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From Regeneration to Escape the Extinction in Population Experiments [1]

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The main idea of the branching stochastic models with immigration for modeling population and re-population and wastewater experiments originates from the problem of estimating the waiting time to the successful experiment in a series of population and re-population experiments with different species, which have disappeared for some reason. It is worth mention here that by "waiting time to a successful experiment" we mean the time before the beginning of that newly introduced population which survives in this environment. Previous works, exploring Bienaymé-Galton-Watson and Bellman-Harris branching processes, are generalized in this paper for Sevast'yanov's age-dependent processes. To estimate the probability density functions of the life cycle and the waiting time to the successful experiment, a software was developed that allows input of a mortality density and a special form of reproduction law.

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1. Introduction

Strongly motivated by the need of models to accurately design, study and predict the development of biological populations, concerning a variety of problems arising, for example in population and re-population experiments, wastewater treatment, evolution of resistance to antibiotics, etc., we focus our efforts to the age-dependent branching models with immigration as a suitable tool in doing such analysis. Specifically, one of the problems of applied ecology is what

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to do, when to do it, and how to assess and improve the actions taken, when particular species disappear. These are, for example population and re-population experiments with trout, birds, and other species [1], or wastewater treatment experiments [14]. In the context of this general concern we propose a technique, motivated by the above mentioned diversity of problems which can be modeled with Sevast'yanov's age-dependent branching processes allowing immigration. Another important motivation for this work is the challenge of natural incorporation of some biological characteristics into a model and their proper interpretation, when applied in biology, ecology, environmental studies, decision making, etc. In this work the stress is on the improvement of the approach applied in [1] and [14] towards the incorporation of the dependence of the particle reproduction on the particle's age. Sevast'yanov's model describes better real life cases (see [13]).

The problem of inference from expected waiting times and expected progeny on fertility rates was proposed for the first time in the context of population and re-population experiments with different types of species in [1]. The classical Bienaymé-Galton-Watson branching process (BGWBP) with immigration in zero state was used as a model describing the population development and exact answers were obtained when all newly introduced populations behave like independent identically distributed (i.i.d.) BGWBP. In [14] similar results were generalized for the distribution of the life-cycle, waiting time to a successful experiment and the estimated total progeny, all conditioned on ultimate extinction, using the so called age-dependent branching model or Bellman-Harris branching process (BHBP) with immigration in zero. In this case the process is called "age-dependent" in sense that the probability for an individual living at time t to die in the interval $(t, t + dt)$ is, in general, a non-constant function of t, but the reproduction is still one and the same random variable, which distribution does not depend on the particle's age. The motivation of paper [14] has arisen in the context of wastewater treatment by bacterial cultures. As it was found in [12] the lifespan of bacteria-like organisms follows a gamma distribution, and reproduction at death is characteristic of bacteria-like organisms, so age-dependent processes can be used as more adequate mathematical models for such real phenomena.

In the discrete-time case the theoretical and simulation results for the life-cycle distribution and the similar characteristics, which appear naturally in the context of bisexual BGWBP, were obtained in [4]. It should be emphasized that all sample paths of the resurrection model are positive.

We would like to point out that in the disctere-time case, the problem concerning the total progeny was investigated in [6], [7]. However, the main interest is focused on the questions of rates of growth, and this conditioned on survival. Some authors, see for example [8], studied the asymptotic behavior of the probabilities of hitting the absorbing states, the times needed to hit these states, and the conditional distributions of the number of particles (for models allowing catastrophes).

On the other hand, however, it is important to pay consideration here to another aspect in the theory of Markov branching processes with instantaneous immigration (MBPII) or resurrection, considered in pertinent literature. In [11] it is shown that a realistic model can be constructed, if the state-space is restricted to the natural numbers. The problem of constructing a version of the MBPI which allows instantaneous resurrection from zero have been tackled in [2]. The authors promote their models as realistic descriptions of situations where populations are quickly restored from extinction, by reintroduction, or rapid migration, as in island biogeography.

The last advancements towards modeling of biological phenomena by branching processes have been recently published in the monograph [5] with lots of real world examples and problems.

The main goal of the present paper is to generalize the results for the life-cycle length and total waiting time for the Sevast'yanov's age-dependent branching model, where not only cell generation times differ between particles, but the offspring distribution may depend on the age of each particle. Such processes in general are non-Markovian. However, the analogous results remain valid in that case, and, we are aware that this is still a simplification of a real world problem but an explicit solution (see Section 3) can be given in terms of Laplace-Stieltjes transforms and generating functions.

