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SUBCRITICAL AGE-DEPENDENT BRANCHING PROCESSES WITH EMIGRATION *

Maroussia Nikiforova Slavtchova-Bojkova, Nickolay Mihailov Yanev

The aim of the study is to present and investigate a new stochastic process for modeling population dynamics, namely Sevastyanov's age-dependent branching process with emigration. Such model appears naturally in applications to cell populations where with positive probability the cells may die before their life-cycle is completed.

1. Introduction. Branching processes with emigration can be considered as one of the possible ways of specifying the general model of controlled (φ- branching) processes (see [10], [11], [14]). For the first time the Bienaymé-Galton-Watson processes with emigration of one particle at every generation (provided there exists at least one particle) was considered by Vatutin in [12]. He studied the critical case, i. e. when the mean offspring of each particle is one. When all moments of the offspring exist the asymptotics of the probability of nonextinction was obtained. He also proved that conditioned on degeneracy the normalized process has the exponential distribution as a limit law.

More general model when a random number of particles is removed from the population (and all these numbers are independent r. v. with given p. g. f. $h(s)$) was considered in [1] and [13] where Vatutin's results about the probability of nonextinction in that more general setting were expanded and again the limit law turned out to be an exponential distribution.

In [4], [7], [8] Pakes has considered continuous-time Markov branching processes with emigration which occurs at the jump moments of a Poisson process, i. e. if emigration occurs at time t, then $\min(Y_t, \eta_t)$ particles are removed from the process. In [4] Pakes has estimated the rate of convergence of $Q(i) = \lim_{t\to\infty} \mathbb{P}\{Y_t = 0|Y_0 = i\}$ to 0 as $i \to \infty$ and $\mathbb{E}\log(1+\eta_t) < \infty$. The asymptotics of the expectation of Y_t and of extinction moment as $Y_0 = i \to \infty$ for subcritical and critical continuous-time Markov branching processes with emigration were studied in [7]. In the same paper it was shown that the limiting stochastic process corresponding to the conditional distributions of Y_t, given that $Y_{t+u} > 0$, $u \to \infty$, is positively recurrent in the subcritical case and transient in the critical one.

Analogous results for Markov branching processes with emigration rate (the same as the rate of jumps upwards caused by the splitting of particles) proportional to the number of particles that are alive have been obtained in [2], [3], [5], [6].

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Our object is to describe a cell population model, general enough to give a good description of biological reality and yet simple enough to cover a large class of cell populations which admit cell degeneracy. For this Sevastyanov age-dependent branching model (see [9]) is considered where additionally each particle is subject to age-dependent emigration. It is investigated the subcritical case when all individual characteristics of the process are finite and the process itself is regular.

2. Model, moments and extinction.

2.1. Definition of the model. Sevastyanov age-dependent branching process $\{Z(t)\}_{t\geq 0}$ with pure emigration is defined as follows. Let $h(t;s) = \sum_{k=0}^{\infty} h_k(t)s^k$ be the offspring p.g.f., where $h_k(t)$ is the probability each particle to have k descendants at age t. The lifetime L of each particle is defined by two independent r.v. X and Y, where $L = \min(X, Y)$. If $L = X$ and $X = u$ then the particle generates random offspring according to the p.g.f. $h(u;s)$ and if $L = Y$ then the particle emigrates from the population or disappears without producing any offspring. It is assumed that the d.f. $F_1(t) = \mathbb{P}(X \leq t)$ and $F_2(t) = \mathbb{P}(Y \leq t)$ are non-lattice.

Denote the p.g.f. $\Phi(t;s) = \mathbb{E}s^{Z(t)} = \sum\limits_{k=0}^{\infty} P_k(t)s^k$, $P_k(t) = \mathbb{P}(Z(t) = k)$, $|s| \leq 1$, with $\Phi(0;s) = s$ and $\mathbb{P}(L \leq t) = G(t)$, where $\bar{G}(t) = \mathbb{P}(L > T) = \bar{F}_1(t)\bar{F}_2(t)$, $\bar{F}_1(t) = 1 - F_1(t)$, $\bar{F}_2(t) = 1 - F_2(t)$.

