Fluctuations and correlations in population models with age structure

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We study the population profile in a simple discrete time model of population dynamics. Our model, which is closely related to certain “bit-string” models of evolution, incorporates competition for resources via a population dependent death probability, as well as a variable reproduction probability for each individual as a function of age. We first solve for the steady–state of the model in mean field theory, before developing analytic techniques to compute Gaussian fluctuation corrections around the mean field fixed point. Our computations are found to be in good agreement with Monte–Carlo simulations. Finally we discuss how similar methods may be applied to fluctuations in continuous time population models.

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The problem of population dynamics has attracted enormous interest over many years (for some introductions and recent applications see Refs. \cite{1-8}). Beginning with simple logistic growth models \cite{1}, a tremendous variety of systems have been studied displaying a diverse range of behavior, varying from stable fixed points to strange attractors. Broadly speaking these models split naturally into two categories: those using continuous and those using discrete time. The simplest discrete time models describe species where there is no overlap between successive generations, leading to difference equations of the form \( N(t + 1) = g[N(t)] \), where \( N(t) \) is the total population at time \( t \). However these models may easily be generalized to species with multiple discrete age generations (for example: eggs, larvae, adults), where one or more generations may be present simultaneously. Instead of a single variable \( N \), information about the age distribution is now carried in a “vector” \( \mathbf{n}(t) \equiv \{n_0(t), n_1(t), \ldots, n_D(t)\} \), where \( n_a(t) \) is the number of individuals of age \( a \) at time \( t \). Note that \( D \) is the maximum age, while \( n_0 \) stands for the number of “newborns”. Beginning with the pioneering work of Leslie \cite{9} models of this type have been extensively analyzed. The simplest Leslie model is linear in \( n \), so that the evolution equation is just \( \mathbf{n}(t + 1) = \mathbf{A} \mathbf{n}(t) \). Here, \( \mathbf{A} \) is the Leslie matrix

\[
\mathbf{A} = \begin{pmatrix}
f_0 & f_1 & \ldots & f_D \\
v_0 & 0 & \ldots & 0 \\
0 & v_1 & \ldots & 0 \\
\vdots & \ddots & \ddots & \vdots \\
0 & \ldots & 0 & v_{D-1}
\end{pmatrix},
\]

where the elements \( f_a \) are the fecundities (number of offspring produced) of individuals of age \( a \), and the \( v_a \) are Verhulst factors (the fraction of individuals of age \( a \) who survive to become age \( a + 1 \)). Though the original Leslie model had all the \( \{f_a\} \) and \( \{v_a\} \) as constants, generalizations have since been made to \( n \)-dependent factors \cite{3,11,12}, so that the evolution dynamics becomes inherently non-linear. For example, \( n \)-dependent Verhulst factors are often used to mimic competition for finite resources.

However one deficiency of the models discussed hitherto is that they are deterministic. Real population systems are of course affected by random fluctuations, coming from the environment and/or from the intrinsic dynamics of the birth/death processes. Such stochastic Leslie models have also been investigated \cite{3,13,14}, however only for cases where the birth/death probabilities were independent of the population vector \( n \). To date no information has been available regarding the more realistic case of fluctuations in stochastic age structured models with population dependent birth/death probabilities \cite{4}. This is the situation we will study in this letter.

Population models have also been intensively studied by physicists in recent years in the context of so-called “bit-string” models of evolution \cite{15}. These models are based on the mutation accumulation hypothesis \cite{16}, which assumes that during the aging process each individual accumulates exclusively late–acting deleterious genetic mutations. In “bit-string” models the genome of a particular species is encoded as a series of ‘0’ s and ‘1’ s (deleterious mutations), and as an individual ages the bits (genes) are activated one by one. When the accumulated sum of bad genes reaches a certain number the individual dies (although death may also occur at younger ages due to Verhulst competition). Note that the “bit–strings” of the offspring may differ from those of the parent due to additional beneficial (‘1’→’0’) or deleterious (‘0’→’1’) mutations. This type of model is clearly well suited to efficient computer simulation \cite{17}. In its simplest case, where individuals die after the first deleterious mutation, “bit-string” models simply correspond to multiple genome population models with age structure, where the different genomes can be distinguished by different maximum ages. Deterministic versions of some of these models have already been treated analytically \cite{18}. However, an analysis of the important role played by fluctuations has so far been lacking. Our calculations form
the first step towards filling this gap.

