The Annals of Applied Probability
1997, Vol. 7, No. 2, 281–298

COUPLING AND POPULATION DEPENDENCE IN BRANCHING PROCESSES[1]

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Consider supercritical general branching processes, where, however, individual reproduction may be influenced by the history of the population, in particular by the total population size. Assume that reproductions approach those of a classical, possibly multitype, supercritical process either from above or from below as the population grows. Conditions are established for the population-history dependent populations to display balanced exponential growth with the same Malthusian parameter as the limiting population. Applications are made to a tumor model with quiescence.

1. Introduction. Recently, two attempts have been made to study interaction in supercritical general branching processes. Olofsson (1994, 1996) used the concept of macroindividuals to analyze populations with interaction, which is local in the pedigree, such as within-sibship-dependence. In that prototype case, each sibship is turned into a macroindividual, these latter forming independent individuals in a new branching population. Jagers (1996) used conditioning on individually adapted historical σ-algebras to obtain asymptotic exponential growth in populations satisfying general criteria of limited collaboration between disjoint daughter processes and a stabilization of the influence of remote history.

The former approach is inherently local and the latter also turns out not to adapt itself readily to situations where individual behavior is affected by global properties of the population, such as the total population size.

Such dependencies have earlier been studied only in the simple Bienaymé–Galton–Watson or real-time Markov branching cases; compare the series of papers by Klebaner (1984, 1985, 1989, 1994), Küster (1983, 1985), Yurachkovskii (1987) and Rittgen's thesis (1986). A special form is what Sevastyanov and Zubkov (1974) called controlled processes, their idea being that the number of reproducing mothers is affected by the population size, the reproduction in itself remaining unaffected. In the other cases, the presumption is that the offspring distribution in a generation is directly determined by the generation size. Kersting (1986) and Keller, Kersting, and Rösler (1987) made a general approach to dependence in discrete time population growth, based on stochastic difference equations.

Received January 1996; revised November 1996.

[1] Support from the Swedish Natural Sciences Research Council is acknowledged.

AMS 1991 *subject classifications*. Primary 60J80; secondary 60F25, 92A15.

Key words and phrases. Branching processes, population dynamics, cell kinetics, population size dependence.

We consider general, abstract multitype, supercritical populations, where individual reproduction may be affected by properties of the whole population, such as its size. The situation we shall focus upon is that where reproduction tends to decrease as the population grows, the limiting individual reproductions being those of a traditional (i.e., population-independent) supercritical branching population. Alternatively, one could think of reproduction as being enhanced by population growth. The purpose is to find conditions for the population dependence not to matter so that, asymptotically, classical Malthusian growth shows up with the same parameters as those of the limiting population where individuals reproduce independently, once they have been born into the population and obtained their types. We shall refer to the these latter reproductions and the whole limiting population they define as imaginary. In contrast, the population-dependent entities will be called actual.

The idea is to couple actual and imaginary reproductions of individuals. If the imaginary reproduction does not exceed the actual, then we can erase actual newborns in a thought experiment, in the hope of mimicking the imaginary reproduction process. In this manner, any individual in the original population gives rise to two populations, an actual daughter population tree and a thinned version. To the extent the mimicking is successful, the latter are classical independently growing branching trees, and their growth is exponential. If the thinning ultimately ceases to have effect, the original population with dependence must also exhibit the same Malthusian behavior, and we have found a successful coupling. There is also a dual theorem for populations approaching the limit reproduction from below, as populations grow, and versions where convergence need not be from a given side could also be stated.

Finally, applications will be made to a tumor model with quiescence, which commands independent interest [Gyllenberg and Webb (1990)]. It will be discussed in two versions, first with dependence upon cell age and tumor size (Jagers, 1997) and then in the original Bell–Anderson formulation, where it is cell size rather than age that matters.

The simple structure of the former highlights the essentials of the whole approach: when a cell is born, assume that it enters the so-called G_0 state of eternal quiescence with a probability $1 - p(n)$, where n is the population (i.e., tumor) size at the moment of birth. Otherwise, with probability $p(n)$ the cell embarks upon the cell cycle, which is assumed to have i.i.d. lengths with an arbitrary but continuous distribution function. Usually it is assumed that the growth rate decreases with tumor size, so that $1 \geq p(n) \downarrow p > 1/2$, as $n \to \infty$. The coupling argument shows that if (and only if)

$$\sum \{ p(n) - p \} < \infty,$$

then after some random but finite time (not a stopping time, though) all individuals will behave as those of an underlying binary splitting Bellman–Harris process with a constant splitting probability p and a quiescent state, entered by nonsplitting cells. Thus the tumor-size dependent model must exhibit the same exponential growth and ultimate asymptotic composition as the classical branching process, and monotonicity in convergence is actually not required.

