Density independent population growth with random survival

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Abstract

A simplified model for the growth of a population is studied in which random effects arise because reproducing individuals have a certain probability of surviving until the next breeding season and hence contributing to the next generation. The resulting Markov chain is that of a branching process with a known generating function. For parameter values leading to non-extinction, an approximating diffusion process is obtained for the population size. Results are obtained for the number of offspring $r_h$ and the initial population size $N_0$ required to guarantee a given probability of survival. For large probabilities of survival, increasing the initial population size from $N_0 = 1$ to $N_0 = 2$ gives a very large decrease in required fecundity but further increases in $N_0$ lead to much smaller decreases in $r_h$. For small probabilities (\textless 0.2) of survival the decreases in required fecundity when $N_0$ changes from 1 to 2 are very small. The calculations have relevance to the survival of populations derived from colonizing individuals which could be any of a variety of organisms.

Keywords: Population ecology; viability; extinction probability.
1 Introduction

The temporal and spatial dynamics of the growth or decline and spread of populations of animals, plants, cells and microorganisms such as bacteria and viruses involves a large number of factors which is mostly species and environment specific. Mathematical models for population growth are thus unlikely to have universal applicability but in some cases may elucidate general principles. The collection of experimental data is mostly a painstaking and sometimes costly task so comparison of data with model predictions is made in relatively few instances. Factors affecting the probability of extinction of a population is one of the main topics of interest in theoretical ecology or theoretical population dynamics and is the subject of the present article.

There is an immense number of population growth models that have been developed since the pioneering models of exponential growth Malthus (1798) and logistic growth Verhulst (1838). See for example Lefever and Horsthemke (1979), Cooke and Witten (1986), Collins and Glenn (1991), Tuckwell and Le Corfec (1998), Tuckwell et al. (2008) and Ferguson and Ponciano (2015). Some of these works concern models with spatial properties and some contain the analysis of experimental data. See Vandermeer and Goldberg (2013) for a useful review.

One of the first models for the random growth of populations due to fluctuations in environmental factors was that of Lewontin and Cohen (1969). Although random processes had been employed and analyzed in population genetics since the 1920s (Wright, 1931) and particularly with diffusion approximations (Kimura, 1964; Crow and Kimura, 1970), it was not until the 1970s that the theory and analysis of stochastic differential equations, developed by Ito (1951) and Kolmogorov (1938), began to be applied in biological modeling. Such coincided with the appearance of many expository texts on stochastic processes and their applications (e.g., Cox and Miller, 1965; Jaswinski, 1970; Gilman and Skorohod, 1972).

One of the models for density independent population growth advanced by Levins (1969) for a population of size \( N(t) \) at time \( t \), with initial value \( N_0 \in (0, \infty) \) took the form of a differential equation

\[
\frac{dN}{dt} = r(t)N + \epsilon(t)\sqrt{v(1-v)N},
\]

where \( r \) is the intrinsic growth rate, \( v \) is called the mean viability and \( \epsilon(t) \) is “a random variable with mean 0 and variance 1”. According to the description of that model “the sampling variation occurs only in the death of adults”. A related stochastic differential equation is

\[
dN = rNdt + \sqrt{v(1-v)N}dW
\]

where \( r \) is the intrinsic growth rate, \( W \) is a standard 1-parameter Wiener process with mean zero and \( Var[W(t)] = t \). This stochastic equation was investigated fully in Tuckwell (1974) who found the associated transition probability density function and the probability of extinction, \( P_E \). The latter was, given by

\[
P_E = 1
\]
\[ P_E = 2N\left(-2\sqrt{\frac{rN_0}{v(1-v)}}\right) \]  

when \( r > 0 \), \( N \) being the normal distribution function.

## 2 Description of model

The model considered in this article has the following assumptions.

- The population has a breeding season (or seasons).
- Only reproducing individuals (often females who can reproduce) are taken into account in enumerating the population size.
- A reproducing individual (female) who is alive at the start of the breeding season produces \( r \) reproducing (female) offspring.
- The probability that a reproducing individual survives to the next breeding season is \( v \).
- Survival of an individual to the next breeding season is independent of the survival of any other individual.