We begin our analysis by defining our discrete time population model. For simplicity, we consider only a single species reproducing asexually, without mutations. Thus, our system can be described by a single vector \( \mathbf{n} \). At each time step we compute the Verhulst factor \( V(\mathbf{n}) \) and let each individual survive with probability \( V \). After this “pruning”, each of the remaining individuals of age \( a \) may give birth to \( F_a \) offspring with probability \( r_a \). At this point the remaining population is aged by one time step, with the exception of the new offspring who make up \( n_0 \). Individuals who exceed the maximum age \( D \) then die immediately and are removed from the system. Since our model allows for a variable reproduction probability \( r_a \) as a function of age, features such as puberty and menopause can be naturally incorporated. However, we do assume that reproductive individuals of puberty and menopause can be naturally incorporated.

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As mentioned above, deterministic versions of this model have been studied \([10,12]\); in particular the population dynamics of a semivoltine species studied in Ref. \([12]\) is quite similar to a \( D = 1 \) version of our model. Our goal is to go beyond these deterministic treatments and analyze the fluctuations and correlations in this system. Therefore, we need to consider \( P(\mathbf{n}, t) \), the probability of finding the population with a particular distribution \( \mathbf{n} \) at time \( t \). Its evolution obeys the master equation

\[
P(\mathbf{n}, t+1) = \sum_{\mathbf{m}} P(\mathbf{m}, t) \times 
\left[ \prod_{a=1}^{D+1} \left( \frac{m_a}{n_a} \right)^{V^{n_a} [1-V]^{m_a-n_a}} \sum_{b_0, \ldots, b_D} \delta \left( n_0 - \sum_{c=0}^{D} F_c b_c \right) \right] \times 
\left[ \prod_{a=1}^{D+1} \left( \frac{n_a}{b_a} \right)^{r_a b_a^{-1} [1 - r_a^{-1}]^{n_a-b_a-1}} \right].
\]

(2)

Note that the \( n_{D+1} \) is just a “temporary” variable, which keeps track of the number of \( m_D \)’s who survive the Verhulst “pruning” so that they can give birth before dying from old age. Let us emphasize that this equation is actually quite complex, since \( V \) is a function of the total population. Multiplying \( (3) \) by \( n_c \) and summing over all the other indices, we obtain

\[
\langle n_a \rangle_{t+1} = \langle V(N) n_{a-1} \rangle_t, \quad (a > 0),
\]

(3)

\[
\langle n_0 \rangle_{t+1} = \sum_d F_d r_d \langle V(N) n_d \rangle_t,
\]

(4)

where \( \langle \bullet \rangle_t \) denotes the average of \( \bullet \) over \( P(\mathbf{n}, t) \). These equations are exact. However, due to the presence of \( N \) through \( V \), all moments of \( P \) may be coupled together. The mean field (MF) approximation consists of replacing the higher order moments by appropriate products of the first moment. Hence we find

\[
\langle n_a \rangle_{t+1}^{\text{MF}} = \left[ V \left( \sum_c \langle n_c \rangle_t^{\text{MF}} \right) \right] \langle n_{a-1} \rangle_{t}^{\text{MF}}, \quad (a > 0),
\]

(5)

\[
\langle n_0 \rangle_{t+1}^{\text{MF}} = \left[ V \left( \sum_c \langle n_c \rangle_t^{\text{MF}} \right) \right] \sum_d F_d r_d \langle n_d \rangle_{t}^{\text{MF}},
\]

(6)

where, to be clear, we have written the explicit expression for \( N \). These non-linear equations are known to contain a rich variety of behavior, depending on the details of \( F_c, r_c, \) and \( V \). For example, if \( \sum_c F_c r_c < 1 \), the reproductive rates are too low and the population will eventually die out. On the other hand, if the reproductive rates are large enough, the population will display period doubling bifurcations and chaos \([13]\). Let us focus on the “moderate” range, so that a simple non–zero steady–state exists. In that case these equations are easily solved to give

\[
\langle n_a \rangle_{t}^{\text{MF}} = N(z) \frac{z^a (1-z)}{(1-z^{D+1})},
\]

(7)

where \( z \) is the unique, positive, real root of the equation

\[
\sum_c F_c r_c z^{c+1} = 1, \quad \text{and} \quad N(z) \text{ is the steady state total population, given by the value that satisfies } V(N) = z.
\]

