Population-Size-Dependent and Age-Dependent Branching Processes *

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Abstract

Supercritical branching processes are considered which are Markovian in the age structure but where reproduction parameters may depend upon population size and even the age structure of the population. Such processes generalize Bellman-Harris processes as well as customary demographic processes where individuals give birth during their lives but in a purely age-determined manner. Although the total population size of such a process is not Markovian the age chart of all individuals certainly is.

We give the generator of this process, and a stochastic equation from which the asymptotic behaviour of the process is obtained, provided individuals are measured in a suitable way (with weights according to Fisher's reproductive value). The approach so far is that of stochastic calculus. General supercritical asymptotics then follows from a combination of L^2 arguments and Tauberian theorems.

It is shown that when the reproduction and life span parameters stabilize suitably during growth, then the process exhibits exponential growth as in the classical case. Application of the approach to, say, the classical Bellman-Harris process gives an alternative way of establishing its asymptotic theory and produces a number of martingales.

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1 Introduction

In age-dependent, Bellman-Harris branching processes a particle lives for a random length of time and on its death produces a random number of offspring, all of which live and reproduce independently, with the same laws as the original particle. In classical demographic theory (female) individuals give birth according to age-specific birth rates. What unifies these two types of processes is that they are *Markovian in the age structure*, cf. Jagers (1975, p. 208).

Now, imagine a collection of individuals with ages $(a^1, \ldots, a^z) = A$. In a population-size-dependent process such an individual of age a has a random life span with hazard rate $h_A(a)$. During life she gives birth with intensity $b_A(a)$, both rates dependent on the individual's age as well as the whole setup of ages. Finally, when she dies, she splits into a random number $Y(a)$ of off-spring with distribution that may depend upon the whole collection A of ages as well as the age a of the individual splitting. Childbearing and life length may thus be affected by population size and age structure, but apart from this individuals live and reproduce independently of each other.

The type of dependence we have in mind is dependence on the total population size $z = |A| = (1, A)$, so that $h_A = h_z$, $b_A = b_z$, and similarly for off-spring at splitting. But a more general influence pattern is also allowed. The aim is to obtain results on the asymptotic behaviour of population-size-dependent such processes in the case of stabilizing reproduction and lifelengths of individuals, namely when $h_z \to h$, $b_z \to b$, and $m_z = \mathbb{E}_z[Y] \to m$, as $z \to \infty$.

We consider only the supercritical case, so that $m > 1$ in the case of pure splitting.

Such results were obtained by Klebaner (1984 and 1989) for Galton-Watson processes and (1994) for Markov population-size-dependent branching process, where life spans are exponential with parameters depending on z. In particular it was shown that the condition $\sum |m_z - m|/z < \infty$ is essentially necessary and sufficient for the process to grow at an exponential rate. Jagers (1997), using a coupling argument, obtained results for population size dependent branching processes more general than presently considered, however a sufficient condition for the exponential growth obtained by this method is $\sum |m_z - m| < \infty$. In Jagers (1998) the sharp necessary and sufficient condition was recovered, but only for processes that possess a symmetric growth property. Here we pursue the line of analysis as for the Markov case by considering the age process.

Our approach combines a stochastic calculus and Markov processes analysis with the method of random characteristics for general branching processes. We identify the compensator of the process and the martingale in section 2. In section 3 we show that this approach leads to new results, as well as recovers known results, for classical branching processes. In section 4 we show the convergence of the Malthusianly normed population-size-dependent and age-dependent branching processes with stabilizing reproduction, provided individuals are counted in a special way, through Fisher's reproductive value. In section 5 we use the population tree formulation and random characteristics to obtain Malthusian asymptotics, exponential growth and stabilization of composition of the population by applying a quadratic mean argument combined with classical Tauberian analysis.

2 Population size dependent processes as Markov processes of ages.

It has been known for a long time that the process of ages in a Bellman-Harris process constitutes a Markov process. It is not difficult to see that the most general classical branching processes that are Markovian in the age structure are those outlined in the introduction, combining a Sevastyanov type splitting (life length and off-spring number at splitting not necessarily independent) with an age-dependent propensity to child-birth during life (or a fertile subinterval thereof).

To be precise one needs to introduce the appropriate state space and topology, for the standard theory of Markov processes cf. Ethier and Kurtz (1986). This has been done in a number of ways in the past. We take the state space to be the finite positive Borel measures on $\mathbb{R}$ with the topology of weak convergence, i.e. $\lim_{n\to\infty} \mu_n = \mu$ if and only if $\lim_{n\to\infty}(f, \mu_n) = (f, \mu)$ for any bounded and continuous function f on $\mathbb{R}$, see Ethier and Kurtz (1986), Section 9.4 and Dawson (1993).

Motivated by sequences of scaled measure valued branching processes and their limits (superprocesses) Métivier (1985) and Borde-Boussion (1990) imbedded the space of measures into a weighted Sobolev space. Oelschläger (1990) took for state space the signed measures with yet another topology. All of the above works defined the process as the solution to the appropriate martingale problem. In our case we study a *single* process by means of martingale techniques, so all we need is the basic representation given by Dynkin's formula. Most of the results below are standard, and we shall not go into details.

Let $A = (a^1, \ldots, a^n)$, where the points $a^i \geq 0$, and n is an integer. The counting measure A defined by these points as $A(B) = \sum_{i=1}^n 1_B(a^i)$, for any Borel set B in $\mathbb{R}^+$. For a function f on $\mathbb{R}$ the following notations are used interchangeably throughout the paper:

$$(f, A) = \int f(x)A(dx) = \sum_{i=1}^{n} f(a^i).$$

Let z_t be the size of the population at t, i.e. the number of individuals alive. If $A_t = (a_t^1, \ldots, a_t^{z_t})$ denotes the age chart of the particles, we shall study processes (f, A_t).

Test functions used on the space of measures are of the form $F((f, \mu))$, where F and f are functions on $\mathbb{R}$. In order not to overburden the presentation we assume, throughout this paper, that births *during* a mother's life are never multiple and the populations are non-explosive in the sense that only a finite number of births can occur in finite time.

We use $\mathbb{P}_A$ and $\mathbb{E}_A$ to indicate that the population started at time $t = 0$ not from one newborn ancestor but rather from $z = (1, A)$ individuals, of ages $A = (a^1, \dots, a^z)$, respectively. No index means start from a given age configuration.