In this model, the growth of the population is partly deterministic (the birth process) and partly governed by random influences (survival to the next breeding season). Note that the number of offspring can easily be made a random variable, but for simplicity this is ignored here. The fact that the number of offspring is the same for all reproducing individuals can be interpreted by assuming that the fecundity \( r \) has been averaged across and within age groups within the population. This averaging should not produce any significant qualitative or quantitative effects. The same can be said to apply to the averaging of survivorship \( v \) over and within age groups.

Note also that in some populations of wild animals, not all females, even if of reproductive age, are allowed to reproduce by the dictates of senior females. In fact, this applies to most human populations as young women are not encouraged to reproduce until they achieve a certain age or social status. The \( r \) (female) offspring per individual may not become reproducing in the breeding season after their birth so a time delay could be introduced to allow for this effect. However, this complication is not taken into account here, with appeal to an averaging argument. Furthermore, there may be an upper limit to the age at which females can reproduce, such being associated with menopause in human and certain other mammalian populations. In the present model passing this age is equivalent to death so that \( v \) is actually the probability that a reproducing female not only survives to the next generation but also continues to contribute offspring, unimpeded by either social rules or by aging.
3 Analysis of model

Reproducing females will hereafter be referred to simply as individuals. Suppose that just prior to a certain breeding season there are $N_0$ individuals. According to the above assumptions, the expectation of the number of individuals $N_1$ just prior to the next breeding season will be

$$E[N_1|N_0] = v(1 + r)N_0,$$  \hspace{1cm} (4)

and the variance of this quantity is

$$\text{Var}[N_1|N_0] = v(1 - v)(1 + r)N_0.$$  \hspace{1cm} (5)

It is seen that the model is equivalent to a Markov chain with transition probabilities

$$P_{N_0,N_0(r+1)-j} = \binom{N_0(r+1)}{N_0(r+1)-j} v^{N_0(r+1)-j}(1-v)^j,$$  \hspace{1cm} (6)

where $j = 0, 1, \ldots, N_0(r+1)$. In particular, the Markov chain constitutes a branching process, which, in the standard notation of Feller (1968, p 295) has the generating function

$$P(s) = \sum_{k=0}^{1+r} \binom{1+r}{k} (vs)^k (1-v)^{1+r-k},$$  \hspace{1cm} (7)

where the number of individuals in the zeroth generation is 1.

Before applying the results for branching processes, we note that if $v = 0$ then the population must go extinct. If at the other extreme, if $v = 1$ the process is one whose continuous approximation grows according to the Malthusian law

$$\frac{dN}{dt} = rN.$$  \hspace{1cm} (8)

If we assume that in Levins’ model, the parameter $v$ is in fact a probability, then these extreme values of $v$ do not yield any difference in the resulting growth process, because setting $v = 0$ or $v = 1$ in the stochastic differential equation (1) yields equation (8).

For the branching process with generating function (7) the following exact results hold. Firstly, the expectation of the population size at the $n$-th generation is

$$E[N_n|N_0 = 1] = (v(1 + r))^n.$$  \hspace{1cm} (9)

Secondly, the variance is

$$\text{Var}[N_n|N_0 = 1] = (1 - v)(v(1 + r))^n \sum_{k=0}^{n-1} (v(1 + r))^k.$$  \hspace{1cm} (10)

Finally, the population is bound to go extinct if

$$r \leq \frac{1}{v} - 1 = r_c.$$  \hspace{1cm} (11)
denoting a critical value.

Furthermore, it is a well-known result for branching processes such as that considered here, that if the population survives then the population size eventually becomes very large. Hence, in the biologically interesting case when condition (11) is violated, we can study the evolution of the population by means of the corresponding diffusion, approximation. This approach has been widely used in the study of the evolution of gene frequencies (Crow and Kimura, 1970). Thus, though it is possible to write down the equations for the probability of extinction in our model in terms of the generating function of the branching process, this quantity may be found more readily as a function of \( v, r \) and \( N_0 \) through the use of a continuous Markov approximation.