Lemma 2.1. *The p.g.f. $\Phi(t;s)$ of the process $Z(t)$ is the unique solution of the equation*

$$\Phi(t;s) = p\int_0^t h(u;\Phi(t-u;s))dA(u) + s(1 - G(t)) + (1-p)B(t), \tag{2.1}$$

where

$$\begin{aligned} p = \mathbb{P}(X \leq Y) &= \int_0^{\infty} \bar{F}_2(u)dF_1(u), \\ A(t) = \mathbb{P}(X \leq t | X \leq Y) &= \frac{1}{p}\int_0^t \bar{F}_2(u)dF_1(u), \\ B(t) = \mathbb{P}(Y \leq t | Y \leq X) &= \frac{1}{(1-p)}\int_0^t \bar{F}_1(u)dF_2(u). \end{aligned} \tag{2.2}$$

Proof. The integral equation (2.1) follows by the law of the total probability considering two cases - when the life-cycle of the first particle $L \leq t$ and $L \geq t$, where $t \geq 0$ is fixed.

(i) If $L \leq t$ then we have two cases:

(i.1) If $Y = L \leq t$ therefore $Z(t) = 0$ with probability

$$\mathbb{P}(Y = L \leq t) = \mathbb{P}(Y \leq t; Y \leq X) = \int_0^t \bar{F}_1(u)dF_2(u) = (1-p)B(t); \tag{2.3}$$

(i.2) If $X = L \leq t$ then the process $Z(t)$ at instant t is equivalent to the classical Sevastyanov's branching process with individual characteristics $(h(t;s), A(t))$.

Since

$$\mathbb{P}(X = L \leq t) = \mathbb{P}(X \leq t; X \leq Y) = \int_0^t \bar{F}_2(u)dF_1(u) = pA(t), \tag{2.4}$$

then we obtain the first term in (2.1).

(ii) If $L \geq t$, then $Z(t) = 1$ with probability 1. On the other hand,

$$\mathbb{P}(L \geq t) = 1 - G(t) = \bar{F}_1(t)\bar{F}_2(t) = 1 - pA(t) - (1-p)B(t). \tag{2.5}$$

Using (2.2)-(2.5) we obtain

$$\begin{aligned} \Phi(t;s) &= p\int_0^t h(u;\Phi(t-u;s))d\mathbb{P}(X \leq u | X \leq Y) \\ &+ s\bar{F}_1(t)\bar{F}_2(t) + (1-p)\mathbb{P}(Y \leq t | Y \leq X). \end{aligned} \tag{2.6}$$

It is clear that the conditional probabilities in (2.6) satisfy

$$\begin{aligned} \mathbb{P}(Y \leq t | Y \leq X) &= \frac{\mathbb{P}(Y \leq t; Y \leq X)}{\mathbb{P}(Y \leq X)} = B(t), \\ \mathbb{P}(X \leq t | X \leq Y) &= \frac{\mathbb{P}(X \leq t; X \leq Y)}{\mathbb{P}(X \leq Y)} = A(t). \end{aligned} \tag{2.7}$$

Finally, from (2.6) and (2.7) we obtain equation (2.1) of the lemma. □

2.2. Moments and extinction. Denote the moments as follows

$$M_1(t) = \left.\frac{\partial \Phi(t;s)}{\partial s}\right|_{s=1} = \mathbb{E}Z(t),\ M_2(t) = \left.\frac{\partial^2 \Phi(t;s)}{\partial s^2}\right|_{s=1} = \mathbb{E}Z(t)[Z(t)-1],$$

$$m(u) = \left.\frac{\partial h(u;s)}{\partial s}\right|_{s=1},\ b(u) = \left.\frac{\partial^2 h(u;s)}{\partial s^2}\right|_{s=1},$$

$$m = \int_0^\infty m(u)dA(u), b = \int_0^\infty b(u)dA(u).$$

After differentiating (2.1) and setting $s = 1$ one obtains the following equations:

$$M_1(t) = \bar{F}_1(t)\bar{F}_2(t) + p\int_0^t m(u)M_1(t-u)dA(u), \tag{2.8}$$

$$M_2(t) = p\int_0^t m(u)M_2(t-u)dA(u) + p\int_0^t b(u)M_1^2(t-u)dA(u). \tag{2.9}$$

