

AN ENVIRONMENT-DEPENDENT BRANCHING PROCESS

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Key words: Alternate renewal process; branching process; coefficient of variation; life-time distribution; population size; random environment.

Summary: A mathematical model of a biological population, taking into account the effect of environmental influences both on the life-time distribution and on the reproductive capacity of the individuals of the population, is considered and analyzed. It is assumed that the environment stays in level 0 and in level 1 alternately for random lengths of time. The sojourn-times of the environment in the levels 0 and 1 form an alternating renewal process and the probability density function (p.d.f.) of the stay-in times of the environment in level i is $\alpha_i e^{-\alpha_i t}$, $i = 0, 1$. Further, assuming that the p.d.f. of the life-time of an individual of the population when the population is in level i , $i = 0, 1$, is $\lambda_i e^{-\lambda_i t}$, an explicit expression for the time-dependent mean size of the population is obtained. The particular case corresponding to the environment independent population is deduced and two other particular cases, corresponding to partial interaction of the environment, are analysed. The coefficient of variation of the population size is also obtained and a numerical illustration is provided to highlight the impact of environment on the population size.

1. Introduction

Branching processes in random environment have been studied very extensively in the past from the theoretical point of view by several researchers (see Harris (1963), Athereya and Ney (1972) and Assmussen and Herin (1983)). The influence of the environment on the life-cycle of the individuals of the population from the point of view of their reproductive nature and the consequent fluctuations in the size of the population have been studied by taking up several experimental case studies with some species (see Andrewartha and Birch (1954), Andrewartha (1961), Silvertown (1987) and Krebs (2002)). Seasonality is quite often the dominant feature of environmental variability experienced by several biological populations due to which the population size and other demographic parameters fluctuate randomly over time. All field studies on the effect of environmental influences such as temperature and rainfall have resulted in the formulation of mathematical models aimed to explain some of the pertinent attributes such as the mean and coefficient of variation of the population density (see Nicholson (1954), Clark et al. (1967)). It has been observed by several researchers in their field studies that a population progressively decreases during some fluctuating conditions which are definitely unfavourable at times, but at the intermittent favourable periods the population tends to adjust itself to the prevailing conditions (see for example Nicholson (1954)). Recently, Saether et al. (2006) have made elaborate comparative studies on the population dynamics of birds and examined whether stochastic fluctuations in the environment (climate and spatio-temporal variation in the wintering areas) can affect annual variation in population change in two different ways (*tap* hypothesis and *tube* hypothesis) by theta-logistic models. In particular, they have made extensive field studies

on the dynamics of different European populations of white stork *Ciconia ciconia* and analysed whether annual changes in population was related to the climate during the breeding period or during the nonbreeding period. Their study has not accounted for the stochastic variation in the life-time of individuals of the population. Although the evidence of fluctuations in the life pattern and in the reproductive capacity of a population has been observed separately in various field studies, not much work has been directed towards building comprehensive models which incorporate environmental influences, not only on the reproductive capacity but also on the life-time distributions. Accordingly, the object of the present paper is to propose and analyse a mathematical model of a biological population taking into account the effect of environmental influences, both on the life-time distribution and on the reproductive capacity of the individuals of the population.

The organization of the paper is as follows: In section 2, a branching process model is described. Section 3 provides the derivation of explicit expressions for the time-dependent mean size of the population. The particular case corresponding to an environment independent population, is deduced in section 4. Two other particular cases corresponding to partial interaction of the environment, are discussed in sections 5 and 6. In section 7, the coefficient of variation of the population size is obtained. A numerical illustration is provided in section 8 to highlight the impact of environment on the population size.

2. The model description

We consider a stochastic population which evolves in a random environment. We assume that the environment stays in level 0 and in level 1 alternately for random lengths of time. Let $X(t)$ be the number of individuals in the population and let $E(t)$ be the level of the environment at any time t . For

simplicity, we let there be just a single new-born individual in the population at time $t = 0$ so that $X(0) = 1$. We assume that the environment has just entered into level 0 at time $t = 0$ so that

$$1 = \lim_{\Delta \rightarrow 0} E(-\Delta) \neq 0 = E(0) = \lim_{\Delta \rightarrow 0} E(\Delta).$$