In the general case, the probabilities $p(n)$ and p are replaced by expected offspring numbers, and the factor influencing individual reproduction need not be precisely population size, somehow measured, but could concern other properties of the population as a whole. For size dependence our results can, however, be summarized as: if $m(n, s)$ denotes the expected total number of children of a type s individual born into a size n population and $m(s)$ denotes the same number in a classical Malthusian supercritical general branching population, $m(n, s) \geq m(s)$, then the convergence

$$\sum \sup_{s} \{m(n, s) - m(s)\} < \infty$$

implies almost sure exponential growth with the same Malthusian parameter and the same stable asymptotic composition as in the classical process.

In the one-type case, this takes the form $\sum_n \{m(n) - m\} < \infty$, $m(n)$ being the expected number of children of an individual born into a size n population. This should be compared to Klebaner's (1984) essentially necessary and sufficient condition for exponential increase of population-size dependent Galton–Watson processes, namely, $\sum_n \{m(n) - m\}/n < \infty$ and similarly in the Markov branching case (1994). Besides smoothness requirements, Gyllenberg and Webb (1990) also arrive at a condition of this form (their H.7 and H.8).

The fact that this very same condition is obtained in two radically different special models makes it plausible that it catches some fundamental property also in more general setups, and shows that exponential increase can occur even though the coupling does not succeed. That requires that the never ending differences be rare and some sort of symmetry in population growth. These matters are discussed in Section 6.

2. Framework.

We quickly recapitulate the framework as given in Jagers (1989). Let

$$I = \bigcup_{n=0}^{\infty} N^n, \qquad N^0 = \{0\}, \qquad N = \{1, 2, \dots\}$$

denote the Ulam–Harris space of all possible individuals. Think of the population as initiated by an Eve, whose name in I is 0, and of $xk := (x, k) \in I$ as x's kth child, twins, *and so on*, numbered in an arbitrary way. Assume that each $x \in I$ has a reproduction process ξ_x, giving x's age at her successive childbearings and the types of the children then born, the latter being elements of a type space $(S, \mathscr{S})$ with a countably generated σ-algebra.

Thus, there is a sequence of maps $(\tau_x(k), \sigma_x(k))$, $k = 1, 2, \dots, 0 \leq \tau_x(1) \leq \tau_x(2) \leq \cdots \leq \infty$, $\sigma_x(k)$ with values in S and the interpretation that $\tau_x(k)$ is x's age at giving birth to her kth child and $\sigma_x(k)$ is that child's type. Of course, if $\tau_x(k) < \tau_x(k+1) = \infty$, then x never has more than k children, and the corresponding individuals in I are not realized. Clearly,

$$\xi_x(A \times B) = \#\{k \in I;\ \sigma_x(k) \in A, \tau_x(k) \in B\}.$$

The birth time and type of an individual $x \in I$ are denoted by τ_x and σ_x, respectively. These are inductively given from a starting type $\sigma_0 \in S$ and $\tau_0 = 0$.

Population size can be measured by random characteristics. That is, at time t the individual x is assumed to have some weight $\chi_x(\sigma_x, t - \tau_x)$, where χ_x is a functional χ as evaluated on x's daughter process. More precisely, define S_x to be the coordinate projection, restricting attention from the space of all lives to only the life of x and all her progeny. In other words S_x renders x the ancestor in a space, which otherwise has the same structure as the original space Ω of all possible life careers of all possible individuals. A characteristic is a measurable map $\chi\colon S \times \mathbb{R}_+ \times \Omega \to \mathbb{R}_+$, which is D-valued in its second coordinate, interpreted as age. Further, $\chi_x := \chi \circ S_x$. Thus, an individual's weight, once her type and age are given, is determined by her own life, and possibly her progeny's lives. We assume characteristics to be nonnegative, bounded and vanishing for negative ages. Typical characteristics would be $1_{S \times \mathbb{R}_+}$, or $1_{A \times [0, \min(\lambda_x, a)]}$ for $A \in \mathscr{S}$. Such characteristics, and many others, are individual in the sense that they actually depend only upon x's own life, type and age, and remain unaffected by x's progeny.

The χ-counted population size at time t is then defined as

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

Thus, the characteristic $1_{S \times \mathbb{R}_+}$ yields the total population, that is, all those born, and the other characteristic mentioned gives the number of those alive of type A and not older than a. Though it is important to vary the characteristics in order to catch the asymptotic composition of the population, we shall usually consider a fixed, but arbitrary such entity χ, and then sometimes write just z_t for z_t^χ.