Our objective is to go beyond such well–known mean field solutions and investigate fluctuations and correlations, i.e., the second moments of \( P \). Thus, we multiply Eq. \( (3) \) by \( n_a n_b \) and sum over all the other indices. For \( a > 0, b > 0 \), we have

\[
\langle n_an_b \rangle_{t+1}^b = \langle V^2 n_{a-1} n_{b-1} \rangle_t + \delta_{ab} \langle V(1-V) n_{a-1} \rangle_t,
\]

(8)

\[
\langle n_0 n_b \rangle_{t+1} = \sum_{c} F_c r_c \langle V^2 n_{a-1} n_{c-1} \rangle_t + F_{a-1} r_{a-1} \langle V(1-V) n_{a-1} \rangle_t,
\]

(9)

\[
\langle n_0 n_0 \rangle_{t+1} = \sum_{c,d} F_{c} r_{c} F_{d} r_{d} \langle V^2 n_{c} n_{d} \rangle_t + \sum_{c} F_{c} r_{c} F_{c} r_{c} \langle V^2 n_{c} n_{c} \rangle_t.
\]

(10)

Note that, like Eqs. \( (3) \) and \( (4) \), these are exact. Assuming \( N_0 > 1 \), and that the system is well away from “critical” points (e.g., bifurcations and the survival/extinction
while the first order result is

\[ P^* (n) = \left( \frac{1}{2\pi N_0} \right)^{(D+1)/2} \frac{1}{\sqrt{\det G}} \times \]

\[ \exp \left[ -\frac{1}{2N_0} \sum_{c,d} (n_c - \bar{n}_c) G^{-1}_{cd} (n_d - \bar{n}_d) \right] , \]

where we expect the unknown (to be determined) parameters \( n \) and \( G \) to be of \( O(N_0) \) and \( O(1) \), respectively. Note that we will integrate \( n \) from \(-\infty \to \infty \) rather than from \(- \infty \to \infty \), a simplification which will introduce only negligible errors of \( O(\exp[-N_0]) \). Averages can now be computed using

\[ \langle f(n_a) \rangle^* = f(\bar{n}_a) + \frac{1}{2} \sum_{c,d} \frac{\partial^2 f}{\partial n_c \partial n_d} N_0 G_{cd} + \ldots . \]

Note that the second term in Eq. (12) is expected to be suppressed by a factor of \( O(1/N_0) \) compared to the first term \( f(\bar{n}_a) \). Hence the right hand side of Eq. (12) is actually an expansion in powers of \( 1/N_0 \). This ordering allows us to set up a systematic perturbation theory, which can be pushed to higher orders if desired.

From now on we drop the bars for clarity (\( \bar{n}_a \to n_a \)). Defining \( \xi = \sum_c n_c / N_0 \) and \( V' = \partial V / \partial \xi \), we have \( \partial V / \partial n_c = V' (\xi) / N_0 \) and \( \partial^2 V / \partial n_c \partial n_d = V'' (\xi) / N_0^2 \), independent of \( c \) or \( d \). Applying Eq. (12) to Eq. (8) gives

\[ n_a = V n_{a-1} + V' \sum_c G_{ca} n_{c-1} + \frac{n_{a-1}}{2N_0} V'' \sum_{c,d} G_{cd} + \ldots . \]

An equation for \( n_0 \) can be similarly derived. With the assumptions \( n \sim O(N_0) \) and \( G \sim O(1) \), the latter two terms in Eq. (13) represent \( O(1/N_0) \) corrections to the mean field results, while the remaining (lowest order) pieces make up the mean field equation (8). Writing a perturbative expansion: \( n_a = n_a^{(0)} + n_a^{(1)} + \ldots \) (with \( n_a^{(k)} \sim O(N_0^{1-k}) \)), we see that \( n_a^{(0)} \) is given by Eq. (6), while the first order result is

\[ n_a^{(1)} = \sum_c \left( \mathbb{I} - S \right)^{-1} \left( \left[ \frac{\partial}{\partial n_c} \right] \right) U_c , \quad \text{with} \]

\[ S_{ab} = \frac{\partial^2 [V n_a - 1]}{\partial n_b} , \quad U_a = \frac{1}{2} \sum_{c,d} \frac{\partial^2 [V n_a - 1]}{\partial n_c \partial n_d} N_0 G_{cd} , \quad (a > 0) , \]

\[ S_{ab} = \sum_c F_c r_c \partial [V n_c] / \partial n_b , \quad U_a = \frac{1}{2} \sum_{c,d} F_c r_c \partial^2 [V n_c] / \partial n_c \partial n_d N_0 G_{cd} , \]