### 3.1 A diffusion approximation

Let \( N(t) \) be the continuous approximation to the population size at time \( t \) and let \( f(N, t|N_0) \) be the transition probability density defined through

\[
f(N, t|N_0)dN = \Pr[N(t) \in (N, N + dN)|N(0) = N_0]. \tag{12}
\]

For a continuous Markov process (diffusion) the transition density satisfies a forward Kolmogorov equation

\[
\frac{\partial f}{\partial t} = -\frac{\partial}{\partial N}[K_1(N)f] + \frac{1}{2}\frac{\partial^2}{\partial N^2}[K_2(N)f], \tag{13}
\]

where \( K_1(N) \) and \( K_2(N) \) are the first and second infinitesimal moments. According to the above reference (Crow and Kimura, 1970) we should, for the diffusion approximation to our branching process, set

\[
K_1(N) = v(1 + r)N \tag{14}
\]

and

\[
K_2(N) = v(1 - v)(1 + r)N \tag{15}
\]

where these two quantities have been obtained from equations (4) and (5). The solution of equation (13) with infinitesimal moments given by (14) and (15) has been obtained as an infinite series by Feller (1951).

Let us put

\[
\alpha = v(1 + r) - 1. \tag{16}
\]

Then from that author’s results we obtain the following expressions for the mean and variance of \( N(t) \).

\[
\mathbb{E}[N(t)|N(0) = N_0] = N_0 \exp[\alpha t] \tag{17}
\]

Secondly, the variance is

\[
\text{Var}[N(t)|N(0) = N_0] = \frac{N_0}{\alpha}v(1 - v)(1 + r)\exp[\alpha t](\exp[\alpha t] - 1). \tag{18}
\]

Furthermore, the probability that the population eventually goes extinct is
\[ P_E = \begin{cases} 
1, & \text{if } r \leq \frac{1}{v} - 1, \\
\exp\left[\frac{-2\alpha N_0}{v(1-v)(1+r)}\right], & \text{if } r > \frac{1}{v} - 1. 
\end{cases} \tag{19} \]

Hence the exact results for the branching process and those for the diffusion approximation agree insofar as the conditions for certain extinction are the same for both.

The diffusion process represented by the Kolmogorov equation for the present model can be considered to be associated with the stochastic differential equation

\[ dN = (v(1+r) - 1)Ndtd + \sqrt{v(1-v)(1+r)}NdW. \tag{20} \]

This equation has the same form as (1) but with different drift and diffusion coefficients. Note that the result of associating a Kolmogorov equation with a stochastic differential equation depends on which definition of stochastic integral is employed, two common examples being those of Ito and Stratonovich (see e.g., Mortensen, 1969).

If we put \( v = 1 \) in Eqn. (20), meaning that the entire population survives from breeding season to breeding season, then we recover the Malthusian growth equation (8), as expected. However, this iterative process could not occur indefinitely because it assumes that individuals may persist indefinitely. On the other hand, if we set \( v = 0 \) we obtain the solution \( N(t) = N_0 \exp(-t) \), which means that the population is destined for extinction. In all cases there is a contribution from both the viability \( v \) and the net growth parameter \( r \) which seems to be a desirable feature in a model describing the evolution of a population whose members have a certain probability of surviving to the next breeding season. The parameter \( v \) can take into account age-dependent death rates when it is between 0 and 1 so that the case \( v = 1 \) and concomitant Malthusian growth does not occur.

### 3.2 Examples

We may use the above results for the diffusion approximation to study the properties of those populations which in the branching process model have a positive probability of ultimate survival. We observe that in the branching process model the number of offspring per individual is restricted to positive integer values.

In populations not bound for certain extinction it is apparent from (17) and (18) that the expectation and variance of \( N(t) \) become infinite as \( t \to \infty \), which is also true for the branching process. It is also clear that there is no value of \( r \in (0, \infty) \) which leads to certain survival if \( 0 \leq v < 1 \). That is, unless the probability of an individual’s survival to the next breeding season is unity, then no matter how great the number of offspring per individual per breeding season, there is always a non-zero chance of ultimate extinction of the population.