The sojourn-times of the environment in the levels 0 and 1 form an alternating renewal process and we assume that the probability density function (p.d.f.) of the stay-in times of the environment in level i is $\alpha_i e^{-\alpha_i t}$, $i = 0, 1$. Let $\lambda_i e^{-\lambda_i t}$ be the p.d.f. of the life-time of an individual of the population when the population in level i , $i = 0, 1$. Let $f_{ij}(t)dt$ be the conditional probability that a particle which was born at time $t = 0$ while the environment was in level i has lived up to time t and branches in $(t, t + dt)$ and the environment is in level j at the time of branching. That is,

$$f_{ij}(t) = \lim_{\Delta \rightarrow 0} \Pr\{X(u) = 1 \text{ for all } u \in [0, t], \\ X(t + \Delta) \neq 1, E(t) = j | X(0) = 1, E(0) = i\} / \Delta, i, j = 0, 1.$$

Then, we have

$$f_{00}(t) = e^{-(\alpha_0 + \lambda_0)t} \lambda_0 + \alpha_0 \int_0^t e^{-(\alpha_0 + \lambda_0)u} f_{10}(t - u) du, \quad (2.1)$$

$$f_{01}(t) = \alpha_0 \int_0^t e^{-(\alpha_0 + \lambda_0)u} f_{11}(t - u) du, \quad (2.2)$$

$$f_{10}(t) = \alpha_1 \int_0^t e^{-(\alpha_1 + \lambda_1)u} f_{00}(t - u) du, \quad (2.3)$$

$$f_{11}(t) = e^{-(\alpha_1 + \lambda_1)t} \lambda_1 + \alpha_1 \int_0^t e^{-(\alpha_1 + \lambda_1)u} f_{01}(t - u) du. \quad (2.4)$$

Using the Laplace transform technique, the equations from (2.1) to (2.4) can be solved and we obtain

$$f_{00}(t) = \frac{\lambda_0}{(a - b)} \{(a + \alpha_1 + \lambda_1)e^{at} - (b + \alpha_1 + \lambda_1)e^{bt}\}, \quad (2.5)$$

$$f_{01}(t) = \frac{\lambda_1 \alpha_0}{(a-b)} \{e^{at} - e^{bt}\}, \quad (2.6)$$

$$f_{10}(t) = \frac{\lambda_0 \alpha_1}{(a-b)} \{e^{at} - e^{bt}\}, \quad (2.7)$$

$$f_{11}(t) = \frac{\lambda_1}{(a-b)} \{(a + \alpha_0 + \lambda_0)e^{at} - (b + \alpha_0 + \lambda_0)e^{bt}\}, \quad (2.8)$$

where a and b are the roots of the equation

$$(s + \alpha_0 + \lambda_0)(s + \alpha_1 + \lambda_1) - \alpha_0 \alpha_1 = 0. \quad (2.9)$$

The discriminant of the equation (2.9) is a positive quantity and hence a and b are real and distinct and are given by

$$a = \frac{-(\alpha_0 + \alpha_1 + \lambda_0 + \lambda_1) + \sqrt{\{(\alpha_0 + \lambda_0) - (\alpha_1 + \lambda_1)\}^2 + 4\alpha_0 \alpha_1}}{2},$$

$$b = \frac{-(\alpha_0 + \alpha_1 + \lambda_0 + \lambda_1) - \sqrt{\{(\alpha_0 + \lambda_0) - (\alpha_1 + \lambda_1)\}^2 + 4\alpha_0 \alpha_1}}{2}.$$

We assume that the offspring generating function of an individual, while splitting when the environment is in level i , is $h_i(\xi)$, $i = 0, 1$. To describe the branching process, we define the following generating functions:

$$G_i(\theta, t) = E\{\theta^{X(t)} | X(0) = 1, E(0) = i\}, i = 0, 1.$$

Using the regeneration point technique, we obtain

$$G_0(\theta, t) = \theta \left[1 - \int_0^t \{f_{00}(u) + f_{01}(u)\} \mathbf{d}u \right]$$

$$+ \int_0^t f_{00}(u) h_0(G_0(\theta, t-u)) \mathbf{d}u + \int_0^t f_{01}(u) h_1(G_1(\theta, t-u)) \mathbf{d}u, \quad (2.10)$$

$$G_1(\theta, t) = \theta \left[1 - \int_0^t \{f_{10}(u) + f_{11}(u)\} \mathbf{d}u \right]$$

$$+ \int_0^t f_{10}(u) h_0(G_0(\theta, t-u)) \mathbf{d}u + \int_0^t f_{11}(u) h_1(G_1(\theta, t-u)) \mathbf{d}u. \quad (2.11)$$

The equations (2.10) and (2.11) are intractable even in the simple case of binary splitting. However, from the equations (2.10) and (2.11), we can derive the

mean number of individuals in the population at any time t . We achieve this in the next section.