Theorem 2.1 *For a bounded differentiable function F on $\mathbb{R}^+$ and a continuously differentiable function f on $\mathbb{R}^+$, the following limit exists*

$$\lim_{t\to 0} \frac{1}{t}\mathbb{E}_A\Big\{F((f, A_t)) - F((f, A))\Big\} = \mathcal{G}F((f, A)), \tag{1}$$

where

$$\mathcal{G}F((f, A)) = F'((f, A))(f', A) + \sum_{j=1}^{z} b_A(a^j)\{F(f(0) + (f, A)) - F((f, A))\} + \\ + \sum_{i=1}^{z} h_A(a^j)\{\mathbb{E}_A[F(Y(a^j)f(0) + (f, A) - f(a^j))] - F((f, A))\}, \tag{2}$$

and $Y(a)$ denotes the number of children at death of a mother, dying at age a.

Proof: Direct calculations. □

Remark. If we were to allow for the possibility of $X(a)$ children if there is a bearing during life and at age a, we would have to replace $F(f(0) + (f, A))$ by $\mathbb{E}_A[F(X(a^j)f(0) + (f, A))]$. $\mathcal{G}$ in (2) defines a generator of a measure valued branching process, in which the movement of the particles is deterministic, namely shift.

The following result is often referred to as Dynkin's formula.

Lemma 2.1 *For a bounded C^1 function F on $\mathbb{R}$ and a C^1 function f on $\mathbb{R}^+$*

$$F((f, A_t)) = F((f, A_0)) + \int_0^t \mathcal{G}F((f, A_s))ds + M_t^F, \tag{3}$$

where M_t^F is a local martingale with the sharp bracket given by

$$\Big\langle M^F, M^F\Big\rangle_t = \int_0^t \mathcal{G}F^2((f, A_s))ds - 2\int_0^t F((f, A_s))\mathcal{G}F((f, A_s))ds. \tag{4}$$

Consequently,

$$\mathbb{E}_A(M_t^F)^2 = \mathbb{E}_A\Big(\int_0^t \mathcal{G}F^2((f, A_s))ds - 2\int_0^t F((f, A_s))\mathcal{G}F((f, A_s))ds\Big),$$

provided $\mathbb{E}_A(M_t^F)^2$ exists.

Proof: The first statement is obtained by Dynkin's formula. Expression (4) is obtained by letting $U_t = f(X_t)$, and an application of the following lemma. □

Lemma 2.2 *Let U_t be a semi-martingale, and $U_t = X_0 + A_t + M_t$, where A_t is a predictable process and M_t is a local martingale. Let $U_t^2 = X_0^2 + B_t + N_t$, where B_t is a predictable process and N_t is a local martingale. Then*

$$\langle M, M \rangle_t = B_t - 2\int_0^t U_{s-} dA_s.$$

Proof: By Itô's formula

$$U_t^2 = U_0^2 + 2\int_0^t U_{s-} dU_s + [U,U]_t = U_0^2 + 2\int_0^t U_{s-} dA_s + 2\int_0^t U_{s-} dM_s + [U,U]_t.$$

Using the representation for U_t^2 given in the conditions of the lemma, we obtain that $[U,U]_t - B_t + 2\int_0^t U_{s-} dA_s$ is a local martingale. Hence the result. □

Let $m_A(a) = \mathbb{E}_A Y(a)$ be the mean and $v_A^2(a) = \mathbb{E}_A Y^2(a)$ be the second moment of the offspring-at-splitting distribution in a population with composition A. Applying Dynkin's formula to the function $F(u) = u$, we obtain the following:

Theorem 2.2 *For a C^1 function f on $\mathbb{R}^+$*

$$(f, A_t) = (f, A_0) + \int_0^t (L_{A_s} f, A_s) ds + M_t^1, \tag{5}$$

where the linear operators L_A are defined by

$$L_A f = f' - h_A f + f(0)(b_A + h_A m_A), \tag{6}$$

and M_t^1 is a local square integrable martingale with the sharp bracket given by

$$\left\langle M^1, M^1 \right\rangle_t = \int_0^t (f^2(0) b_{A_s} + f^2(0) v_{A_s}^2 h_{A_s} + h_{A_s} f^2 - 2f(0) m_{A_s} h_{A_s} f), A_s) ds. \tag{7}$$

Proof: The first statement is Dynkin's formula for $F(u) = u$. This function is unbounded and the standard formula cannot be applied directly. However, the statement follows from the formula for bounded functions by taking smooth bounded functions that agree with u on bounded intervals, $F_n(u) = u$ for $u \le n$, moreover the sequence of stopping times $T_n = \inf\{(f, A_t) > n\}$ serves as a localizing sequence, as was done in, for example, Oelschläger (1984). The form of the operator L_A follows from (2). Note that with $F(u) = u^2$

$$\begin{aligned}
\mathcal{G}F((f,A)) \;=\;& 2(f,A)(f',A) + (b_A, A)(f^2(0) + 2f(0)(f,A)) \\
& + f^2(0)(v_A^2 h_A, A) + (h_A f^2, A) + 2f(0)(m_A h_A, A)(f,A) \\
& - 2f(0)(m_A h_A f, A) - 2(h_A f, A)(f, A),
\end{aligned}$$

so that (7) follows from (4). A similar argument given to the one above but for $F(u) = u^2$ shows that M_t^1 is locally square integrable. □

An equation similar to (5) is given in Métivier (1985) and Borde-Boussion (1990) for (f, A_t) with $f \in C_K^\infty$, infinitely differentiable functions with a compact support. Since a smooth function can be approximated on a finite interval by C_K^∞ functions, equation (5) can also be deduced from that equation.

It is important to give conditions that assure the integrability of the processes appearing in the Dynkin's formula (5). Typically, to achieve integrability it is assumed that functions are bounded, and in this case the local martingales appearing in Dynkin's formula are true martingales. However, integrability holds also for some unbounded functions. In the case of pure jump processes not too stringent conditions for it to hold were given in Hamza and Klebaner (1995). However, the age process considered here includes a deterministic motion, thus it is not a pure jump process, and the condition given in the above paper can not be used directly. A similar condition for integrability to hold for some unbounded functions, condition (H1) is given below. We restrict ourselves to positive functions, since these are the ones we use.