In the following we will establish asymptotic properties of the moments and will prove limit theorems for the processes using integral equations (2.8) and (2.9).

Define real number α (which is so-called Malthusian parameter) as the root of the equation

$$p\int_0^\infty e^{-\alpha u}m(u)dA(u) = 1. \tag{2.10}$$

If $mp > 1$, then $\alpha > 0$ exists and it is unique. If $\tilde{m} = mp = 1$ then $\alpha = 0$. If $\tilde{m} < 1$, then the equation (2.10) may not have a root. But if it exists, then it is negative. In the following considerations it will be supposed that there exists a unique root of equation (2.10).

Let $q = \lim_{t\to\infty} P_0(t)$, where $P_0(t) = \mathbb{P}(Z(t) = 0)$. Then from equation (2.1) with

$s = 0$ as $t \to \infty$ we obtain that q is the smallest root of the equation $\tilde{h}(u) = s$, where $\tilde{h}(u) = p\int_0^\infty h(u;s)dA(u) + (1-p)$. Then the criticality parameter of the process $Z(t)$ with emigration component turned out to be $\tilde{m} = mp = p\int_0^\infty m(t)dA(t)$.

3. Limit theorems ($\tilde{m} = mp < 1$).

Theorem 3.1. *Let* $\tilde{m} < 1$, $\int_0^\infty te^{-\alpha t}dG(t) < \infty$, $\int_0^\infty te^{-\alpha t}m(t)dA(t) < \infty$, *and there exists the Malthusian parameter* $\alpha < 0$, *defined by (2.10),* $G(t)$ *and* $A(t)$ *are defined by* (2.2). *Then*

$$\lim_{t\to\infty} M_1(t)e^{-\alpha t} = c_1. \tag{3.1}$$

If in addition $\int_0^\infty b(t)e^{-\alpha t}dA(t) < \infty$ *and* $\int_0^\infty tb(t)e^{-\alpha t}dA(t) < \infty$, *then*

$$\lim_{t\to\infty} M_2(t)e^{-\alpha t} = c_2, \tag{3.2}$$

where c_1 *and* c_2 *are positive constants.*

Proof. From equation (2.8) by substitution $\tilde{M}_1(t) = M_1(t)e^{-\alpha t}$, it follows

$$\tilde{M}_1(t) = \bar{F}_1(t)\bar{F}_2(t)e^{-\alpha t} + \int_0^t \tilde{M}_1(t-u)d\tilde{A}(u), \tag{3.3}$$

where

$$\tilde{A}(u) = p\int_0^u e^{-\alpha x}m(x)dA(x) \quad (\tilde{A}(+\infty) = 1). \tag{3.4}$$

To apply basic renewal theorem (see [9], Theorem 8.7.6, p.271) we have to prove, that $\bar{F}_1(t)\bar{F}_2(t)e^{-\alpha t} \in L_1(0,\infty)$ and $\bar{F}_1(t)\bar{F}_2(t)e^{-\alpha t} \downarrow 0$, as $t \to \infty$. We will show that $\bar{G}(t)e^{-\alpha t}$ can be presented as sum of two non-increasing functions belonging to $L_1(0,\infty)$. First of all, as $\alpha < 0$, then $e^{-\alpha t}(1-G(t)) \le \int_t^\infty e^{-\alpha u}dG(u)$, and that is why $e^{-\alpha t}(1-G(t)) \to 0$, as $t \to \infty$.