3. The population mean

Let $\xi_i, i = 0, 1$ be the event that the environment has just entered into the level i at time $t = 0$ and the population has just one newly born individual at time $t = 0$. We define the conditional means

$$M_i(t) = E\{X(t)|\xi_i\}, i = 0, 1.$$

Differentiating the equations (2.22) and (2.23) with respect to θ and putting $\theta = 1$, we obtain

$$M_0(t) = \left[1 - \int_0^t \{f_{00}(u) + f_{01}(u)\} du \right] + m_0 \int_0^t f_{00}(u) M_0(t-u) du + m_0 \int_0^t f_{01}(u) M_1(t-u) du, \quad (3.1)$$

$$M_1(t) = \left[1 - \int_0^t \{f_{10}(u) + f_{11}(u)\} du \right] + m_0 \int_0^t f_{10}(u) M_0(t-u) du + m_0 \int_0^t f_{11}(u) M_1(t-u) du, \quad (3.2)$$

where $m_i = h_i'(1), i = 0, 1$. The equations (3.1) and (3.2) can be solved explicitly by the Laplace transform technique and we obtain the population means

$$M_0(t) = \frac{1}{\tilde{a} - \tilde{b}} \left[(\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1) e^{\tilde{a}t} - (\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1) e^{\tilde{b}t} \right], \quad (3.3)$$

$$M_1(t) = \frac{1}{\tilde{a} - \tilde{b}} \left[(\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0) e^{\tilde{a}t} - (\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0) e^{\tilde{b}t} \right], \quad (3.4)$$

where \tilde{a} and \tilde{b} are the roots of the equation

$$\{s + \alpha_0 + \lambda_0(1 - m_0)\} \{s + \alpha_1 + \lambda_1(1 - m_1)\} - \alpha_0 \alpha_1 = 0. \quad (3.5)$$

Clearly \tilde{a} and \tilde{b} are real and distinct. In fact $\tilde{a} > \tilde{b}$. If we choose m_0 and m_1 such that

$$\frac{\tilde{b}(\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1)}{\tilde{a}(\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1)} > 1,$$

then $M_0(t)$ has a unique turning point at time t^{0*} given by

$$t^{0*} = \frac{1}{\tilde{a} - \tilde{b}} \log \left\{ \frac{\tilde{b}(\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1)}{\tilde{a}(\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1)} \right\}. \quad (3.6)$$

On the other hand, if we choose m_0 and m_1 such that

$$\frac{\tilde{b}(\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0)}{\tilde{a}(\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0)} > 1,$$

then $M_1(t)$ has a unique turning point at time t^{1*} given by

$$t^{1*} = \frac{1}{\tilde{a} - \tilde{b}} \log \left\{ \frac{\tilde{b}(\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0)}{\tilde{a}(\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0)} \right\}. \quad (3.7)$$

The expressions (3.3) and (3.4) are quite new and in the following sections we recover the classical results pertaining to the simple Markov branching process.

4. The particular case $\lambda_0 = \lambda_1 = \lambda$ and

$$m_0 = m_1 = m$$

This corresponds to the situation where the environment has no influence on the life-time and reproductive capacity of the individuals of the population. In other words, we have the situation that the individuals never change their life-time and their reproductive capacity irrespective of the changes in the environmental surroundings. In this case, the equation (3.5) becomes

$$\{s + \alpha_0 + \lambda(1 - m)\}\{s + \alpha_1 + \lambda(1 - m)\} - \alpha_0\alpha_1 = 0.$$

Consequently, we have

$$a = -\lambda, b = -(\alpha_0 + \alpha_1 + \lambda),$$

$$\tilde{a} = -\lambda(1 - m),$$

$$\begin{aligned}\tilde{b} &= -\{\alpha_0 + \alpha_1 + \lambda(1 - m)\}, \\ \tilde{\lambda}_0 &= \tilde{\lambda}_1 = \lambda(1 - m).\end{aligned}$$