Theorem 2.3 *Let $f \geq 0$ be a C^1 function on $\mathbb{R}^+$ that satisfies*

$$|(L_A f, A)| \leq C(1 + (f, A)), \tag{$H1$}$$

for some constant C and any A, and assume that (f, A_0) is integrable. Then (f, A_t) and M_t^1 in (5) are also integrable with $\mathbb{E}M_t^1 = 0$.

Proof: Let T_n be a localizing sequence, then

$$(f, A_{t \wedge T_n}) = (f, A_0) + \int_0^{t \wedge T_n} (L_{A_s} f, A_s) ds + M_{t \wedge T_n}^1, \tag{8}$$

where $M_{t \wedge T_n}^1$ is a martingale. Taking expectations we have

$$\mathbb{E}(f, A_{t \wedge T_n}) = \mathbb{E}(f, A_0) + \mathbb{E} \int_0^{t \wedge T_n} (L_{A_s} f, A_s) ds. \tag{9}$$

Using the condition (H1)

$$\begin{aligned} |\mathbb{E} \int_0^{t \wedge T_n} (L_{A_s} f, A_s) ds| &\leq \mathbb{E} \int_0^{t \wedge T_n} |(L_{A_s} f, A_s)| ds \\ &\leq Ct + C\mathbb{E} \int_0^{t \wedge T_n} (f, A_s) ds. \end{aligned}$$

Thus we have from (9)

$$\begin{aligned} \mathbb{E}(f, A_{t \wedge T_n}) &\leq \mathbb{E}(f, A_0) + Ct + C\mathbb{E} \int_0^{t \wedge T_n} (f, A_s) ds \\ &\leq \mathbb{E}(f, A_0) + Ct + C\mathbb{E} \int_0^t I(s \leq T_n)(f, A_s) ds \\ &\leq \mathbb{E}(f, A_0) + Ct + C \int_0^t \mathbb{E}(f, A_{s \wedge T_n}) ds. \end{aligned}$$

It now follows by Gronwall's inequality that

$$\mathbb{E}(f, A_{t\wedge T_n}) \leq (\mathbb{E}(f, A_0) + 1)e^{Ct} < \infty. \tag{10}$$

Taking $n \to \infty$ we obtain by Fatou's lemma that

$$\mathbb{E}(f, A_t) \leq (\mathbb{E}(f, A_0) + 1)e^{Ct} < \infty. \tag{11}$$

Now it follows from (11) that (f, A_t) is integrable, as it is nonnegative. Now by the condition (H1)

$$\begin{aligned} \mathbb{E}\left|\int_0^t (L_{A_s} f, A_s) ds\right| &\leq \int_0^t \mathbb{E}|(L_{A_s} f, A_s)| ds \\ &\leq \int_0^t C(1 + \mathbb{E}(f, A_s)) ds < \infty, \end{aligned}$$

where the last inequality is by (11). Thus $\int_0^t (L_{A_s} f, A_s) ds$ is integrable, which together with (11) implies that

$$M_t^1 = (f, A_t) - (f, A_0) - \int_0^t (L_{A_s} f, A_s) ds \tag{12}$$

is also integrable with zero mean. □

By taking $f(u) = 1 =$ constantly, Theorem 2.2 yields the following corollary. Recall that $z_t = (1, A_t)$ is the population size at time t.

Theorem 2.4 *The compensator of z_t is given by $\int_0^t (b_{A_s} + h_{A_s}(m_{A_s} - 1), A_s) ds$.*

Before considering populations with stabilizing reproductions, we shall have a look at classical, population-size independent branching processes, which have a Markovian age structure.

3 Classical branching processes which are Markovian in the age structure

In traditional branching processes, as well as demography or population dynamics, the reproduction rate, hazard function and offspring-at-splitting distribution are all population independent. We write b and h for the former two, and G for the lifespan distribution. Its density is denoted by g and the first two moments of offspring-at-splitting distribution by m and v^2. Not that the latter may still be functions of age at split, unless we are in the Bellman-Harris case of independence between life span and reproduction.

This section is confined to the case of i.i.d. individuals. For simplicity we assume that $G(u) < 1$ for all $u \in \mathbb{R}^+$, and write $S = 1 - G$ for the survival function. The results of the previous section are summarized in the following theorem.

Theorem 3.1 *1. For a C^1 function f on $\mathbb{R}^+$*

$$(f, A_t) = (f, A_0) + \int_0^t (Lf, A_s)ds + M_t^f, \tag{13}$$

where the linear operator L is defined by

$$Lf = f' - hf + f(0)b + f(0)mh \tag{14}$$

and M_t^f is a local square integrable martingale with the sharp bracket given by

$$\left\langle M^f, M^f \right\rangle_t = \int_0^t (f^2(0)b + h(f^2 + f^2(0)v^2 - 2f(0)mf), A_s)ds. \tag{15}$$

2. If $f \geq 0$ satisfies

$$|(Lf, A)| \leq C(1 + (f, A)), \qquad (H2),$$

for some constant C, and (f, A_0) is integrable, then (f, A_t) and M_t^f in (13) are also integrable with $\mathbb{E}M_t^f = 0$.

Equation (13) can be analyzed through the eigen-value problem for the operator L given in (14).

Theorem 3.2 *Let L be the operator in (14). Then*
1. The equation

$$Lq = rq \tag{16}$$

has a solution q_r for any r. The corresponding eigen-function (normed so that $q(0) = 1$) is given by

$$q_r(u) = \frac{e^{ru}}{S(u)}\Big(1 - \int_0^u e^{-rs}\{m(s)g(s) + b(s)S(s)\}ds\Big). \tag{17}$$

2. Provided b and m are bounded, there is only one bounded positive eigenfunction V, the reproductive value function, corresponding to the eigen-value known as the Malthusian parameter α,

$$V(u) = \frac{e^{\alpha u}}{S(u)} \int_u^\infty e^{-\alpha s}\{m(s)g(s) + b(s)S(s)\}ds. \tag{18}$$