Our main interest here is to ascertain quantitative estimates of the effects of the parameters \( v \), the viability, and \( r \), the fecundity, on survival. These estimates will mainly be presented graphically. Recall that \( r_c \) is the critical value of \( r \) defined in (11). We also define the number of offspring \( r_h(v, P_E) \) which gives a probability \( P_E \) of ultimate
extinction when the viability is \( v \). This is given by the expression

\[
{r_h}(v, P_E) = \frac{v^{-1}}{1 + \frac{(1-v) \ln(P_E)}{2N_0}} - 1.
\]  

(21)

Equivalently this gives a probability of ultimate survival

\[
P_S = 1 - P_E.
\]  

(22)

Some algebra shows that apart from a singularity at \( v = 0 \), \( r_h \) has another singularity at

\[
v^* = 1 + \frac{2N_0}{\ln P_E}.
\]  

(23)

The second singularity only occurs at positive values if

\[
P_E < \exp[-2N_0] = P_E^*.
\]  

(24)

so formula (21) is only valid when \( P_E > P_E^* \). The smallest initial population is technically \( N_0 = 1 \) for which the requirement for a non singular \( r_h \) is \( P_E > \exp[-2] \approx 0.1353 \). However, for \( N_0 = 2 \) the value of \( P_E^* \approx 0.0183 \) and for \( N_0 = 3 \) it is \( P_E^* \approx 0.0025 \), so that only in very few cases is there a singularity for positive values of \( v \).

Similarly, another rearrangement of (19) gives the value of the viability \( v_h(r, P_E) \) which gives a probability \( P_E \) of extinction when the fecundity is \( r \),

\[
v_h(r, P_E) = \frac{1}{2\gamma} \left(\gamma - 2N_0 + \sqrt{\left(\gamma - 2N_0\right)^2 + \frac{8\gamma N_0}{1 + r}}\right),
\]  

(25)

where \( \gamma = -\log P_E \).

3.2.1 Graphical results

Figures 1 and 2 show plots of \( r_h \) versus \( v \) for four values of the probability of ultimate survival \( P_S = 0.1, 0.15, 0.5, 0.85 \) and for four values of the initial number of reproducing females \( N_0 = 1, 2, 10, 100 \). Values of \( P_S \) are indicated on each plot, but only the two extreme values of \( N_0 \) are indicated on the plot for \( P_S = 0.85 \). In order to make the pictures clearer, in Figure 1 values of \( v \) are small, being less than 0.15, whereas in Figure 2 they are large with 0.15 \( \leq v \leq 1 \). In all calculations of \( r_h \), only values of \( v \) greater than or equal to 0.01 were considered in order to stay away from the singularity at \( v = 0 \). In Figure 1 are also shown the critical values \( r_c \) (diamonds) from (11) below which value of \( v \) extinction is certain. This curve is almost coincident with the values of \( r_h \) for very large initial population sizes as

\[
\lim_{N_0 \to \infty} r_h = r_c.
\]  

(26)

The most noticeable features of the results shown in Figures 1 and 2 are as follows.
• When the probability of survival is large, increasing the initial population size from $N_0 = 1$ to $N_0 = 2$ results, for a given $v$, in a very large decrease in the required fecundity $r_h$. For example, with $P_S = 0.85$ and $v = 0.1$, increasing $N_0$ from 1 to 2 gives rise to a drop in $r_h$ from about 65 to less than 20. Further increases in $N_0$ do not lead to very large changes in $r_h$.

• The smaller the probability of survival, at a given value of $v$, the smaller the change in required $r_h$ when $N_0$ increases from 1 to 2.

• When the probability of survival is small, for a given $v$, changing the initial population size has very little effect on the required fecundity $r_h$ - see for example the results for $P_S = 0.10$ in Figure 1.

• Regardless of the probability of survival or the initial population size, $r_h$ decreases as $v$ increases in an exponential-like fashion.