Consequently, from the equations (3.3) and (3.4), we deduce the classical result

$$\begin{aligned}M_0(t) &= e^{\lambda(m-1)t}, \\ M_1(t) &= e^{\lambda(m-1)t}.\end{aligned}$$

5. The particular case $\alpha_0 = 0$

This corresponds to the situation where the environment, once enters into level 0, remains in level 0 for ever and never changes its level from 0 thereafter. In this case, we obtain

$$\tilde{a} = -\alpha_1 - \tilde{\lambda}_1, \tilde{b} = -\tilde{\lambda}_0.$$

Consequently, from the equations (3.3) and (3.4), we deduce the classical results

$$\begin{aligned}M_0(t) &= e^{-\tilde{\lambda}_0 t}, \\ M_1(t) &= \frac{(\tilde{\lambda}_0 - \tilde{\lambda}_1)e^{(-\tilde{\lambda}_1 - \alpha_1)t} - \alpha_1 e^{-\tilde{\lambda}_0 t}}{\tilde{\lambda}_0 - \tilde{\lambda}_1 - \alpha_1}.\end{aligned}$$

6. The particular case $\alpha_1 = 0$

This corresponds to the situation where the environment, once enters into level 1, remains in level 1 for ever and never changes its level from 1 thereafter. In this case, we obtain

$$\tilde{a} = -\tilde{\lambda}_1, \tilde{b} = -\alpha_0 - \tilde{\lambda}_0.$$

Consequently, from the equations (3.3) and (3.4), we deduce the classical results

$$M_0(t) = \frac{\alpha_0 e^{-\tilde{\lambda}_1 t} - (\tilde{\lambda}_1 - \tilde{\lambda}_0)e^{(-\tilde{\lambda}_0 - \alpha_0)t}}{\tilde{\lambda}_0 - \tilde{\lambda}_1 + \alpha_0}, \quad M_1(t) = e^{-\tilde{\lambda}_1 t}.$$

In addition to the population mean, we require the variance of the population to give a complete picture of how the stochastic changes are dispersed in the

dynamics of the population. Accordingly, we proceed to obtain the coefficient of variation in the next section.

7. The coefficient of variation

We define the second factorial moment

$$D_i(t) = E[X(t)\{X(t) - 1\} | X(0) = 1, E(0) = i], i = 0, 1.$$

From the equations (2.10) and (2.11), we obtain

$$\begin{aligned} D_0(t) &= \int_0^t f_{00}(u) \left\{ h'_0(1)D_0(t-u) + h''_0(1)M_0^2(t-u) \right\} du \\ &\quad + \int_0^t f_{01}(u) \left\{ h'_1(1)D_1(t-u) + h''_1(1)M_1^2(t-u) \right\} du, \end{aligned} \quad (7.1)$$

$$\begin{aligned} D_1(t) &= \int_0^t f_{10}(u) \left\{ h'_0(1)D_0(t-u) + h''_0(1)M_0^2(t-u) \right\} du \\ &\quad + \int_0^t f_{11}(u) \left\{ h'_1(1)D_1(t-u) + h''_1(1)M_1^2(t-u) \right\} du. \end{aligned} \quad (7.2)$$

Substituting for $M_0(t-u)$ and $M_1(t-u)$ from (3.3) and (3.4), the equations (7.1) and (7.2) become

$$\begin{aligned} D_0(t) &= \int_0^t f_{00}(u) \left\{ h'_0(1)D_0(t-u) + h''_0(1) \left(\beta_0 e^{\tilde{a}(t-u)} - \gamma_0 e^{\tilde{b}(t-u)} \right)^2 \right\} du \\ &\quad + \int_0^t f_{01}(u) \left\{ h'_1(1)D_1(t-u) + h''_1(1) \left(\beta_1 e^{\tilde{a}(t-u)} - \gamma_1 e^{\tilde{b}(t-u)} \right)^2 \right\} du, \end{aligned} \quad (7.3)$$

$$\begin{aligned} D_1(t) &= \int_0^t f_{10}(u) \left\{ h'_0(1)D_0(t-u) + h''_0(1) \left(\beta_0 e^{\tilde{a}(t-u)} - \gamma_0 e^{\tilde{b}(t-u)} \right)^2 \right\} du \\ &\quad + \int_0^t f_{11}(u) \left\{ h'_1(1)D_1(t-u) + h''_1(1) \left(\beta_1 e^{\tilde{a}(t-u)} - \gamma_1 e^{\tilde{b}(t-u)} \right)^2 \right\} du, \end{aligned} \quad (7.4)$$

where

$$\beta_0 = \frac{\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1}{\tilde{a} - \tilde{b}}, \gamma_0 = \frac{\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_1}{\tilde{a} - \tilde{b}},$$

$$\beta_1 = \frac{\tilde{a} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0}{\tilde{a} - \tilde{b}}, \gamma_1 = \frac{\tilde{b} + \alpha_0 + \alpha_1 + \tilde{\lambda}_0}{\tilde{a} - \tilde{b}}.$$