Proof: 1. Since eigen-functions are determined up to a multiplicative constant, we can take $q(0) = 1$. Equation (16) is a first order linear differential equation, and solving it we obtain the solution (17).
2. The Malthusian parameter α is defined as the value of r which satisfies

$$\int_0^\infty e^{-ru}\{m(u)g(u) + b(u)S(u)\}du = 1.$$

It follows that for $r > \alpha$, $\int_0^\infty e^{-ru}\{m(u)g(u) + b(u)Su)\}du < 1$ and the eigen-function q_r in (17) is positive and grows exponentially fast or faster. For $r < \alpha$, $\int_0^\infty e^{-ru}\{m(u)g(u) + b(u)S(u)\}du > 1$ and the eigenfunction q_r in (17) takes negative values. When $r = \alpha$, $q^\alpha = V$ in (18) is the eigen-function. To see that it is bounded, write

$$V(u) = \frac{e^{\alpha u}}{S(u)} \int_u^\infty e^{-\alpha s} m(s)g(s)ds + \frac{e^{\alpha u}}{S(u)} \int_u^\infty e^{-\alpha s} b(s)S(s)ds \leq m^* + b^*, \tag{19}$$

where $m^* = \sup m(s)$ and $b^* = \sup b(s)$. Replace $e^{-\alpha s}$ by its largest value $e^{-\alpha u}$ in the first integral to see that it does not exceed m^* and replace $b(s)$ by b^* in the second integral to see that it does not exceed b^*.

□

Theorem 3.3 *Let q_r be the eigenfunction of L corresponding to the eigenvalue $r \geq \alpha$. Then $Q_r(t) = e^{-rt}(q_r, A_t)$ is a positive martingale.*

Proof: Using (13) and the fact that q_r is an eigen-function for L, we have

$$(q_r, A_t) = (q_r, A_0) + r \int_0^t (q_r, A_s)ds + M_t^{q_r}, \tag{20}$$

where $M_t^{q_r}$ is a local martingale. Functions q_r, $r \geq \alpha$, clearly satisfy the condition (H2), therefore (q_r, A_t) is integrable, and it follows from (20) by taking expectations that

$$\mathbb{E}(q_r, A_t) = e^{rt}\mathbb{E}(q_r, A_0). \tag{21}$$

Using integration by parts for $e^{-rt}(q_r, A_t)$, we obtain from (20) that

$$dQ_r(t) = d(e^{-rt}(q_r, A_t)) = e^{-rt}dM_t^{q_r},$$

and

$$Q_r(t) = (q_r, A_0) + \int_0^t e^{-rs}dM_s^{q_r} \tag{22}$$

is a local martingale as an integral with respect to the local martingale M^{q_r}. Since a positive local martingale is a super-martingale, and $Q_r(t) \geq 0$, $Q_r(t)$ is a super-martingale. But from (21) it follows that $Q_r(t)$ has a constant mean. Thus the super-martingale $Q_r(t)$ is a martingale. □

Taking $r = \alpha$, we obtain an important corollary:

Theorem 3.4 *Let V be the reproductive value function. Then $W_t = e^{-\alpha t}(V, A_t)$ is a positive martingale, which converges almost surely to a limit $W \geq 0$.*

By the martingale convergence theorem a positive martingale converges almost surely to a nonnegative limit, but the limit W may be degenerate, $P(W > 0) = 0$. However, under additional assumptions W is nondegenerate.

Theorem 3.5 *Assume that $\sigma^2(a) = Var(Y^2(a)) < \infty$ and for some r, $\alpha \leq r < 2\alpha$, and some constant C*

$$b(a) + (\sigma^2(a) + (V(a) - m(a))^2)h(a) \leq Cq_r(a). \tag{23}$$

(which holds in particular when b, h and m are bounded.) Then W_t is a square integrable martingale, and therefore converges almost surely and in L^2 to the nondegenerate limit $W \geq 0$.

Proof: It follows from (15) that

$$\left\langle M^V, M^V \right\rangle_t = \int_0^t \Big(b + (\sigma^2 + (m - V)^2)h, A_s\Big)ds. \tag{24}$$

Since (see (22))

$$W_t = (V, A_0) + \int_0^t e^{-\alpha s} dM_s^V, \tag{25}$$

we obtain that

$$\langle W, W \rangle_t = \int_0^t e^{-2\alpha s} d\left\langle M^V, M^V \right\rangle_s = \int_0^t e^{-2\alpha s}\Big(b + (\sigma^2 + (m - V)^2)h, A_s\Big)ds. \tag{26}$$

It follows by the assumption (23) that

$$\Big(b + (\sigma^2 + (m - V)^2)h, A_s\Big) \leq C(q_r, A_s), \tag{27}$$

and by Theorem 3.3

$$\mathbb{E}\int_0^\infty e^{-2\alpha s}\Big(b + (\sigma^2 + (m - V)^2)h, A_s\Big)ds \leq C\int_0^\infty e^{-2\alpha s}\mathbb{E}(q_r, A_s)ds < C\int_0^\infty e^{(r-2\alpha)s} < \infty, \tag{28}$$

where for the last inequality the assumption $r < 2\alpha$ was used. This implies from (26) that $\mathbb{E}\langle W, W \rangle_\infty < \infty$. Therefore W_t is a square integrable martingale, see for example Protter (1992) or Liptser and Shiryayev (1989), and the proof is complete. $\square$

Remark. For Bellman-Harris processes the martingale $\{W_t\}$ was given in Harris (1963) and Athreya and Ney (1972). For the processes we consider, with a Markovian age structure, it appeared in (Jagers, 1975, p. 213). It is the conditional expectation, given the age chart, of Nerman's (1981) martingale intrinsic in general (Crump-Mode-Jagers) branching processes.

4 Processes with stabilizing reproduction

Consider now population-size-dependent and age-dependent branching processes. Recall that by Theorem 2.2 the following stochastic equation holds for a bounded smooth function f on $\mathbb{R}$.

$$(f, A_t) = (f, A_0) + \int_0^t (L_{A_s} f, A_s) ds + M_t^f, \tag{29}$$

where M_t^f is a local square integrable martingale, and $L_A f = f' - h_A f + f(0)(b_A + h_A m_A)$ as given by (6).

Assume that reproduction stabilizes as the population size gets large, that is,
$m_A \to m$, $h_A \to h$, and $b_A \to b$, as $z = (1, A) \to \infty$.
Then the operator L_A in (6) can be represented as

$$L_A f = Lf + D_A f, \tag{30}$$

where

$$D_A f = L_A f - Lf = m(h_A - h) f(0) + (m_A - m) h_A f(0) + (h - h_A) f + (h_A - h) f(0), \tag{31}$$

so that all the terms are small when $z \to \infty$.