where \( \mathbb{I} \) is the unit matrix and \( S \) is the stability matrix associated with the mean field (zeroth order) stationary solution. Note that both \( S \) and \( U \) need to be evaluated at zeroth order only. With our assumptions about \( F_c, r_c \), and \( V(N) \), the eigenvalues of the stability matrix \( S \) usually lie within the unit circle, implying that our mean field solution is stable. However, for sufficiently high reproductive rates, perturbations with \( \delta n_a \propto n_a \) (i.e., populations with the same relative age distribution, but with different total numbers of individuals) can have eigenvalues of less than \(-1 \). This is the signal of a period doubling bifurcation, leading to the breakdown of our Gaussian perturbation expansion (see also below).

Applying the same analysis to the second moments, we obtain, after some lengthy algebra,

\[ G_{ab} - \sum_{c,d} S_{ac} S_{bd} G_{cd} = K_{ab} , \quad \forall a, b , \]

where

\[ K_{ab} = \delta_{ab} (1 - V) \frac{n_a}{N_0} , \quad a, b > 0 , \]

\[ K_{aa} = K_{0a} = F_{a-1} r_{a-1} (1 - V) \frac{n_a}{N_0} , \quad a > 0 , \]

\[ K_{00} = \frac{1}{N_0} \sum_b V F_b^2 r_b n_b (1 - V r_b) . \]

Again, all quantities need to be evaluated only at the zeroth order, so that, e.g., \( V \) is just \( z \). In compact form this equation can be written as \( G - S G S^T = K \), which may be solved by series

\[ G = K + SKS^T + S^2 K (S^T)^2 + \ldots = \sum_n S^n K (S^T)^n . \]

Since the eigenvalues and eigenvectors of \( S \) are known, let us write \( S = \mathbb{M} \mathbb{E} \mathbb{M}^{-1} \), where \( \mathbb{E} \) is in Jordan form, with the eigenvalues on the diagonal, and \( \mathbb{M} \) is the matrix (with its columns) composed of the corresponding right eigenvectors. Note that \( \mathbb{M} \) is not necessarily orthogonal or unitary. If we define \( \mathbb{G} = \mathbb{M}^{-1} G (\mathbb{M}^T)^{-1} \) and \( \mathbb{K} = \mathbb{M}^{-1} K (\mathbb{M}^T)^{-1} \), then it is straightforward to show that \( \mathbb{G} = \sum_n (\mathbb{E}^n \mathbb{K} \mathbb{E}^n) \). For simplicity, let us focus on the case where \( \mathbb{E} \) is diagonal. Then the sum is easily performed, so that

\[ \mathbb{G}_{ab} = \mathbb{K}_{ab} / (1 - c_a c_b) \quad (\text{no sum}), \]

where the \( \{c\} \) are the eigenvalues. Since \( G = \mathbb{M} \mathbb{G} \mathbb{M}^T \), we can directly obtain the matrix \( G \) and with it all the information about the Gaussian probability distribution.
The explicit formula for computing $G$ is our principal result. Given a particular form of $V(N)$ and reproductive parameters $r_a, F_a$, we can compute $G$ and find the fluctuations in, as well as the correlations between, the populations of various ages.

The result (21) contains a further appealing feature: the signal of bifurcation. From stability analysis, we know that period doubling emerges when the eigenvalue associated with $\delta_{n_a} \propto n_a$ reaches $-1$. Examining Eq. (21), we see that it is precisely this feature which signals the breakdown of the Gaussian approximation. Furthermore, in many studies of, e.g., the Penna “bit-string” model [4], menopause sets in before death, so that $E$ is not diagonal. Then the final expression for $\bar{G}$ will be slightly more complicated, although the above conclusions will remain qualitatively unchanged.

To check the above analysis, we study the simplest possible case: a 2 age system (i.e. $D = 1$), with $r_a = F_a = 1$. Choosing the exponential form for $V$ with $s_0 = 1$ and $N_0 = 100$, mean field theory yields $n_0(0) = 157.4$ and $n_1(0) = 119.3$. Performing our analysis, we arrive at the first order corrections to $n_0$ and $n_1$, the fluctuations in the populations of each age, and the correlation between the populations of the two ages. The results are listed in Table I, alongside those from Monte–Carlo simulations [1]. The agreement is excellent, validating our approach. Note that the corrections $n_a^{(1)}/n_a^{(0)}$ are less than 1%, vindicating our assertion that they should be $O(1/N_0)$.