Moreover, from relations

$$\begin{aligned}\int_0^\infty dt\int_t^\infty e^{-\alpha u}dG(u) &= t\int_0^\infty e^{-\alpha u}dG(u)\Big|_0^\infty + \int_0^\infty te^{-\alpha t}dG(t)\\ &= \int_0^\infty te^{-\alpha t}dG(t) < \infty,\end{aligned}$$

we obtain that $\int_t^\infty e^{-\alpha t}dG(t) \in L_1(0,\infty)$.

On the other hand, integrating by parts gives

$$\begin{aligned}\textstyle\int_t^T e^{-\alpha u}dG(u) &= -\int_t^T e^{-\alpha u}d(1-G(u))\\ &= -e^{-\alpha u}(1-G(u))\Big|_t^T - \alpha\int_t^T e^{-\alpha u}(1-G(u))du.\end{aligned}$$

Let $T \to \infty$, then $\displaystyle\int_t^\infty e^{-\alpha u} dG(u) = e^{-\alpha t}(1 - G(t)) - \alpha \int_t^\infty e^{-\alpha u}(1 - G(u))du$.

In the last equation the left hand side and the second term on the righthand side belong to $L_1(0,\infty)$ and it is clear that $e^{-\alpha t}(1 - G(t)) \in L_1(0,\infty)$, as the sum of two non-increasing functions of $L_1(0,\infty)$.

Then, it is easy to obtain from equation (3.3) that

$$\lim_{t\to\infty} \tilde{M}_1(t) = \frac{\displaystyle\int_0^\infty e^{-\alpha t}\bar{F}_1(t)\bar{F}_2(t)dt}{p\displaystyle\int_0^\infty um(u)e^{-\alpha u}dA(u)} = c_1, \tag{3.5}$$

which proves (3.1).

Now, to establish (3.2) let us make the substitutions $\tilde{M}_1(t) = M_1(t)e^{-\alpha t}$, $\tilde{M}_2(t) = M_2(t)e^{-\alpha t}$ in (2.9), where $\alpha < 0$ is defined by (2.10). We obtain

$$\tilde{M}_2(t) = \int_0^t \tilde{M}_2(t-u)d\tilde{A}(u) + e^{\alpha t}\int_0^t \tilde{M}_1^2(t-u)b(u)e^{-2\alpha u}dA(u), \tag{3.6}$$

where $\tilde{A}(u)$ is defined by (3.4).

In order to apply Theorem 8.7.9 (see [9], p. 272) we need to prove that the second term on the righthand side in (3.6) belongs to $L_1(0,\infty)$. Using (3.5) it is clear that it is non-negative and bounded from above function by some constant multiplied by $e^{\alpha t}\displaystyle\int_0^t e^{-2\alpha u}dA_b(u)$, where $A_b(u) = \displaystyle\int_0^u b(y)dA(y)$. As $\alpha < 0$, then we have $e^{\alpha t}\displaystyle\int_0^t e^{-2\alpha u}dA_b(u) \le e^{\alpha t}[\int_0^{t/3} e^{-2\alpha u}dA_b(u) + \int_{t/3}^t e^{-2\alpha u}dA_b(u)] \le Be^{\alpha t/3} + \displaystyle\int_{t/3}^\infty e^{-\alpha u}dA_b(u)$, where $Be^{\alpha t/3} \in L_1(0,\infty)$ and the second term also belongs to $L_1(0,\infty)$, as $\displaystyle\int_0^\infty tb(t)e^{-\alpha t}dA(t) < \infty$. Finally, we can apply Theorem 8.7.9 (see [9], p. 272) to equation (3.6), which gives (3.2) and the proof is completed. □

Theorem 3.2. *If $\tilde{m} < 1$ and the conditions of Theorem 3.1 are satisfied, then*

$$Q(t) = \mathbb{P}(Z(t) > 0) \sim Q_0 e^{\alpha t}, t \to \infty, \tag{3.7}$$

where $\alpha < 0$ is the Malthusian parameter defined by (2.10).