Using the Laplace transform technique, the equations (7.3) and (7.4) can be solved explicitly and we obtain

$$\begin{aligned} D_0(t) &= d_{01}e^{\tilde{a}t} + d_{02}e^{\tilde{b}t} + d_{03}e^{2\tilde{a}t} + d_{04}e^{2\tilde{b}t} + d_{05}e^{(\tilde{a}+\tilde{b})t}, \\ D_1(t) &= d_{11}e^{\tilde{a}t} + d_{12}e^{\tilde{b}t} + d_{13}e^{2\tilde{a}t} + d_{14}e^{2\tilde{b}t} + d_{15}e^{(\tilde{a}+\tilde{b})t}, \end{aligned}$$

where

$$\begin{aligned} d_{01} &= \frac{\lambda_0 h_0''(1)(\tilde{a} + \alpha_1 + \tilde{\lambda}_1)\{2\delta_1(\tilde{a} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)\alpha_0\{2\delta_0(\tilde{a} + \delta_0) + \tilde{a}\tilde{b}\}}{\tilde{a}\tilde{b}(\tilde{a} - \tilde{b})(\tilde{a} - 2\tilde{b})}, \\ d_{02} &= \frac{\lambda_0 h_0''(1)(\tilde{b} + \alpha_1 + \tilde{\lambda}_1)\{2\delta_1(\tilde{b} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)\alpha_0\{2\delta_0(\tilde{b} + \delta_0) + \tilde{a}\tilde{b}\}}{\tilde{a}\tilde{b}(\tilde{a} - \tilde{b})(2\tilde{a} - \tilde{b})}, \\ d_{03} &= \frac{\lambda_0 h_0''(1)(2\tilde{a} + \alpha_1 + \tilde{\lambda}_1) + \lambda_1 h_1''(1)\alpha_0}{2(\tilde{a} - \tilde{b})^2} \\ &+ \frac{\lambda_0 h_0''(1)(2\tilde{a} + \alpha_1 + \tilde{\lambda}_1)\{2\delta_1(2\tilde{a} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)\alpha_0\{2\delta_0(2\tilde{a} + \delta_0) + \tilde{a}\tilde{b}\}}{2\tilde{a}(2\tilde{a} - \tilde{b})(\tilde{a} - \tilde{b})^2}, \\ d_{04} &= \frac{\lambda_0 h_0''(1)(2\tilde{b} + \alpha_1 + \tilde{\lambda}_1) + \lambda_1 h_1''(1)\alpha_0}{2(\tilde{a} - \tilde{b})^2} \\ &- \frac{\lambda_0 h_0''(1)(2\tilde{b} + \alpha_1 + \tilde{\lambda}_1)\{2\delta_1(2\tilde{b} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)\alpha_0\{2\delta_0(2\tilde{b} + \delta_0) + \tilde{a}\tilde{b}\}}{2\tilde{b}(\tilde{a} - 2\tilde{b})(\tilde{a} - \tilde{b})^2}, \\ d_{05} &= -\frac{\lambda_0 h_0''(1)(\tilde{a} + \tilde{b} + \alpha_1 + \tilde{\lambda}_1) + \lambda_1 h_1''(1)\alpha_0}{(\tilde{a} - \tilde{b})^2} \\ &- \frac{\lambda_0 h_0''(1)(\tilde{a} + \tilde{b} + \alpha_1 + \tilde{\lambda}_1)\{2\delta_1(\tilde{a} + \tilde{b} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)\alpha_0\{2\delta_0(\tilde{a} + \tilde{b} + \delta_0) + \tilde{a}\tilde{b}\}}{\tilde{a}\tilde{b}(\tilde{a} - \tilde{b})^2}, \\ d_{11} &= \frac{\lambda_0 \alpha_1 h_0''(1)\{2\delta_1(\tilde{a} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)(\tilde{a} + \alpha_0 + \tilde{\lambda}_0)\{2\delta_0(\tilde{a} + \delta_0) + \tilde{a}\tilde{b}\}}{\tilde{a}\tilde{b}(\tilde{a} - \tilde{b})(\tilde{a} - 2\tilde{b})}, \\ d_{12} &= \frac{\lambda_0 \alpha_1 h_0''(1)\{2\delta_1(\tilde{b} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)(\tilde{b} + \alpha_0 + \tilde{\lambda}_0)\{2\delta_0(\tilde{b} + \delta_0) + \tilde{a}\tilde{b}\}}{\tilde{a}\tilde{b}(\tilde{a} - \tilde{b})(2\tilde{a} - \tilde{b})}, \\ d_{13} &= \frac{\lambda_0 \alpha_1 h_0''(1) + \lambda_1 h_1''(1)(2\tilde{a} + \alpha_0 + \tilde{\lambda}_0)}{2(\tilde{a} - \tilde{b})^2} \\ &+ \frac{\lambda_0 \alpha_1 h_0''(1)\{2\delta_1(2\tilde{a} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)(2\tilde{a} + \alpha_0 + \tilde{\lambda}_0)\{2\delta_0(2\tilde{a} + \delta_0) + \tilde{a}\tilde{b}\}}{2\tilde{a}(2\tilde{a} - \tilde{b})(\tilde{a} - \tilde{b})^2}, \end{aligned}$$