Up to this point we have been considering models with discrete time steps. However it is perfectly possible, and sometimes more appropriate biologically, to analyze models in continuous time [3]. Let us conclude with some brief remarks about fluctuations in this context. A suitable equation for the mean field population dynamics is

$$\frac{\partial n(x, t)}{\partial t} = -\frac{\partial n(x, t)}{\partial x} - \lambda n(x, t) \int_0^D n(x', t) dx', \quad (21)$$

with boundary conditions for birth at $x = 0$ and certain death at $x = D$. However the birth/death/aging processes giving rise to Eq. (21) can also be written as a ballistic reaction model on a discrete spatial lattice but with continuous time. As is well known [1], starting from the corresponding microscopic lattice master equation, techniques now exist to map this model onto a field theory in continuous space–time. The ensuing action can be recast as a Langevin equation, with the result being Eq. (21), but with extra multiplicative noise terms. The form of these noise terms would then be completely specified, without any ad–hoc guesses. Unfortunately the field–theoretic action is rather awkward, due to the presence of non–local interactions and non–local, multiplicative noise (from fluctuations in the birth process at $x = 0$). However, simplifications occur if we are interested only in the simple, non–zero steady state, where expansions about the mean field solution should be adequate. In this case the leading noise terms enter additively, so that a perturbation theory analogous to the above approach can be set up.

In conclusion, we have developed analytic techniques for dealing with fluctuation effects in a general class of population models with age structure. The results we have presented also form a first step towards an improved analytic understanding of the “bit–string” models of evolution. Finally, it would be interesting to perform further investigations near the bifurcation point, since interesting collective behavior can be expected in that region.

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### Table I. Comparison of results for the 2 age model.

|                | Gaussian Approximation | Simulations |
|----------------|------------------------|------------|
| $\langle n_0 \rangle$ | 156.4                  | 156.4      |
| $\langle n_1 \rangle$ | 118.6                  | 118.6      |
| $\langle n_0^2 \rangle - \langle n_0 \rangle^2$ | 122.0                  | 130.7      |
| $\langle n_0 n_1 \rangle - \langle n_0 \rangle \langle n_1 \rangle$ | 63.9                   | 67.8       |
| $\langle n_1^2 \rangle - \langle n_1 \rangle^2$ | 69.9                   | 71.7       |

[1] J.D. Murray, *Mathematical Biology* (Springer-Verlag, Berlin, 1989).
[2] E.C. Pielou, *Mathematical Ecology* (John Wiley, New York, 1977).
[3] J.H. Pollard, *Models for Human Populations* (Cambridge University Press, Cambridge, 1973).
[4] B. Charlesworth, *Evolution in Age–Structured Populations* (Cambridge University Press, Cambridge, 1994).
[5] M. Rose, *Evolutionary Biology of Aging* (Oxford University Press, New York, 1991).
[6] T.J.P. Penna, J. Stat. Phys. 78, 1629 (1995); T.J.P. Penna and D. Stauffer, Int. J. Mod. Phys. C 6, 233 (1995).
[7] A.F.R. de Toledo Piza, Physica A 242, 195 (1997); R.M.C. de Almeida, S. Moss de Oliveira, and T.J.P. Penna, Physica A 253, 366 (1998).
[8] W. Hwang, P.L. Krapivsky, and S. Redner, Phys. Rev. Lett. 83, 1251 (1999); cond-mat/9912004.
[9] P.H. Leslie, Biometrika 33, 183 (1945); 35, 213 (1948).
[10] L. Liu and J.E. Cohen, J. Math. Biol. 25, 73 (1987); R.A. Desharnais and L. Liu, J. Anim. Ecol. 56, 885 (1987).
[11] A. Wikan, Theor. Pop. Biol. 53, 85 (1998).
[12] R.M. Nisbet and L.C. Onyiah, J. Math. Biol. 32, 329 (1994).
[13] S. Tuljapurkar, Theor. Pop. Biol. 35, 227 (1989).
[14] S. Engen and B.-E. Sarther, Oikos 83, 345 (1998).
[15] J. Guckenheimer, G. Oster, and A. Ipaktchi, J. Math. Biol. 4, 101 (1977).
[16] R.J. Astalos, private communication.
[17] L. Peliti, J. Phys. (Paris) 46, 1469 (1984); J. Cardy in Proceedings of the mathematical beauty of physics, ed. J.-B. Zuber, Adv. Ser. in Math. Phys. 24, 113 (1997); cond-mat/9907163.