Suppose now that the limiting operator L has the eigenfunction V given in (18) with the corresponding eigenvalue α. Then it follows that

$$(V, A_t) = (V, A_0) + \alpha \int_0^t (V, A_s) ds + \int_0^t (D_{A_s} V, A_s) ds + N_t^V, \tag{32}$$

where N_t^V is a local martingale. In fact, it is easy to see that, under the condition (A1) given below (coefficients of L_A and L are bounded), the condition (H1) of Theorem 2.2 is satisfied, and N_t^V is integrable with zero mean. Let

$$W_t = e^{-\alpha t} (V, A_t).$$

Using integration by parts for $e^{-\alpha t}(V, A_t)$, we obtain

$$W_t = W_0 + \int_0^t e^{-\alpha s} (D_{A_s} V, A_s) ds + \int_0^t e^{-\alpha s} dN_s^V. \tag{33}$$

Letting $w(t) = \mathbb{E} W_t$ we have

$$w'(t) = e^{-\alpha t} E(D_{A_t} V, A_t). \tag{34}$$

We show below, in a way similar to the case of a Markov branching process as in Klebaner (1994), that if the convergence to the limit of L_A to L (or D_A to zero) is fast enough, see Assumption (A3), then $w(t)$ has a limit as $t \to \infty$ and this limit is positive.

ASSUMPTIONS.

(A1). The functions b, b_A, m, m_A, h, h_A are bounded from above.

(A2). V is bounded from below, $V \geq c > 0$.

(A3). There is a function ε such that $\sum_1^\infty \varepsilon(z)/z < \infty$ and

$$\sup_u |m_A(u) - m(u)| + \sup_u |h_A(u) - h(u)| + \sup_u |b_A(u) - b(u)| \leq \varepsilon(z), \quad z = (1, A).$$

Of course, if the functions b, m and h are bounded, then (A3) implies (A1).

Theorem 4.1 *Assume that (A1) - (A3) hold. Then*

1. $w(t) = \mathbb{E}W_t$ has a limit as $t \to \infty$ and this limit is positive, provided z_0 is large enough.

2. W_t converges almost surely to a limit $W \geq 0$.

3. If in addition v_A^2 is bounded, then W_t converges almost surely and in L^2, and the limit W is nondegenerate. Moreover, $P(z_t \to \infty) > 0$, and $\log z_t/t$ converges almost surely to α on the set $\{z_t \to \infty\}$.

Proof: In what follows C stands for a constant that may be different in different formulae.
1. It is easy to see that under the stated assumptions the function $D_A V$ satisfies

$$|D_A V| \leq C(|m_A - m| + |h_A - h| + |b_A - b|) \leq C\varepsilon(z). \tag{35}$$

Therefore

$$|(D_{A_t}V, A_t)| \leq C\varepsilon(z_t)z_t. \tag{36}$$

We wish to take expectations and to obtain a bound by carrying it inside the function. To do so one can replace the function $x\varepsilon(x)$ by a dominating increasing and concave function with the same behaviour at infinity, see Lemma 2 of Klebaner (1994). Therefore without loss of generality we can take the function $\delta(x) = x\varepsilon(x)$ to be increasing and concave. Hence

$$\mathbb{E}|(D_{A_t}V, A_t)| \leq C\delta(\mathbb{E}Z_t) \leq C\delta(e^{\alpha t}w(t)/c), \tag{37}$$

where the lower bound $V \geq c > 0$ was used to obtain $(V, A_t) \geq cZ_t$. Thus we have from (34)

$$|w'(t)| \leq e^{-\alpha t}\mathbb{E}|(D_{A_t}V, A_t)| \leq e^{-\alpha t}C\delta(e^{\alpha t}w(t)/c) = Cw(t)\varepsilon(e^{\alpha t}w(t)/c). \tag{38}$$

Since $\varepsilon(x)$ satisfies (A3), $\int^\infty \varepsilon(x)/x dx < \infty$, the above bound on the growth of $|w'(t)|$ implies convergence of $w(t)$, see Lemma 1 of Klebaner (1994). That result also shows that $\lim_{t\to\infty} w(t) > 0$ provided $w(0)$ is large enough. But $w(0) = (V, A_0) = \sum_{i=1}^{z_0} V(a_0^i) \geq cz_0$.
2. By the estimate in (38) it follows that

$$\mathbb{E}\int_0^\infty e^{-\alpha t}|(D_{A_t}V, A_t)|dt \leq C\int_0^\infty w(t)\varepsilon(e^{\alpha t}w(t)/c)dt < \infty, \tag{39}$$

since $\lim w(t) > 0$ and $\int_1^\infty \varepsilon(t)/t dt < \infty$. This implies that $\int_0^t e^{-\alpha s}(D_{A_s}V, A_s)ds$ converges in L^1 to $\int_0^\infty e^{-\alpha s}(D_{A_s}V, A_s)ds$.

Let $N^1_t = \int_0^t e^{-\alpha s} dN^V_s$. Then

$$\left\langle N^1, N^1 \right\rangle_t = \int_0^t e^{-2\alpha s} d\left\langle N^V, N^V \right\rangle_s = \int_0^t e^{-2\alpha s}\Big(b_{A_s} + h_{A_s}(V^2 + v^2_{A_s} - 2m_{A_s}V), A_s\Big)ds. \quad (40)$$

Under the imposed assumptions $b_A + h_A(V^2 + v^2_A - 2m_AV) \le C$, hence

$$\int_0^t e^{-2\alpha s}\Big(b_{A_s} + h_{A_s}(V^2 + v^2_{A_s} - 2m_{A_s}V), A_s\Big)ds < C\int_0^t e^{-2\alpha s}(1, A_s)ds < C\int_0^t e^{-2\alpha s}(V, A_s)ds,$$

where the last inequality is by (A2), $V \ge c$. Since $w(s) = \mathbb{E}e^{-\alpha s}(V, A_s)$ converges, it follows from (40) that

$$\mathbb{E}\left\langle N^1, N^1 \right\rangle_\infty < C\int_0^\infty e^{-\alpha s} w(s)ds < \infty. \quad (41)$$