Proof. Using equation (2.1) it follows that the probability of non-extinction $Q(t) = 1 - \Phi(t;0)$ satisfies the equation

$$Q(t) = 1 - p\int_0^t h(u;\Phi(t-u;0))dA(u) + (1-p)B(t). \tag{3.8}$$

From (3.8) using the following expansion $h(u;s) = 1 + m(u)(s-1) + \frac{b(u)}{2}\varphi(s)(s-1)^2$, where $\varphi(s)$ is p.g.f., with $\varphi(1) = 1$ and $\varphi(s) = \displaystyle\sum_{k=0}^\infty \varphi_k s^k$, $0 \le \varphi_k \le 1$, one obtains that

$$Q(t) \;=\; 1 - G(t) + p\int_0^t m(u)Q(t-u)dA(u)$$

$$-\quad p\int_0^t \frac{b(u)}{2}Q^2(t-u)\varphi(1-Q(t-u))dA(u). \tag{3.9}$$

Making the substitution $Q(t)=Q_0e^{\alpha t}$ in (3.9) we obtain

$$Q_0(t)=\int_0^t Q_0(t-u)d\tilde{A}(u)+W(t), \tag{3.10}$$

where $\tilde{A}(t)$ is defined by (3.4) and

$$W(t)=e^{-\alpha t}[1-G(t)]-\frac{pe^{\alpha t}}{2}\int_0^t Q_0^2(t-u)e^{-2\alpha u}\varphi(1-Q(t-u))dA_b(u). \tag{3.11}$$

For the first term on the righthand side of (3.11) it was already proved in Theorem 3.1 that $e^{-\alpha t}[1-G(t)]\in L_1(0,\infty)$. Moreover, from the same theorem and the inequality $Q(t)\le M_1(t)$, it follows that $Q_0(t)$ is bounded.

Therefore the second term in (3.11) will not exceed $Kpe^{\alpha t}\int_0^t e^{-2\alpha u}b(u)dA(u)$, as $|\varphi(1-Q(t-u))|\le 1$. But in Theorem 3.1 we also proved that the last function belongs to $L_1(0,\infty)$. Finally, we can apply Theorem 8.7.8 (see [9]) to equation (3.10) and it implies that $Q_0(t)\to Q_0$, as $t\to\infty$. □

Next we will turn our attention to the existence of a stable distribution of the population size. The tool we used is non-markovian renewal theory.

Theorem 3.3. *Under the assumptions of the Theorem 3.1 it follows that there exists*

$$\lim_{t\to\infty}\mathbb{P}(Z(t)=k|Z(t)>0)=P_k,\quad k=1,2,\dots,\sum_{k=1}^{\infty}P_k=1.$$

Proof. Denote $R(t;y)=1-\Phi(t;1-y)$, $|y|\le 1$. Then the equation (2.1) admits the following renewal-type representation

$$R(t;y)=p\int_0^t[1-h(u;1-R(t-u;y))]dA(u)+y\bar{F}_1(t)\bar{F}_2(t). \tag{3.12}$$

Using (3.9) it follows that

$$R(t;y)=p\int_0^t m(u)R(t-u;y)dA(u)+$$

$$+p\int_0^t\frac{b(u)}{2}R^2(t-u;y)\varphi(1-R(t-u;y))dA(u)+y\bar{F}_1(t)\bar{F}_2(t). \tag{3.13}$$

Making the substitution $R(t;y)=e^{\alpha t}\bar{R}(t;y)$ in (3.13) we obtain

$$\bar{R}(t;y)=\int_0^t\bar{R}(t-u;y)d\tilde{A}(u)+pe^{\alpha t}\tilde{W}(t,y)+ye^{-\alpha t}\bar{F}_1(t)\bar{F}_2(t), \tag{3.14}$$

where $\tilde{W}(t,y)=\int_0^t\frac{b(u)}{2}\bar{R}^2(t-u;y)e^{-2\alpha u}\varphi(1-R(t-u;y))dA(u)$ and $\tilde{A}(u)$ is defined by (3.4).