In the classical case of independent reproduction, the reproduction process depends upon the past only through the individual type and the form of supercritical population growth is essentially governed by the reproduction kernel μ, defined as the expected number of births of children of various types and at various ages:

$$\mu(r, ds \times dt) := E_r[\xi(ds \times dt)],$$

r being the type of the individual with reproduction ξ. The usual assumption is that the population is Malthusian and supercritical, this meaning that there is a number $\alpha > 0$, the Malthusian parameter, such that the kernel $\hat{\mu}(\alpha)$,

$$\hat{\mu}(r, ds; \alpha) := \int_0^\infty e^{-\alpha t} \mu(r, ds \times dt)$$

has Perron root one and is what Shurenkov (1989) calls conservative. [This corresponds to irreducibility and α-recurrence in the terminology of Niemi and Nummelin (1986).] By the abstract Perron–Frobenius theorem [Shurenkov (1989), page 43, or Nummelin (1984), page 70], there is then a σ-finite measure π on the type space $(S, \mathscr{S})$ and a strictly positive a.e. $[\pi]$ finite measurable function h on the same space such that

$$\int_S \hat{\mu}(r, ds; \alpha)\pi(dr) = \pi(ds),$$

$$\int_S h(s)\hat{\mu}(r, ds; \alpha) = h(r).$$

Further, strong or positive α-recurrence holds in the sense that $h \in L^1[\pi]$ is required and

$$0 < \beta = \int_{S\times S\times R_+} te^{-\alpha t}h(s)\mu(r, ds \times dt)\pi(dr) < \infty.$$

(In population dynamics this entity might be interpreted as the long-run stable age at childbearing.) Then, one norms to

$$\int_S h\, d\pi = 1$$

and makes the homogeneity assumption that $\inf h > 0$. Then π is finite and can (and will) also be normed to a probability measure. These are the conditions (i.e., those concerning μ) for the general Markov renewal theorem of Shurenkov [(1989), page 107], which in the nonlattice case lead to the expected asymptotics

$$\mathbb{E}_s[z_t^\chi] \sim h(s)\mathbb{E}_\pi[\hat{\chi}(\alpha)]e^{\alpha t}/\alpha\beta,$$

as $t \to \infty$. [Here the hat denotes Laplace transform, so that

$$\hat{\chi}(\alpha) = \alpha\int_0^\infty e^{-\alpha t}\chi(\sigma, t)\, dt,$$

where σ denotes the type, following the stable type distribution π, as indicated by the suffix of the expectation, $\mathbb{E}_\pi := \int_S \mathbb{E}_s\pi(ds)$, and the necessary direct-Riemann-type regularity assumptions on the expected characteristic are tacitly assumed.]

The fundamental finding of the theory of general, supercritical branching processes is that under very broad conditions this leads to a similar behavior of the process itself, in L^1, in L^2, in probability, or a.s. for π-almost-all $\mathbb{P}_s$,

$$z_t^\chi \sim w\mathbb{E}_\pi[\hat{\chi}(\alpha)]e^{\alpha t}/\alpha\beta,$$

where w is a random variable, vanishing precisely if the process dies out and with mean value $\mathbb{E}_s[w] = h(s)$. The fact that this holds for many different χ's is what is referred to as balanced exponential growth in certain branches of biology and as asynchronous exponential growth in (deterministic) mathematical population dynamics. Here we shall bypass the technical conditions for such growth [cf. Jagers (1989), Nerman (1981)], and instead assume directly that the limiting, classical independent-individual, branching population exhibits balanced exponential growth. Somewhat inadvertently, we shall summarize this by referring to the (latter) population as (nonlattice) Malthusian, adding the particular character of the asymptotics (a.s., in probability, or in the mean) whenever necessary. The populations under study will be referred to as actual or history-dependent. It will be assumed that they are always finite (at finite times). If they exhibit the exponential asymptotics of the formula above, they will also be called Mathusian and the entities α, h, and π will be referred to as their Malthusian parameter, fitness function and stable type distribution, as for populations with independently acting individuals.

3. Minorized reproduction. By the assumption that history-dependent populations remain finite at finite times, individuals can be numbered as they appear, starting from the ancestor X_1 and continuing $X_2, X_3, \dots,$ with simultaneously born individuals—if any—so numbered that progeny can never precede their ancestors. A filtration $\{\mathscr{F}_n\}$ of σ-algebras is defined by letting $\mathscr{F}_n$ be generated by the complete lives of all individuals $X_1, X_2, \dots, X_n$. Define $\mathscr{G}_x$ by

$$A \in \mathscr{G}_x \Leftrightarrow A \cap \{X_n = x\} \in \mathscr{F}_{n-1},$$

for all n. If no individuals are ever born together, this means that $\mathscr{G}_x$ is the σ-algebra generated by the complete lives of all individuals born before x. The reason for this seemingly complicated, stopping line type definition is to cover possible simultaneous births. The time τ_x when $x \in I$ is born is measurable with respect to $\mathscr{G}_x$, as is x's type σ_x (with a suitable convention for never-realized individuals).