Thus N^1_t is a square integrable martingale which converges almost surely and in L^2 to $\int_0^\infty e^{-\alpha s} dN^V_s$. The L^2 convergence of W_t now follows from equation (33). L^2 convergence of W_t to W implies $\mathbb{E}W = \lim_{t\to\infty} \mathbb{E}W_t > 0$, hence $P(W > 0) > 0$. Since by assumption $V \ge c$, $CZ_t > (V, A_t) > cZ_t$. The rest of the statement follows from this and convergence of W_t to the nondegenerate limit. □

Remark. Convergence of a suitably normed process follows directly from the martingale property of W_t for simple branching models, such as Markov branching processes (in this case the function V is a constant and the (V, A_t) is proportional to the population size). However, in Bellman-Harris process and Crump-Mode-Jagers process it is not straightforward to obtain such convergence by martingale methods. For such methods see Athreya and Ney (1972), and Schuh (1982) for Bellman-Harris processes, and Nerman (1981) for Crump-Mode-Jagers processes. Note here that direct analysis of the stochastic equation (29) for $z_t = (1, A_t)$ does not seem to yield the convergence of $e^{-\alpha t}z_t$, and this is achieved by a different method in the next section.

5 Asymptotics of the population size

The last section established that $(V, A_t) \sim e^{\alpha t}W$. From the point of view of general branching processes (Jagers, 1975) this process is obtained from measuring the population in one of many possible ways: at any time t an individual, born into the population, is counted if she is still alive, and her weight is V, evaluated at her age. This is a particular *random characteristic* (ibid., p. 167 ff., for general multi-type processes cf. Jagers, 1989).

In order to proceed to other characteristics and more natural population sizes, like the number of individuals alive, $z_t = (1, A_t)$, we shall have to rely upon the traditional population tree definition of branching populations. Thus we quickly review it, in the single-type case.

With any individual $x \in I$ in a Ulam-Harris family tree space

$$I := \bigcup_{n=0}^{\infty} N^n,$$

$N^0 := \{0\}, N = \{1, 2, 3, \ldots\}$ there is associated a reproduction point process telling at which ages x begets children. Those are numbered $x1, x2$ etc according to the Ulam-Harris convention. The population starts from Eve $= 0$ at time zero (or from another conventional set of ancestors though the family tree space has then to be trivially modified), and the birth-times τ_x are then recursively defined (as x's mother's birth time plus her age at x's birth, $\tau_x = \infty$ meaning that x is never born).

The basic process is the total number of births by $t \geq 0$,

$$y(t) := \#\{x \in I; \tau_x \leq t\}.$$

A host of other "population sizes" can now be defined through the mentioned additive functionals called random characteristics: a random characteristic $\chi := \{\chi_x; x \in I\}$ is a set of D-valued, stochastic processes $\chi_x(u)$ vanishing for negative arguments, and measurable with respect to the σ-algebra generated by the complete lives of x and all her progeny, i.e. x's *daughter process.* We shall assume throughout that the populations are non-explosive in the sense that only a finite number of births can occur in finite time, and also that characteristics are bounded.

The χ-counted or -weighted population size at t is defined as the sum of all χ values of those born, evaluated at their actual ages $t - \tau_x$ now at time t,

$$z_t^\chi := \sum_{x \in I} \chi_x(t - \tau_x) = \sum_{\tau_x \leq t} \chi_x(t - \tau_x).$$

Clearly,

$$y(t) = z_t^{1_{\mathbb{R}+}},$$

and if $x \in I$ has a life span λ_x, and we allow ourselves to write $\Lambda := \{1_{[0,\lambda_x)}; x \in I\}$, then

$$z_t = z_t^\Lambda = \sum_{x \in I} 1_{[0,\lambda_x)}(t - \tau_x)$$

and $(f, A_t) = z_t^{f\Lambda}$ in the obvious notation

$$z_t^{f\Lambda} = \sum_{x \in I} f(t - \tau_x) 1_{[0,\lambda_x)}(t - \tau_x).$$

Thus in the symbols of the tree formulation, we have shown that $e^{-\alpha t} z_t^{V\Lambda} \to W$. The question is what other characteristics we can have instead of $V\Lambda$ (and what change in W we are then lead to).

For any $x \in I$ let $\mathcal{B}_x$ denote the σ-algebra generated by the complete lives of all individuals *not* stemming from x (with the convention that x stems from herself).

Lemma 5.1 *Let $\chi = \{\chi_x\}$ be a characteristic such that $\mathbb{E}[\chi_x(a)|\mathcal{B}_x] = 0$ for any $x \in I$ and $a \geq 0$. Then*
$$\mathbb{E}[(z_t^\chi)^2] = \mathbb{E}[z_t^{\chi^2}].$$

Proof: If $x \neq x'$, then one of the two is not in the daughter process of the other. Say that x' does not stem from x. Then

$$\mathbb{E}[\chi_{x'}(t-\tau_{x'})\chi_x(t-\tau_x)] = \mathbb{E}[\chi_{x'}(t-\tau_{x'})\mathbb{E}[\chi_x(t-\tau_x)|\mathcal{B}_x]] = 0,$$

since τ_x is measurable with respect to $\mathcal{B}_x$. Hence,

$$\mathbb{E}[(z_t^\chi)^2] = \mathbb{E}[(\sum_x \chi_x(t-\tau_x))^2] = \mathbb{E}[\sum_x \chi_x^2(t-\tau_x)] = \mathbb{E}[z_t^{\chi^2}].$$

□

Corollary 5.1 *Assume that $\mathbb{P}(\lambda_x \leq u|\mathcal{B}_x) = G(u)$ for some distribution function G, independently of the population. Write $S = 1-G$ for the survival function. Then, for any càdlàg and bounded f*
$$\mathbb{E}[(z_t^{f\Lambda} - z_t^{fS})^2] = \mathbb{E}[z_t^{f^2(\Lambda-S)^2}].$$

□

By Theorem 4.1

$$w(t) = e^{-\alpha t}\mathbb{E}[z_t^{V\Lambda}] = e^{-\alpha t}\int_0^t V(t-u)S(t-u)\mathbb{E}[y(du)]$$

remains bounded, as $t \to \infty$, firsthand in the special case of i.i.d life spans now under consideration, but also more generally.