2. Model formulation.

Consider a population branching process $(Z_t : t \geq 0)$ having as state-space the non-negative integers with zero as an absorbing state. Let $Z_0 = 1$, and $T = \inf\{t : Z_t = 0\} \leq \infty$. Next, let $\{(Z_t(n)) : n = 1, 2, \ldots\}$ be independent identically distributed (i.i.d.) copies of Z_t with $Z_0(n) = 1$. Let $T_0 = H_0 = 0$ and for all $n \geq 1$ let $T_n = \inf\{t : Z_t(n) = 0\}$ and $H_n = \sum_{0 \leq j \leq n} T_j, (n \geq 1)$. Note that $\{T_n\}$ are i.i.d. random variables. Thus H_n is the time of the $n-$th extinction event, provided it is finite, and the convention $H_0 = 0$ implies the entire process begins with an extinction at $t = 0^-$. Hence $N = \sup\{n : T_n = \infty\}$ is the number of the index of the first infinite cycle. In addition, let us suppose that $(Z_t : t \geq 0)$ is Sevast'yanov's age-dependent branching process, starting at time 0 with a single progenitor of age 0, whose life-length τ has distribution $G(t) = P(\tau \leq t)$, $G(0^+) = 0$. With probability $h_t(k)$, $t > 0$, $k \geq 0$ it produces at the end of its life k similar individuals of age 0, with the same life-length distribution as that of τ and reproduction distribution $\{h_t(k)\}$, where $h_t(k) = P(\xi = k|\tau = t)$, $\sum_{k=0}^{\infty} h_t(k) = 1$, for every $t > 0$. Let us denote the probability generating function (p.g.f.) of the number of offspring ξ generated at age t by

$$h(t; s) = \sum_{k=0}^{\infty} h_t(k)s^k, \quad |s| \leq 1.$$

Then, the process we are interested in is

$$\widetilde{Z}_t = Z_{t-H_{n-1}}(n) \quad \text{if} \quad H_{n-1} \leq t < H_n \quad (n = 1, \ldots, N).$$

The discrete version, i.e. BGWBP with immigration in zero state was first studied (in the critical case) in the papers [3], [9], [10] .

Life cycles

For the branching process $(\widetilde{Z}_t)_{t\geq 0}$ we shall call life cycles the intervals (H_{n-1}, H_n), $n = 1, 2, \ldots, N-1$. Thus $(\widetilde{Z}_t)$ may have several life cycles, the last one always being infinite, provided the process is super-critical. If the process is sub-critical it will have a.s. infinitely many life cycles.

Lifetime of the process $(\widetilde{Z}_t)_{t\geq 0}$ before escaping from extinction.

Lifetime of the process $(\widetilde{Z}_t)_{t\geq 0}$ before escaping from extinction will be defined as $L = H_{n-1}$, i.e. the "birth time" of the first infinite life cycle. We shall also study the expectation of the lifetime L. Finally, we shall analyze the total progeny during the lifetime of the process $(\widetilde{Z}_t)_{t\geq 0}$ and shall obtain its expectation and variance.

Criticality and extinction

Let $q = \lim_{t\to\infty} P_0(t)$, where $P_0(t) = P(Z_t = 0)$. It is known that q is the smallest root of the equation

$$\int_0^{\infty} h(t; s)dG(t) = s$$

(see e.g. [3]).

Then the criticality parameter of the process Z_t turns out to be

$$m = \int_0^\infty m(t) dG(t),$$

where $m(t) = h'_s(t; 1)$ and $q = 1$ iff $m \leq 1$. The parameter m is called the reproduction mean, and the super-critical, critical and sub-critical cases correspond to the relations $m > 1$, $m = 1$ and $m < 1$, respectively. So, if $Z_0 = 1$ we have $P\{L = 0\} = P\{\text{first process does not die out}\} = 1 - q$.

3. Results

Suppose $q = P(T < \infty) < 1$, so that $\tau(\theta) = E(e^{-\theta T})$ satisfies $\tau(0) = q$. Thus $L = 0$ if the initial population is immortal, i.e. $T_1 = \infty$.

Let

$$F(t) = P(T \leq t) = \int_0^t h(u; F(t-u)) dG(u). \tag{1}$$

Proposition *The Laplace-Stieltjes transform* $\lambda(\theta) := E(e^{-\theta L})$, *is:*

$$\lambda(\theta) := \frac{1-q}{1-\tau(\theta)}.$$

Proof. It follows by

$$\lambda(\theta) := E(e^{-\theta L}) = \sum_{n \geq 0} E(e^{-\theta H_n}; T_{n+1} = \infty) = (1-q) \sum_{n \geq 0} \tau^n(\theta) = \frac{1-q}{1-\tau(\theta)}.$$

■

The total progeny of a life cycle.