$$d_{14} = \frac{\lambda_0 \alpha_1 h_0''(1) + \lambda_1 h_1''(1)(2\tilde{b} + \alpha_0 + \tilde{\lambda}_0)}{2(\tilde{a} - \tilde{b})^2}$$

$$- \frac{\lambda_0 \alpha_1 h_0''(1)\{2\delta_1(2\tilde{b} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)(2\tilde{b} + \alpha_0 + \tilde{\lambda}_0)\{2\delta_0(2\tilde{b} + \delta_0) + \tilde{a}\tilde{b}\}}{2\tilde{b}(\tilde{a} - 2\tilde{b})(\tilde{a} - \tilde{b})^2},$$

$$d_{15} = -\frac{\lambda_0 \alpha_1 h_0''(1) + \lambda_1 h_1''(1)(\tilde{a} + \tilde{b} + \alpha_0 + \tilde{\lambda}_0)}{(\tilde{a} - \tilde{b})^2}$$

$$- \frac{\lambda_0 \alpha_1 h_0''(1)\{2\delta_1(\tilde{a} + \tilde{b} + \delta_1) + \tilde{a}\tilde{b}\} + \lambda_1 h_1''(1)(\tilde{a} + \tilde{b} + \alpha_0 + \tilde{\lambda}_0)\{2\delta_0(\tilde{a} + \tilde{b} + \delta_0) + \tilde{a}\tilde{b}\}}{\tilde{a}\tilde{b}(\tilde{a} - \tilde{b})^2}.$$

Now, the variance of $X_i(t)$ is given by

$$V_i(t) = D_i(t) + M_i(t) - \{M_i(t)\}^2, i = 0, 1.$$

Then,

$$V_0(t) = (d_{01} + \beta_0)e^{\tilde{a}t} + (d_{02} - \gamma_0)e^{\tilde{b}t} + (d_{03} - \beta_0^2)e^{2\tilde{a}t} + (d_{04} - \gamma_0^2)e^{2\tilde{b}t}$$

$$+ (d_{05} + 2\beta_0\gamma_0)e^{(\tilde{a} + \tilde{b})t},$$

$$V_1(t) = (d_{11} + \beta_1)e^{\tilde{a}t} + (d_{12} - \gamma_1)e^{\tilde{b}t} + (d_{13} - \beta_1^2)e^{2\tilde{a}t} + (d_{14} - \gamma_1^2)e^{2\tilde{b}t}$$

$$+ (d_{15} + 2\beta_1\gamma_1)e^{(\tilde{a} + \tilde{b})t}$$

and the coefficient of variation of $X_i(t)$ is given by

$$CV_i(t) = \frac{\sqrt{V_i(t)}}{M_i(t)}, i = 0, 1.$$

Let us consider the particular case,

$$\lambda_0 = \lambda_1 = \lambda, h_0'(1) = h_1'(1) = m, h_0''(1) = h_1''(1) = K.$$