![Figure 1](image-url): Showing the number $r_h$ of offspring per individual per breeding season as a function of the survival probability $v$ of individuals for four values of the probability $P_S$ of ultimate survival and for four values of the initial population size $N_0$. In this figure results are restricted to small values of $v \in [0.01, 0.15]$. The diamonds indicate the values of $r_c$ from (11) below which extinction is certain.

It is of interest to examine the dependence of the probability of extinction, $P_E$, on the fecundity for various values of the survival probability $v$ and the initial population
For the population to have any chance of survival $r$ must be greater than the critical value $r_c$ given by (11).

- When $v$ is small $P_E$ is unity until $r$ is large as in the case $v = 0.05$ where $P_E = 1$ until $r = 19$. The rate of decline in $P_E$ for larger $r$ is slowest with an initial population of $N_0 = 1$, becoming faster as $N_0$ increases. By $r = 30$, the values of $P_E$ have fallen to approximately 0.49, 0.22 and 0.11 for initial populations of 1, 2 and 3 respectively.

- When $v$ is large, $P_E$ drops dramatically after $r$ increases beyond the critical value. For example, when $v = 0.5$ the critical value of $r_c = 1$. With $r = 3$ the values of $P_E$ are about 0.14, 0.02 and 0.003 for $N_0 = 1, 2$ and 3 respectively, representing jumps from zero probability of ultimate survival to 86%, 98% and 99.7% by an increase from 1 to three offspring per reproducing female.

Table 1 contains calculated values for $P_E$ for a wide range of values of $v$ with two values of $r$ for each and with 4 values of $N_0$. Only when $v$ is small (0.01 or 0.05) is $P_E$ substantial for any of the given values of $r$ and $N_0$. When $v = 0.95$ the probabilities of extinction are always essentially zero, even when $N_0 = 1$. 

Figure 2: As in the previous figure but that $v \in [0.15, 1.0]$. 

Figure 3 shows $P_E$ versus $r$ for three values of $v = 0.05$, 0.15 and 0.5 (blue, red and black curves respectively) and for three values of $N_0 = 1, 2$ and 3 (solid, dashed and dot-dash curves respectively).
Figure 3: Plots of probability of ultimate extinction versus $r$ for various values of survival probability $v$ and initial population size $N_0$. Blue, red and black curves for values of $v$ which are small (0.05), intermediate (0.15) and large (0.5), respectively. Solid, dashed and dot-dashed curves for initial populations of 1, 2 and 3 respectively.

Table 1: Numerical values for $P_E$=extinction probability

| $v$   | $r_c$ | $r$  | $N_0 = 1$ | $N_0 = 10$ | $N_0 = 100$ | $N_0 = 1000$ |
|-------|-------|------|-----------|------------|-------------|--------------|
| 0.01  | 99    | 100  | 0.9802    | 0.8187     | 0.1353      | 2.1x10-9     |
| 0.01  | 99    | 200  | 0.3624    | 3.9x10-5   | 8.2x10-45   | ≈0           |
| 0.05  | 19    | 20   | 0.9046    | 0.3670     | 4.3x10-5    | 2.9x10-44    |
| 0.05  | 19    | 50   | 0.2781    | 2.8x10-6   | 2.7x10-56   | ≈0           |
| 0.95  | 0.053 | 1    | 5.9x10-9  | 5.2x10-83  | ≈0          | ≈0           |
| 0.95  | 0.053 | 10   | 2.0x10-16 | 8.1x10-158 | ≈0          | ≈0           |
4 Summary and conclusions

We have considered a simple approximate model for population growth in which reproducing females, which must be carefully defined, produce \( r \) offspring, and have a probability \( v \) of surviving to the next breeding season. Using results from branching process theory and that of diffusion processes, the probability of survival is obtained in terms of the parameters \( r \) and \( v \) and the initial population size. Numerical results are presented both graphically and in tabular form. When the probability of ultimate survival of the population is large, small increases in \( N_0 \) change the fecundity required by large amounts whereas when the probability of survival is small, the initial population size is found to have little influence. These calculations have relevance to the survival of colonizing individuals which could be from populations of animals, plants, insects, cells or microorganisms such as bacteria and viruses.

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