It is clear, that if $|y|\le 1$, then

$$|R(t;y)|=|1-\Phi(t;1-y)|\le M_1(t).|y|\le C_1e^{\alpha t}, \tag{3.15}$$

where $\alpha<0$ is the Malthusian parameter.

Using (3.15) yields

$$\left|\int_0^\infty \tilde{W}(t,y)dt\right| = \int_0^\infty \left[\int_0^t \frac{b(u)}{2}\bar{R}^2(t-u;y)e^{-2\alpha u}\varphi(1-R(t-u;y))dA(u)\right]dt$$

$$= \left|\int_0^\infty \frac{b(u)}{2}e^{-2\alpha u}dA(u)\int_0^\infty \bar{R}^2(t-z;y)\varphi(1-R(t-z;y))dz\right| \leq$$

$$\leq C_1^2\left|\int_0^\infty b(u)e^{-2\alpha u}dA(u)\right|\left|\int_0^\infty M_1^2(t)e^{2\alpha t}dt\right| < \infty,$$

as $\displaystyle\int_0^\infty b(u)e^{-2\alpha u}dA(u) < \infty$.

Applying the basic renewal theorem to the equation (3.14), one concludes that there exists

$$\lim_{t\to\infty}\bar{R}(t;y) = \frac{p\displaystyle\int_0^\infty e^{\alpha t}\tilde{W}(t,y)dt + y\int_0^\infty e^{-\alpha t}\bar{F}_1(t)\bar{F}_2(t)dt}{p\displaystyle\int_0^\infty ue^{-\alpha u}m(u)dA(u)} = R(y),$$

as $|y| \leq 1$, i.e. $R(t;y) = R(y)e^{\alpha t}(1+o(1))$, uniformly in $0 < y \leq 1$.

If we denote by $\tilde{\Phi}(t;s) = \sum\limits_{k=1}^{\infty} P(Z(t)=k|Z(t)>0)s^k$, i.e. $\tilde{\Phi}(t;s)$ is the conditional p.g.f. conditioned on the event $\{Z(t)>0\}$, we have the following representation

$$\tilde{\Phi}(t;s) = 1 - \frac{1-\Phi(t;s)}{1-\Phi(t;0)} = 1 - \frac{R(t;1-s)}{Q(t)}. \tag{3.16}$$

Then (3.16) yields that $\tilde{\Phi}(t;s)$ is uniformly convergent as $0 \leq s \leq 1$ and its limit is $1 - \dfrac{R(1-s)}{Q_0}$, which completes the proof.

□

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Maroussia N. Slavtchova-Bojkova
Department of Probability and Statistics
Institute of Mathematics and Informatics
Bulgarian Academy of Sciences
Acad. G. Bontchev Str., Bl. 8
1113 Sofia, Bulgaria
e-mail: bojkova@math.bas.bg

Nickolay M. Yanev
Department of Probability and Statistics
Institute of Mathematics and Informatics
Bulgarian Academy of Sciences
Acad. G. Bontchev Str., Bl. 8
1113 Sofia, Bulgaria
e-mail: yanev@math.bas.bg

ДОКРИТИЧНИ РАЗКЛОНЯВАЩИ СЕ ПРОЦЕСИ, ЗАВИСЕЩИ ОТ ВЪЗРАСТТТА НА ЧАСТИЦИТЕ С ЕМИГРАЦИЯ

Марусия Никифорова Славчова-Божкова, Николай Михайлов Янев

Изследван е един нов модел разклоняващи се процеси, зависещи от възрастта на частиците с емиграция в докритичния случай. Доказано е съществуването на стационарно гранично разпределение при условие за неизраждане. Такива модели възникват естествено при изследване на клетъчни популации, при които клетките могат да дегенерират с положителна вероятност.