The primary concern of this section is the situation where individual reproduction tends to exceed what it would have been in an imaginary infinite population, "tends to exceed" being interpreted as "stochastically larger than." In other words, if $x \in I$, $\tau_x < \infty$, and η is a generic imaginary reproduction point process, then the basic assumption is that for all u and sets A, B,

$$\mathbb{P}(\xi_x(A \times B) > u \mid \mathscr{G}_x) \geq \mathbb{P}_{\sigma_x}(\eta(A \times B) > u),$$

where the right-hand side $\mathbb{P}$-suffix indicates the dependence upon type of reproduction in a general branching process. Let $\mathbb{P}^x$ denote a regular version of the conditional distribution, given $\mathscr{G}_x$, supposed to exist. By Strassen's theorem [Lindvall (1992), page 129] we may assume that for each $x \in I$ there is a pair of reproduction point processes (ξ_x, η_x) such that ξ_x is x's original reproduction, whereas η_x is the imaginary reproduction, "if the population were already infinite," and $\mathbb{P}^x(\xi_x \geq \eta_x) = 1$ in the obvious partial order of measures. By an Ionesco–Tulcea construction [cf. Jagers (1989)] we may then assume the pairs (ξ_x, η_x) to be defined on a joint population probability space with the proper conditional distributions and still satisfying $\xi_x \geq \eta_x$ a.s.

Now define

$$\tau := \inf\{t \geq 0; t \leq \tau_x < \infty \Rightarrow \xi_x = \eta_x\},$$

so that any individual born into the actual population after τ has coinciding actual and imaginary daughter population trees. Let

$$I_u := \{x \in I;\ \tau_{x\text{'s mother}} < u \le \tau_x < \infty\}.$$

If $\tau < \infty$, then I_τ is a well-defined finite random set, and in terms of the daughter processes

$$z_t^{\chi}(x) := \sum_{x' \text{ stems from } x} \chi_{x'}(t - \tau_{x'}),$$

we can write

$$z_t^{\chi} = \sum_{\tau_x \le \tau} \chi_x(t - \tau_x) + \sum_{x \in I_\tau} z^{\chi}_{t - \tau_x}(x),$$

which is the fundamental decomposition at τ. Since the real and imaginary trees growing out from any $x \in I_\tau$ coincide by definition, there is a $w(x)$ with

$$z_t^{\chi}(x) \sim w(x)\mathbb{E}_\pi[\hat{\chi}(\alpha)]e^{\alpha t}/\alpha\beta,$$

and we may hope that

$$z_t^{\chi} \sim \left\{\sum_{x \in I_\tau} \exp(-\alpha\tau_x)w(x)\right\}\mathbb{E}_\pi[\hat{\chi}(\alpha)]\exp(\alpha t)/\alpha\beta,$$

in suitable senses, as $t \to \infty$.

This sketchy argument is correct if the characteristic is determined by reproductions, so that the χ_x, $\tau_x > \tau$ follow the same law as they would in a branching population with the imaginary reproductions η_x. One such characteristic is $1_{S\times\mathbb{R}_+}$. Others are those counting the number of individuals of certain types, $1_{A\times\mathbb{R}_+}$, $A \in \mathscr{S}$. But already the living population, counted by $1_{S\times[0,\lambda]}$, need not have this property, unless life span is a function of reproduction. Certainly, it is conceivable that life continues to, say, shrink, while the population increases, even though reproductions do not change any further.

One could think of different conditions to preclude such phenomena, the most natural maybe being to require that conditionally, given x's type σ_x and all the reproductions $\xi_{x'}$ of individuals x' stemming from x, the χ_x are i.i.d. Call such characteristics conditionally population independent.

THEOREM 1. *Consider a history-dependent population, counted by a conditionally population-independent characteristic. Assume reproductions ξ to be finite and stochastically minorized by the reproductions of a general Malthusian branching population with the finite reproduction kernel μ. If*

$$\sum_{\tau_x < \infty} \mathbb{E}_s[\xi_x(S \times \mathbb{R}_+) \mid \mathscr{G}_x] - \mu(\sigma_x, S \times \mathbb{R}_+) < \infty,$$

then the individual reproductions in the history-dependent population coincide with those of a version of the minorizing process from some finite random time on. Thus it is also Malthusian, a.s. if the branching population is Malthusian a.s., or in probability if that was the case for the latter. The *exponential growth parameter* α, *fitness function and stable asymptotic composition also remain the same*, *as defined by* μ.

PROOF. By assumption, all reproductions $\xi_{X_i}(S \times \mathbb{R}_+)$ are finite. Since a.s. $\xi_x \geq \eta_x$, $\tau = \infty \Leftrightarrow \xi_{X_i} > \eta_{X_i}$ i.o. $\Leftrightarrow \xi_{X_i}(S \times \mathbb{R}_+) > \eta_{X_i}(S \times \mathbb{R}_+)$ i.o. But by the conditional Borel–Cantelli lemma [Breiman (1968), page 96], a.s.,

$$\begin{aligned}
&\xi_{X_i}(S \times \mathbb{R}_+) > \eta_{X_i}(S \times \mathbb{R}_+) \text{ i.o.}\\
&\quad\Leftrightarrow \sum \mathbb{P}_s\big(\xi_{X_i}(S \times \mathbb{R}_+) > \eta_{X_i}(S \times \mathbb{R}_+) \mid \mathscr{F}_{i-1}\big) = \infty\\
&\quad\Rightarrow \sum \mathbb{E}_s\big[\xi_{X_i}(S \times \mathbb{R}_+) - \eta_{X_i}(S \times \mathbb{R}_+) \mid \mathscr{F}_{i-1}\big] = \infty\\
&\quad\Rightarrow \sum_{\tau_x < \infty} \mathbb{E}_s[\xi_x(S \times \mathbb{R}_+) \mid \mathscr{G}_x] - \mu(\sigma_x, S \times \mathbb{R}_+) = \infty,
\end{aligned}$$

the second to last implication being by Markov's inequality.

