotes the normal density function.

By including five terms in the Taylor series expansion of $g(n)$ about $n = K$ we find that $g(n)$ can be approximated as follows:

$$g(n) \sim g_0 g_b(n), \quad y_1(n) = O(1), \quad N \to \infty,$$

where

$$g_0 = \frac{1}{\sqrt{R_0}}$$

and

$$g_b(n) = 1 + g_1 y_1(n) + g_2 y_1^2(n) + g_3 y_1^3(n) + g_4 y_1^4(n).$$

This approximation is asymptotic, since g_k is of order $O(1/N^{k/2})$.

Inclusion of five terms in the Taylor expansion of $f_a(n)$ about $n = K$ leads to the following approximation:

$$f_a(n) \sim f_{0b} f_b(n), \quad y_1(n) = O(1), \quad N \to \infty,$$

where

$$f_b(n) = 1 + f_1 y_1(n) + f_2 y_1^2(n) + f_3 y_1^3(n) + f_4 y_1^4(n),$$

with $f_k = O(1/N^{k/2})$. Also, we put $f_0 = f_{0a} f_{0b}$.

The asymptotic approximation of $s(n)$ is derived in steps, as follows:

$$s_0 = \mathscr{A}_2(s_{0a}),$$

$$s_{1b}(n) = \mathscr{A}_2(s_1(n)),$$

$$s_{2b}(n) = \mathscr{A}_2(s_2(n)),$$

$$s_b(n) = \mathscr{A}_2(s_{1b}(n) s_{2b}(n)).$$

A result of these evaluations is that the asymptotic approximation for π_n can be expressed as follows:

$$\pi_n \sim \sqrt{2\pi} \pi_0 \pi_b(n) \varphi(y_1(n)), \quad y_1(n) = O(1), \quad N \to \infty,$$

where

$$\pi_0 = \mathscr{A}_2(s_0 f_0 g_0 h_0)$$

and

$$\pi_b(n) = \mathscr{A}_2(s_b(n) f_b(n) g_b(n) h_b(n)).$$

It is useful to express the function $\pi_b(n)$ in the following way:

$$\pi_b(n) = \sum_{j=0}^{12} k_j y_1^j(n).$$

By using the well-known formulas for the moments of a normal random variable we are led to the following relation:

$$\sum_{n=1}^{N} y_1^j(n) \varphi(y_1(n))/\sigma \sim \begin{cases} 0, & j = 1, 3, 5, \ldots, \\ 1 \cdot 3 \cdot 5 \cdots (j-1), & j = 2, 4, 6, \ldots . \end{cases}$$

Applying this, we get

$$\sum_{n=1}^{N} \pi_n = \sqrt{2\pi} \pi_0 \sigma p_d,$$

where

$$p_d = k_0 + k_2 + 3k_4 + 15k_6 + 105k_8 + 945k_{10} + 10395k_{12}.$$

It follows that

$$p_n^{(0)} \sim \frac{\pi_b(n) \varphi(y_1(n))}{\sigma p_d}, \quad y_1(n) = O(1), \quad N \to \infty.$$

This approximation of the stationary distribution $p_n^{(0)}$ in its body can be used to derive approximations of the moments. We get the following approximation for the expectation:

$$EX^{(0)} \sim K + \frac{\sigma(k_1 + 3k_3 + 15k_5 + 105k_7 + 945k_9)}{p_d}, \quad N \to \infty,$$

since $k_{11} = 0$. Similarly, the variance is approximated by

$$VX^{(0)} = E(X^{(0)} - EX^{(0)})^2 \sim \frac{\sigma^2(k_0 + 3k_2 + 15k_4 + 105k_6 + 945k_8 + 10395k_{10} + 135135k_{12})}{p_d} - (EX^{(0)} - K)^2, \quad N \to \infty,$$

and the third central moment by

$$E(X^{(0)} - EX^{(0)})^3 \sim \frac{\sigma^3(3k_1 + 15k_3 + 105k_5 + 945k_7 + 10395k_9)}{p_d} - 3VX^{(0)}(EX^{(0)} - K) - (EX^{(0)} - K)^3, \quad N \to \infty,$$

since $k_{11} = 0$.

The evaluations in the Maple worksheet in Nåsell (2002a) of these complicated expressions for the asymptotic approximations of the first three cumulants lead very surprisingly to the simple results in (3)–(5). (The same Maple worksheet also gives approximations of the first three cumulants of the stationary distribution $\{p_n^{(1)}\}$.)

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