First, we are interested in the total progeny V of a life cycle and its expectation, in order to make some inferences on the fertility rates of the particles. So, let $g(t; s) = E(s^V; T \leq t)$.

Proposition

The expected total progeny V *of a life cycle satisfies the following equation:*

$$\nu(t) := E(V; T \leq t) = F(t) + \int_0^t \nu(t-y) h'_s(y; F(t-y)) dG(y), \tag{2}$$

where $F(t)$ is defined by (1).

In the case $m \neq 1$ (i.e. non-critical cases) the expected total progeny of a life cycle is:

$$E(V; T < \infty) = \frac{q}{1 - \displaystyle\int_0^\infty h'(t; q) dG(t)}. \tag{3}$$

Proof. It is obvious from the branching property that the p.g.f. $g(t; s)$ of the total progeny of a life cycle satisfies the recurrence relation

$$g(t; s) = s \int_0^t h(y; g(t-y; s)) dG(y). \tag{4}$$

Since $g(1; t) = F(t)$, after differentiating (4) we obtain (2).

From $q = F(\infty)$ and $\nu(t) \uparrow \nu := E(V; T < \infty)$, dominated convergence yields (3). ■

The total progeny of the $(\widetilde{Z}_t)_{t \geq 0}$ before explosion.

Suppose that $\{Z_t(n)\}$ are supercritical Sevast'yanov's branching processes, in which case with probability one will appear a process that is going to explode. We are interested in the total progeny W of the process $\widetilde{Z}_t$, i.e. the number of all existing particles during the all finite cycles before explosion. Assume $p_0 > 0$ and let V_n denote the total progeny within $Z_t(n), n = 1, 2, \ldots$. Then

$$W = \sum_{n=1}^{\infty} [V_1 \mathbb{I}\{T_1 < \infty\} + \ldots + V_n \mathbb{I}\{T_n < \infty\}] \mathbb{I}\{T_{n+1} = \infty\}, \tag{5}$$

where the summands $V_i, i = 1, \ldots, n$ are i.i.d. and independent of $\{T_{n+1}\}$.

Let denote $g(s) := E(s^{V_n} | Z_0(n) = 1) = E(s^{V_n}; T_n < \infty | Z_0(n) = 1)$, because $V_n = \infty$ if $\mathbb{I}\{T_n = \infty\} = 1$.

Moreover, $g(1) = P(T_n < \infty | Z_0(n) = 1) = q$, the extinction probability starting with one particle. Observing that $W = 0$ if $T_1 = \infty$, (5) yields

$$E(s^W) = (1-q) + \sum_{n\geq 1} g^n(s)(1-q) = \frac{1-q}{1-g(s)}. \tag{6}$$

Now, for a given p.g.f. $h(t;s)$ of a Sevast'yanov's branching process using the relation (3) we obtain that the expected total progeny within extinct cycles is

$$EW = \frac{q}{(1-q)(1-\int_0^\infty h'_s(t;q)dG(t))}.$$

After differentiating (5) once more at $s=1$ it is a matter of straightforward computations to verify that

$$E[W(W-1)] = \frac{1}{1-q}\left\{\frac{2q}{(1-q)(1-\int_0^\infty h'_s(t;q)dG(t))} + \mu\right\},$$

where

$$\mu := \frac{\nu\left(2\int_0^\infty h'_s(t;q)dG(t) + \int_0^\infty h''_{ss}(t;q)dG(t)\right)}{1-\int_0^\infty h'_s(t;q)dG(t)}.$$

4. Simulation results

In general, one of the best features of branching processes is that the exact theoretical results have a natural interpretation and can be directly used for numerical and simulation studies.

When using Bellman-Harris branching model allowing immigration, the computation procedure was implemented by recursive equations to compute the probability of extinction by certain epoch (see [14]). It was illustrated how the duality between sub-critical and super-critical branching processes given extinction can make decision - makers take the wrong decision.