But the last sum was assumed to converge. If, therefore, the population with reproductions η is a.s. Malthusian, the fundamental decomposition yields without further ado that so is the history-dependent population. Similarly Malthusianness in probability carries over to history-dependent populations, since I_τ must still have finitely many members a.s. □

That the theorem holds literally for stochastically majorized reproductions goes without saying. What may be more intriguing is that the obvious stochastic order we have been using could possibly be replaced by weaker orderings. For example, define $\xi \succcurlyeq \eta$ to mean that $\xi(A \times B) \geq \eta(A \times B)$ for all $A \in \mathscr{S}$ but only for intervals $B = [0, t]$, $t \geq 0$. This is a partial order in which the requirement that the conditional reproduction of an individual tends to exceed the imaginary reproduction in an infinite population has the interpretation that large surrounding populations possibly do not only tend to abort births but may as well just postpone them. Like the ordering "$\geq$" it is closed in the weak topology and so Strassen's theorem applies. However, elegant convergence criteria seem harder to formulate.

4. Population size dependence.

The seemingly abstract main theorem takes a neater form if history expresses itself through population size, z_t, as measured by some implicit characteristic. As in the Introduction, we assume that the expected number of children of an s-type individual born into a population of size z is $m(z, s)$. Correspondingly, write $m(s) := \mu(s, S \times \mathbb{R}_+)$ for infinite populations. In this situation we call history-dependent reproductions population-size dependent.

The condition of Theorem 1 takes the form

$$\sum_{\tau_x < \infty} m(z_{\tau_x}, \sigma_x) - m(\sigma_x) < \infty$$

or

$$\sum_n m(z_{\tau_{X_n}}, \sigma_{X_n}) - m(\sigma_{X_n}) < \infty,$$

which is more suitable in the present context, since many characteristics lead to $z_{\tau_{X_n}} = O(n)$. If the relevant population size is the total number of births, y_t, this is even exact, $y_{\tau_{X_n}} = n$, provided individuals are born one by one. If this is not required but the natural assumption made that $\sup_n(y_{\tau_{X_n}} - y_{\tau_{X_n -}}) < \infty$, it remains true that $y_{\tau_{X_n}} \sim n$, as $n \to \infty$.

With a more general but bounded ($\le c$, say) characteristic, the resulting z_t will not exceed cy_t. In many cases it is easy to see that also

$$\liminf_{n \to \infty} z_{\tau_{X_n}} / y_{\tau_{X_n}} > 0,$$

by martingale or law-of-large-numbers type arguments (and the same for values immediately before births, $z_{\tau_{X_n -}} / y_{\tau_{X_n -}}$): assume that there is an age interval $[a, b]$ and a number $d > 0$ such that $\mathbb{E}_s[\chi_x(t) \mid \mathscr{G}_x] \ge d$ for $a \le t \le b$. Then, by conditional population independence often $\liminf_{t \to \infty} z_t / (y_{t-a} - y_{t-b}) \ge d$. If not only $y_{\tau_{X_n}} = O(n)$, but also $y_{\tau_{X_{n-a}}} - y_{\tau_{X_{n-b}}} = O(n)$, as $n \to \infty$, then $z_{\tau_{X_n}} = O(n)$.

Corollary 2. *In the setting of Theorem* 1, *assume that the characteristic is bounded*, *that*

$$\sup_n(y_{\tau_{X_n}} - y_{\tau_{X_n -}}) < \infty,\ 0 < \liminf z_{\tau_{X_n}}/n \le \limsup z_{\tau_{X_n}}/n < \infty,$$

and that $\mathbb{E}_s[\xi_x(S \times \mathbb{R}_+) \mid \mathscr{G}_x] = m(z_{\tau_x}, \sigma_x)$. *Write* $m(s) := \mu(s, S \times \mathbb{R}_+)$. *If*

$$\sum_n \sup_s \{m(n, s) - m(s)\} < \infty,$$

then the population with population-size dependent reproductions is Malthusian together with the limiting branching population and shares its Malthusian parameters.