Theorem 5.1 *Assume Conditions (A1)-(A3), and also that v_A^2 is bounded, so that*

$$w_t^{V\Lambda} := W_t = e^{-\alpha t}z_t^{V\Lambda} \to W,$$

a.s. and in L^2, as $t \to \infty$. If $\mathbb{P}(\lambda_x \leq u|\mathcal{B}_x) = G(u)$, then also

$$w_t^{VS} := e^{-\alpha t}z_t^{VS} \to W$$

in mean square. If further the reproduction intensity $\phi := mg + bS$ decreases slowly in the sense that

(A4) there are constants $a, b > 0$ such that $\phi(t+u) \geq (1-au)\phi(t)$ for all $t \geq 0$ and all $0 \leq u \leq b$

then the convergence holds a.s. as well.

Proof: Since $\sup V < \infty$ by (A1) and the second statement of Theorem 3.2, Corollary 5.1 yields

$$\mathbb{E}[(w_t^{V\Lambda} - w_t^{VS})^2] = \mathbb{E}[w_t^{V^2(\Lambda-S)^2}] \leq \sup V e^{-2\alpha t}\mathbb{E}[z_t^{V(\Lambda-S)^2}].$$

But

$$\mathbb{E}[z_t^{V(\Lambda-S)^2}] = \mathbb{E}[\sum_x V(t-\tau_x)\mathbb{E}[(1_{[0,\lambda_x)}(t-\tau_x) - S(t-\tau_x))^2|\mathcal{B}_x] =$$

$$= \mathbb{E}[\sum_x V(t-\tau_x)G(t-\tau_x)S(t-\tau_x)] \leq \mathbb{E}[\sum_x V(t-\tau_x)S(t-\tau_x)] =$$

$$= \mathbb{E}[\sum_x V(t-\tau_x)\mathbb{E}[1_{[0,\lambda_x)}(t-\tau_x)|\mathcal{B}_x]] =$$

$$= e^{\alpha t}\mathbb{E}[W_t] \leq K e^{\alpha t},$$

for som $K < \infty$, by Theorem 4.1 (1). Hence, $w_t^{V\Lambda} - w_t^{VS} \to 0$ in L^2. Since by Theorem 4.1 $W_t = w_t^{V\Lambda} \to W$ a.s. and in L^2, we can conclude the same in L^2 for w_t^{VS}, as $t \to \infty$.

In order to proceed to a.s. convergence, note that

$$\int_0^\infty \mathbb{E}[(w_t^{V\Lambda} - w_t^{VS})^2]dt = \int_0^\infty \mathbb{E}[w_t^{V^2(\Lambda-S)^2}]dt \leq$$

$$\sup V \int_0^\infty e^{-2\alpha t}\mathbb{E}[z_t^{V(\Lambda-S)^2}]dt \leq K\int_0^\infty e^{-\alpha t}dt < \infty.$$

Then, use Fubini's theorem to see that

$$\int_0^\infty (w_t^{V\Lambda} - w_t^{VS})^2 dt < \infty$$

a.s. Here $w_t^{V\Lambda}$ can be replaced by W, and thus provided w_t^{VS} does not oscillate too wildly the convergence of the integral implies a. s. convergence of

$$w_t^{VS} = \int_0^t e^{-\alpha(t-u)}V(t-u)S(t-u)e^{-\alpha u}y(du).$$

Indeed,

$$e^{-\alpha t}V(t)S(t) = \int_t^\infty e^{-\alpha u}\phi(u)du$$

and (A4) leads to

$$w_{t+u}^{VS} \geq (1-cu)w_t^{VS}$$

for a $c > 0$ and $0 \leq u \leq$ some $\gamma > 0$. Continue as in Harris (1963), p. 148, to see that if $w_{t_i}^{VS} \geq (1+\delta)W, t_{i+1} - t_i \geq \gamma$, then

$$\int_0^\infty (w_t^{VS} - W)^2 dt \geq \sum_i \int_0^\gamma (w_{t_i+u}^{VS} - W)^2 du = \infty,$$

provided $W > 0$ and $(1-c\gamma)(1+\delta) > 1$. Hence, under (A3) $\limsup w_t^{VS} > W > 0$ implies divergence of the integral.

In the same vein we can mimic Harris's argument that $\liminf w_t^{VS}$ cannot be strictly smaller than W, and the theorem follows

$\square$

In the convolution notation

$$\int_0^t e^{-\alpha(t-u)} V(t-u) S(t-u) e^{-\alpha u} y(du) \to W$$

it is natural to associate the proved convergence with Wiener's general Tauberian theorem (Widder, 1946, p. 214) in order to arrive at conclusions about the growth of $y(t)$, or about integrals where V has been replaced by other functions f, and in a later step by characteristics with conditional expectation f.

For Wiener's theorem it suffices that the Fourier transform of $e^{-\alpha t} V(t) S(t)$ never vanishes, that $e^{-\alpha u} y(du)$ gives finite measure to any finite interval, and that

$$\int_t^{t+1} e^{-\alpha u} y(du) \leq \int_t^{t+1} \frac{e^{-\alpha(t-u)} V(t-u) S(t-u)}{e^{-\alpha} V(1) S(1)} e^{-\alpha u} y(du),$$

which is bounded by some (stochastic) constant. The integrand $e^{-\alpha t} V(t) S(t)$ is clearly directly Riemann integrable, and further

$$\int_0^\infty e^{itu} e^{-\alpha u} V(u) S(u) du = \int_0^\infty e^{itu} du \int_u^\infty e^{-\alpha s} \phi(s) ds =$$

$$\int_0^\infty e^{-\alpha s} \phi(s) (e^{its} - 1) ds / it,$$

for $t \neq 0$. Thus, the condition of a non-vanishing Fourier transform reduces to

$$\int_0^\infty e^{its} e^{-\alpha s} \phi(s) ds \neq 1, t \neq 0,$$

always satisfied, since $e^{-\alpha s} \phi(s)$ is a probability density, cf. e.g. Durrett (1995), p. 131.