However, as it does not look easy to derive analogous results for the Sevast'yanov's population models, we develop a code for a simulation system of different branching models with immigration, including BGWBP, BHBP and

Sevast'yanov's ones. No programming is necessary and all input data can be entered in user-friendly dialog boxes and graphics and (numerical) results can be easily and quickly obtained. The results can be stored in the database table and may be analyzed easily. The code can be used for actual design, prediction and estimation of the parameters of different classes of branching processes, both in discrete and continuous time. The simulation system is a simple professional tool that might be used by biologists, engineers and decision-makers for simulation of the processes which could appear to be suitable for modeling of some real world problems related to population and re-population experiments. Moreover, the simulation software system allows input of a mortality density and a special form of the reproduction law with particle's age dependence. Up to now exponential, logarithmic and polynomial functions are proposed to model the age-dependency. We apply the Monte-Carlo method to approach the behaviour of the variables $T|T < \infty$ and L. For the variable $T|T < \infty$, we simulate the process $(Z_t : t \geq 0)$ whereas the process $(\widetilde{Z}_t : t \geq 0)$ is considered to study the variable L. All runs are with $\Gamma(6, 1)$ life-time distribution of each particle and Poisson reproduction distribution, depending in logarithmic way from the particle's age.

As an example we have simulated 100 000 paths of each process. In Figure 1 and Figure 2 we show the estimate density functions for the variables $T|T < \infty$ and L. From the simulation we estimate the probability of extinction of the process $(Z_t : t \geq 0)$ by 0.1447. Moreover, the sample mean for $T|T < \infty$ is 6.6650 and for L the sample mean is 1.1255.

5. Conclusions

In population experiments it is usually easier to see if a new introduction has been successful than to know whether, and when, extinction has occurred. In many cases statistical data are only provided by interest groups, hunters, photographers, etc. Independent control studies to assess the prior probability of extinction are likely to be environment-biased. On the other hand, it is not always possible to reduce the prior probability of extinction by releasing a large numbers of individuals. The point is that extinction involves a very strong bias. The discrete mass in the origin for the density function of L is the consequence of $P(L = 0) = 1 - q$. Indeed, the estimated extinction probability of the process $(Z_t : t \geq 0)$ equals to 0.1447.

To generalize the inference results on fertility rates and illustrate how the duality between sub-critical and super-critical branching processes given extinction can mislead decision-makers, the study of the behaviour of the extinction probability by given time when using Sevast'yanov's model, will be reserved for future research.

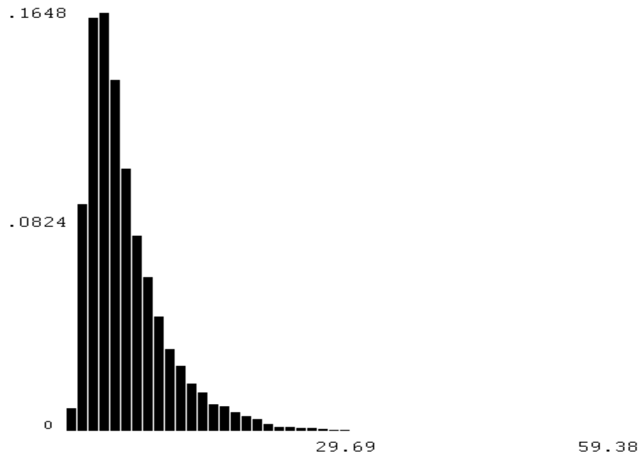

Figure 1: Histogram of probability densities of a life cycle $T|T<\infty$ with $\Gamma(6,1)$ life-time of each particle and Poisson reproduction distribution, depending logarithmic from the particle's age.

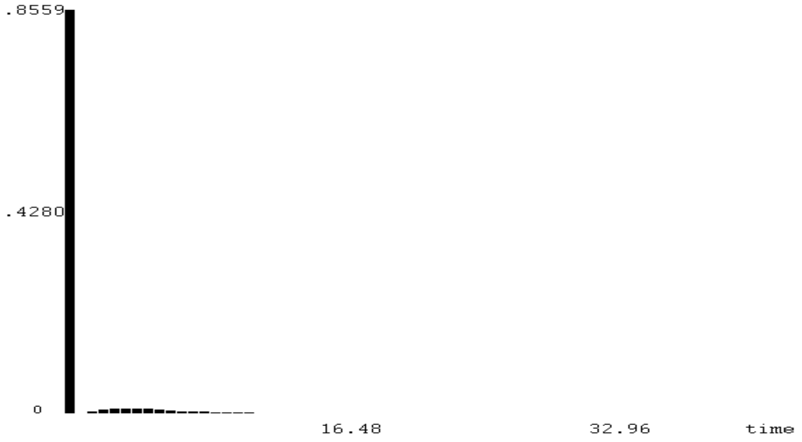

Figure 2: Histogram of probability densities of a total waiting time L with $\Gamma(6,1)$ life-time of each particle and Poisson reproduction distribution, depending logarithmic from the particle's age.

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