Example. Besides the total population y_t, the most natural choice of z_t is the number of individuals alive. For this purpose, let λ_x denote x's life span, so that for any $a \le t$,

$$z_t := \sum_{\tau_x \le t} 1_{\{\lambda_x > t - \tau_x\}} \ge \sum_{t - a \le \tau_x \le t} 1_{\{\lambda_x > a\}}.$$

If, say, life spans are i.i.d. with distribution L (so that population size may only influence reproduction and not life span), clearly

$$\begin{aligned} 1 &\ge z_{\tau_{X_n}}/n \\ &\ge \left\{ (y_{\tau_{X_n}} - y_{\tau_{X_{n-a}}}) / y_{\tau_{X_n}} \right\} \frac{1}{y_{\tau_{X_n}} - y_{\tau_{X_{n-a}}}} \sum_{i = y_{\tau_{X_{n-a}}}}^{y_{\tau_{X_n}}} 1_{\{\lambda_{X_i} > a\}} \to 1 - L(a) > 0, \end{aligned}$$

if a is small enough, newborns do not necessarily face immediate death, and $y_{\tau_{X_{n-a}}} - y_{\tau_{X_{n-b}}} = O(y_{\tau_{X_n}})$, as $n \to \infty$.

5. Uniform integrability. Usually expected asymptotics are easy, and the asymptotics of the processes themselves hard. Here it is the other way round: since the coupling time τ is not necessarily a stopping time, expected

Malthusian growth is no immediate consequence of a.s. Malthusian growth plus Malthusianness in L^1 of the limiting population with imaginary reproductions.

LEMMA 3. *Let* $D_n \geq \mathbb{E}_s[\, \xi_{X_n}(S \times \mathbb{R}_+) \mid \mathscr{F}_{n-1}] - m(\sigma_{X_n})$, *under the minorization assumptions of Theorem* 1. *Then*, *for* $p \geq 1$,

$$\sum_n n^p \mathbb{E}_s[D_n] < \infty \Rightarrow \mathbb{E}_s[y_\tau^p] < \infty.$$

PROOF. If $\nu := \inf\{n; k \geq n \Rightarrow \xi_{X_k} = \eta_{X_k}\}$, then $y_\tau = y_{\tau_{X_\nu}}$ and

$$\begin{aligned} \mathbb{P}_s(\nu > n) &\leq \sum_{k>n} \mathbb{P}_s(\xi_{X_k} > \eta_{X_k}) \\ &\leq \sum_{k>n} \mathbb{E}_s\big[\xi_{X_k}(S \times \mathbb{R}_+) - \eta_{X_k}(S \times \mathbb{R}_+)\big] \\ &= \sum_{k>n} \mathbb{E}_s\big[\mathbb{E}_s\big[\xi_{X_k}(S \times \mathbb{R}_+) \mid \mathscr{F}_{k-1}\big] - m(\sigma_{X_k})\big] \\ &\leq \sum_{k>n} \mathbb{E}_s[D_k]. \end{aligned}$$ □

Often, for example, in the total population-size dependent case, D_n can be chosen in a nonstochastic fashion, as $\sup_s\{m(n, s) - m(s)\}$.

LEMMA 4. *Let* $\{U_n\}$ *be an* L^2*-bounded sequence of random variables and* ν *positive*, *integer valued*, *and in* L^p *for some* $p > 2$. *Then*,

$$\sum_{n=1}^{\nu} U_n \in L^1.$$

PROOF. By Schwarz's inequality

$$\begin{aligned} \mathbb{E}\left[\left|\sum_{n=1}^{\nu} U_n\right|\right] &\leq \sum_{n=1}^{\infty} \mathbb{E}[|U_n|; \nu > n] \\ &\leq \sum_{n=1}^{\infty} \mathbb{E}^{1/2}[U_n^2]\mathbb{P}^{1/2}(\nu > n) \leq C \sum_{n=1}^{\infty} \mathbb{P}^{1/2}(\nu > n), \end{aligned}$$

for some constant C. However, if $\{a_n\}$ is $\{\mathbb{P}(\nu > n)\}$, or any nonnegative sequence with $\sum n^{p-1}a_n < \infty$, then

$$\sum_n \sqrt{a_n} = \sum_n \sqrt{n^r a_n}\, n^{-r/2} \leq \Big\{\sum n^r a_n\Big\}^{1/2} \Big\{\sum_n n^{-r}\Big\}^{1/2} < \infty,$$

if $r = p - 1 > 1$. □

REMARK. The moment condition was chosen by conventionality; a sharper criterion is the convergence of $\sum \sqrt{\mathbb{P}(\nu > n)}$. Note that $\sum \sqrt{\mathbb{P}(\nu > n)} < \infty \Rightarrow \mathbb{E}[\nu^2] < \infty$ but not conversely (choose $a_n = 1/n^2 \log^2 n$).

Now, write

$$\begin{aligned} w_t &:= e^{-\alpha t} y_t, \qquad w_t(x) := e^{-\alpha t} y_t(x) \\ &= e^{-\alpha t}\#\{x' \in I \text{ which stem from } x \text{ and } \tau_{x'} \le t\}, \end{aligned}$$

and add bars when referring to the limiting classical population with reproduction processes η. Assume that the latter population is L^2-Malthusian. Then $\sup_t \mathbb{E}_s[\overline{w}_t^2] < \infty$, and

$$w_t \le y_\tau + \sum_{x \in I_\tau} w_{t-\tau_x}(x) = y_\tau + \sum_{x \in I_\tau} \overline{w}_{t-\tau_x}(x).$$