Then, we obtain

$$D_0(t) = D_1(t) = \frac{K}{1-m} (e^{-\lambda t} - e^{-2\lambda t}).$$

and consequently, we recover the classical result for the variance of $X(t)$

$$V_0(t) = V_1(t) = \left(\frac{1 - h'(1) + h''(1)}{h'(1) - 1} \right) (e^{2\lambda(m-1)t} - e^{\lambda(m-1)t}).$$

8. A numerical illustration

We provide below a numerical illustration to highlight the environmental impact on the population size. For the purpose of illustration, we fix the values of the parameters as follows:

$$\alpha_0 = 1.0, \alpha_1 = 2.0, \lambda_0 = 0.1, \lambda_1 = 0.4.$$

We consider two illustrations. First, we consider the case of binary splitting in both the levels of the environment. Specifically, we assume

$$h_0(s) = 0.55 + 0.45s^2, h_1(s) = 0.4 + 0.6s^2.$$

By varying the time t , we have computed the conditional means $M_i(t)$, $i = 0, 1$ and the conditional coefficient of variation $CV_i(t)$, $i = 0, 1$. The results are tabulated in table 3.1.

Table 1

$$h_0'(1) = h_0''(1) = 0.9, h_1'(1) = h_1''(1) = 1.2$$

t	$M_0(t)$	$M_1(t)$	$CV_0(t)$	$CV_1(t)$
0.131	0.99937284	1.00916564	0.12410917	1.41242194
0.132	0.99937266	1.00922668	0.12464499	1.41216385
0.133	0.99937260	1.00928760	0.12517934	1.41190660
0.134	0.99937254	1.00934851	0.12571226	1.41165030
0.135	0.99937254	1.00940919	0.12624376	1.41139495
0.136	0.99937260	1.00946987	0.12677385	1.41114044
0.137	0.99937272	1.00953043	0.12730254	1.41088688
0.138	0.99937296	1.00959074	0.12782985	1.41063440
0.139	0.99937320	1.00965106	0.12835582	1.41038275
0.140	0.99937350	1.00971115	0.12888043	1.41013217

From the above table, we find that $M_0(t)$ decreases initially and then increases exhibiting a concave shape having a turning point at $t^*t_0 = 0.135$. The mean $M_1(t)$ exhibits a strictly increasing behaviour having no stationary point on the

time axis. We also find that the coefficient of variation $CV_0(t)$ strictly increases and the coefficient variation $CV_1(t)$ strictly decreases.

Next, we consider another illustration where we assume

$$h_0(s) = 0.4 + 0.6s^4, h_1(s) = 0.75 + 0.25s^2.$$

By varying the time t , we have computed the conditional means $M_i(t)$, $i = 0, 1$ and the conditional coefficient of variations $CV_i(t)$, $i = 0, 1$. The results are tabulated in table 3.2.

Table 2

$$h_0'(1) = 2.4, h_0''(1) = 7.2, h_1'(1) = h_1''(1) = 0.5$$

t	$M_0(t)$	$M_1(t)$	$CV_0(t)$	$CV_1(t)$
0.57	1.04859245	0.95639008	0.55577224	3.11609507
0.58	1.04913568	0.95632750	0.56045681	3.11550903
0.59	1.04967391	0.95627695	0.56509966	3.11495233
0.60	1.05020690	0.95623815	0.56970197	3.11442399
0.61	1.05073512	0.95621061	0.57426476	3.11392355
0.62	1.05125856	0.95619416	0.57878900	3.11344957
0.63	1.05177736	0.95618832	0.58327562	3.11300206
0.64	1.05229175	0.95619285	0.58772558	3.11258006
0.65	1.05280185	0.95620739	0.59213978	3.11218262
0.66	1.05330777	0.95623171	0.59651893	3.11180902
0.67	1.05380964	0.95626545	0.60086399	3.11145902

From table 2, we find that $M_0(t)$ strictly increases for the whole time while the mean $M_1(t)$ decreases initially and then increases thus exhibiting a concave shape having a turning point at $t^*_1 = 0.63$. As in illustration 1, we also find here that the coefficient of variation $CV_0(t)$ strictly increases and the coefficient of variation $CV_1(t)$ strictly decreases.

Acknowledgements

V.S.S. Yadavalli is thankful to NRF for their financial support.

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