In other words, under the conditions of the theorem

$$e^{-\alpha t} z_t^f = \int_0^t e^{-\alpha(t-u)} f(t-u) e^{-\alpha u} y(du) \to \hat{f}(\alpha) w,$$

a.s and in quadratic mean, provided only $e^{-\alpha t} f(t)$ is directly Riemann integrable. Here hat denotes Laplace transform and w is $W/\widehat{VS}(\alpha)$. Indeed, the very same convergence

$$e^{-\alpha t} z_t^\chi \to \hat{f}(\alpha) w,$$

holds true for any bounded characteristic $\chi = \{\chi_x\}$ such that $\mathbb{E}[\chi_x | \mathcal{B}_x] = f$. In particular,

$$e^{-\alpha t} z_t \to \hat{S}(\alpha) w.$$

However, this is all under the assumption that $\mathbb{P}(\lambda_x \leq u | \mathcal{B}_x) = G(u)$, which we shall now free ourselves from.

Lemma 5.2 *Let χ be a bounded characteristic tending to zero as $z_t \to \infty$ in the sense that for any $\epsilon > 0$ there is a z such that $|\chi_x| < \epsilon$ if only $z_t > z$ for $t \geq \tau_x$. Then, provided $e^{-\alpha t} z_t^{V\Lambda}$ is bounded by an L^2 random variable Z, then a. s. and in mean square $e^{-\alpha t} z_t^{V\chi\Lambda} \to 0$, as $t \to \infty$ on the set where $z_t \to \infty$.*

Proof: For ϵ and z as above, let $z_t > z$ for $t \geq t_\epsilon$. Then,

$$|z_t^{V\chi\Lambda}| \leq Cy(t_\epsilon) + \epsilon z_t^{V\Lambda}.$$

On the set where t_ϵ is finite, this yields

$$\limsup e^{-\alpha t} |z_t^{V\chi\Lambda}| \leq \epsilon Z.$$

□

Theorem 5.2 *Assume Conditions (A1),(A2), (A3), and also that v_A^2 is bounded. Then, for any bounded, non-negative characteristic $\chi = \{\chi_x\}$ such that $\mathbb{E}[\chi_x|\mathcal{B}_x] \to f$, as $z_t \to \infty$,*

$$e^{-\alpha t} z_t^\chi \to \hat{f}(\alpha) w$$

in quadratic mean, provided $e^{-\alpha t} f(t)$ is directly Riemann integrable. If further Assumption (A4) holds, then we can also conclude a. s. convergence.

The theorem has two direct but important ($f = S$ or 1) special cases:

Corollary 5.2 *Under the asumptions given, $e^{-\alpha t} y(t) \to w/\alpha$ and $e^{-\alpha t} z_t \to \hat{S}(\alpha) w$ a.s. and in mean square, the latter convergence requiring, say, that h_A be majorized by some L^1-function.*

Proof: The fact that $e^{-\alpha t} z_t^{V\Lambda} \to W$ entails that also $e^{-\alpha t} z_t^{V\mathbb{E}[\Lambda|\mathcal{B}]} \to W$, where $\mathbb{E}[\Lambda|\mathcal{B}]$ denotes the characteristic $\{\mathbb{P}(\lambda_x > \cdot|\mathcal{B}_x)\}$. But

$$\mathbb{P}(\lambda_x > a|\mathcal{B}_x) = \mathbb{E}[e^{-\int_a^\infty h_{A_{\tau_x+u}}(u)du}|\mathcal{B}_x] \to$$
$$\to \mathbb{E}[e^{-\int_a^\infty h(u)du}] = S(a),$$

the arrow describing convergence in the sense of Lemma 5.2, and we have used dominated convergence of h_{A_t}, as $z_t \to \infty$. By the lemma therefore

$$e^{-\alpha t} z_t^{VS} \to W.$$

The rest of the proof runs as in the argument preceding Lemma 5.2. □

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6 References

1. Athreya K.B. and Ney P. *Branching Processes.* Springer 1972.

2. Borde-Boussion A-M. (1990) Stochastic demographic models: age of a population. *Stoch. Proc. Appl.* 35, 279-291.

3. Durrett, R. *Probability: Theory and Examples.* 2nd ed. Duxbury Press 1996.

4. Ethier S.N. and Kurtz T.G. *Markov Processes.* Wiley 1986.

5. Hamza K. and Klebaner F.C. (1995) Conditions for integrability of Markov chains. *J. Appl. Prob.* 32, 541-547.

6. Harris T.E. *The Theory of Branching Processes.* Springer 1963, Dover 1989.

7. Jagers P. *Branching Processes with Biological Applications.* Wiley 1975.

8. Jagers P. (1989) Branching Processes as Markov Fields. *Stochastic Process. Appl.* 32, 183-242.

9. Jagers P. (1997) Coupling and population dependence in branching processes. *Ann. Appl. Prob.* 7, 281 - 298.

10. Jagers P. (1998) Branching processes with dependence but homogeneous growth. Preprint 1998:31, Dep. Mathematics, Chalmers and Gothenburg Universities.

11. Klebaner F.C. (1984) Geometric rate of growth in population size dependent branching processes. *J. Appl. Prob.* 21, 40-49.

12. Klebaner F.C. (1989) Geometric growth in near-supercritical population size dependent multitype Galton-Watson processes. *Ann. Prob.* 17, 4, 1466-1477.

13. Klebaner F.C. (1994) Asymptotic behaviour of Markov population processes with asymptotically linear rate of change. *J. Appl. Prob.* 31, 614-625.

14. Liptser R.S. and Shiryayev A.N. *Theory of Martingales.* Kluwer, 1989.

15. Metivier M. (1987) Weak convergence of measure valued processes using Sobolev imbedding techniques. *Lect. Notes in Maths.,* Vol. 1236 (Springer 1987), 172-183.

16. Nerman O. (1981) On the convergence of supercritical general (C-M-J) branching processes. *Z. Wahrscheinlichkeitstheorie verw. Gebiete* 57, 365-395.

17. Oelschläger K. (1984) A martingale approach to the Law of Large Numbers for weakly interacting stochastic processes. *Ann. Prob.* 12, 458-479.

18. Oelschläger K. (1990) Limit theorems for age-structured populations. *Ann. Prob.* 18, 290-318. 458-479.

19. Protter P. *Stochastic Integration and Differential equations.* Springer-Verlag, 1992.

20. Schuh H.-J. (1982) Seneta constants for the supercritical Bellman-Harris process. *Adv. Appl. Prob.* 14, 732-751.

21. Widder D.V. *The Laplace Transform.* Princeton University Press 1946.