THEOREM 5. *Suppose that the limiting population is a.s. and L^2-Malthusian, that some sequence $\{D_n\}$ satisfies Lemma 5 with $p > 2$, and finally that $\sup_x \mathbb{E}_s[\hat{\xi}_x(2\alpha)] < \infty$. Then $\sup_t w_t \in L^1$. Hence Malthusianness follows not only a.s. but also in L^1.*

PROOF. By Lemma 5, $y_\tau \in L^p$. With $\nu = y_\tau$ and $\nu_n := \xi_{X_n}(S \times \mathbb{R}_+)$,

$$\sum_{x \in I_\tau} \overline{w}_{t-\tau_x}(x) \le \sum_{n=1}^{\nu} \left\{ \sum_{i=1}^{\nu_n} \overline{w}_{t-\tau_{X_n i}}(X_n i) \exp(-\alpha \tau_i(X_n)) \right\};$$

recall that $\tau_i(x)$ denotes x's age at begetting her ith child. In this

$$\mathbb{E}_s\left[\overline{w}^2_{t-\tau_{X_n i}}(X_n i) \mid \mathscr{F}_n\right]$$

is bounded by some constant K. Since ν_n and the $\tau_i(X_n)$ are measurable with respect to $\mathscr{F}_n$, and the different $\overline{w}_{t-\tau_{X_n i}}(X_n i)$, $i = 1, \dots, \nu_n$ conditionally independent, it follows that

$$\begin{aligned} &\mathbb{E}_s\left[\left\{\sum_{i=1}^{\nu_n} \exp(-\alpha\tau_i(X_n))\overline{w}_{t-\tau_{X_n i}}(X_n i)\right\}^2\right] \\ &\quad = \mathbb{E}_s\left[\operatorname{Var}_s\left[\sum_{i=1}^{\nu_n} \exp(-\alpha\tau_i(X_n))\overline{w}_{t-\tau_{X_n i}}(X_n i)\middle| \mathscr{F}_n\right]\right] \\ &\qquad + \mathbb{E}_s\left[\mathbb{E}_s^2\left[\sum_{i=1}^{\nu_n} \exp(-\alpha\tau_i(X_n))\overline{w}_{t-\tau_{X_n i}}(X_n i)\middle| \mathscr{F}_n\right]\right] \\ &\quad \le 2K\mathbb{E}_s\left[\hat{\xi}_{X_n}(2\alpha)\right] < \infty, \end{aligned}$$

by assumption. Hence we can apply Lemma 4 to conclude the proof. □

COROLLARY 6. *For population-size dependent reproductions, strengthen the conditions of Corollary 2 so that the limiting imaginary population is also L^2-Malthusian and*

$$\sum_n \sup_s n^p\{m(n,s) - m(s)\} < \infty,$$

for some $p > 2$. *Then*

$$z_t^{\chi} \sim \left\{ \sum_{x \in I_\tau} \exp(-\alpha\tau_x) w(x) \right\} \mathbb{E}_\pi[\hat{\chi}(\alpha)] \exp(\alpha t)/\alpha\beta,$$

in L^1 *as well as a.s.*

6. When the coupling barely fails....

The difference between our criterion and the Klebaner and Gyllenberg and Webb condition renders it plausible that cases exist where the coupling is not successful, and possibly $\tau = \infty$, but nevertheless differences between the imaginary and actual reproductions are rare enough for the actual process ultimately to display the Malthusian behavior of the imaginary population.

In order to catch such situations, note that the strict ordering $\xi_x \geq \eta_x$ means that the imaginary reproduction can be thought of as arising from the actual, population-history dependent reproduction through abortion of some children. Write δ_x to indicate abortion or not of x, so that

$$\eta_x(A \times B) = \sum_{k=1}^{\infty} (1 - \delta_{xk}) 1_{\{\tau_x(k) \in A,\, \sigma_x(k) \in B\}}.$$

Recall the definitions of age at kth birth, and type of the child then born; the Ulam–Harris numbering consistently refers to the actual population. Note that the latter is not affected by the value of δ_x, so that given $\mathscr{G}_x$, δ_x and the actual population are independent. Define

$$\varepsilon_x := \mathbb{E}_s[\delta_x \mid \mathscr{G}_x],$$

and write $\varepsilon(z_{\tau_x})$ for ε_x in case of population-size dependence. (It could well be argued that ε should be determined by the size immediately before birth, z_{τ_x-}, instead.)

THEOREM 7. *Let* $\{z_t^{\chi}\}$ *be the population as counted by a conditionally population independent characteristic* χ. *Assume reproductions* χ *are finite and stochastically minorized by the reproductions of a general Malthusian branching population with the finite reproduction kernel* μ (*defining the Malthusian parameter* α, *stable type distribution* π, *and fitness* h). *Assume that* $w_t := e^{-\alpha t} z_t^{\chi}$ *is tight.*

Further, suppose that for some constant K,

$$\mathbb{E}_s\left[z_{t-\tau_x}^{\chi}(x)/z_t^{\chi} \mid \mathscr{G}_x \right] \leq K/z_{\tau_x}^{\chi}$$

for all $x \in I$ *and* $t \geq \tau_x$, *and that*

$$\sum_x \mathbb{E}_s\left[\varepsilon_x / z_{\tau_x}^{\chi} \right] < \infty.$$

Then, w_t *tends in probability to some finite* $w \geq 0$, *not identically zero.*

We shall refer to the basic condition

$$\mathbb{E}_s\left[z^{\chi}_{t-\tau_x}(x)/z^{\chi}_t \mid \mathscr{G}_x \right] \le K/z^{\chi}_{\tau_x}$$

as the condition of symmetric growth.

The theorem has one direct and two less immediate corollaries.

COROLLARY 8. *In the population-size dependent case, besides tightness and symmetric growth assume that* $\mathbb{E}_s[z^{\chi}_{\tau_{X_n}}] = O(n)$ *and that* $\varepsilon(t)/t$ *is ultimately concave, as* $t \to \infty$. *Then*

$$\sum \varepsilon(n)/n < \infty$$

implies that Malthusianness carries over.

COROLLARY 9. *For population-size-dependent Galton–Watson processes with* $z_t = z^{\chi}_t = z_{[t]}$ *and* $m(n)$ *denoting the expected individual offspring in a generation of size* n,

$$\sum \varepsilon(n)/n < \infty \Leftrightarrow \sum \{m(n) - m\}/n < \infty \Rightarrow z_n \sim m^n w$$

for a nonzero random variable w, *provided* ε *can be interpreted as concave.*

For the tumor example we need a concept of growth fraction, elaborating the ideas of Section 4: let c_t be the number of cycling cells at time t and z_t the total tumor size, that is, cycling plus quiescent cells. The growth fraction is called strictly positive if $\limsup_{T\to\infty} \mathbb{E}[z_T/c_T] < \infty$, the lim sup being over larger and larger stopping times.

COROLLARY 10. *Provided it has a strictly positive growth fraction and the process* $w_t := e^{-\alpha t} z_t$ *is tight, then the cell age and tumor size dependent growth model exhibits balanced exponential growth with the same Malthusian parameter* α *as the limiting nontumor-size dependent model, provided only*

$$\sum \varepsilon(n)/n < \infty.$$

PROOF OF THEOREM 7. First some notation: twiddled processes count only imaginary individuals; $\tilde{z}^{\chi}_{t-\tau_x}(x)$ thus stands for the imaginary process starting from the individual x in the actual population at time τ_x. Similarly, $\tilde{w}^{\chi}_{t-\tau_x}(x) := \exp(-\alpha(t-\tau_x))\tilde{z}^{\chi}_{t-\tau_x}(x)$ and so on.

For any u, z^u_t records the summed χ-values at time $t+u$ of all individuals born up to u and all individuals not stemming from an aborted individual after u. If $\delta_{xu} = 0$ precisely if x stems from an x' with $\tau_{x'} > u$ and $\delta_{x'} = 1$, and $\delta_{xu} = 1$ otherwise, then

$$z^u_t = \sum_{\tau_x \le t+u} \delta_{xu}\, \chi_x(t+u-\tau_x).$$

In analogy with other notation, $w^u_t := e^{-\alpha(t+u)} z^u_t$.

Clearly,

$$0 \le z^{\chi}_{t+u} - z^{u}_{t} \le \sum_{\tau_x > u} \delta_x z^{\chi}_{t+u-\tau_x}(x)$$

and

$$|w_{t+u} - w^{u}_{t}| \le w_{t+u} \sum_{\tau_x > u} \delta_x \frac{z^{\chi}_{t+u-\tau_x}(x)}{z^{\chi}_{t+u}}.$$

Thus for any ε', $v > 0$,

$$\mathbb{P}_s\big(|w_{t+u} - w^{u}_{t}| > \varepsilon', w_{t+u} \le v\big) \le (v/\varepsilon')K\mathbb{E}_s\left[\sum_{\tau_x > u} \delta_x / z^{\chi}_{\tau_x}\right]$$

for all t and starting types $s \in \mathcal{S}$. But

$$|w_{t+u} - w_{t'+u}| \le |w_{t+u} - w^{u}_{t}| + |w^{u}_{t} - w^{u}_{t'}| + |w_{t'+u} - w^{u}_{t'}|.$$

Since

$$w^{u}_{t} = \sum_{x \in I_u} \exp(-\alpha\tau_x)\tilde{w}_{t+u-\tau_x}(x) \to \sum_{x \in I_u} \exp(-\alpha\tau_x)\tilde{w}(x),$$

as $t \to \infty$, the twiddled daughter processes being independent individual supercritical branching process with Malthusian parameter α, it follows that

$$\lim_{t, t' \to \infty} \mathbb{P}_s\big(|w^{u}_{t} - w^{u}_{t'}| > \varepsilon'\big) = 0.$$

Hence,

$$\limsup_{t, t' \to \infty} \mathbb{P}_s\big(|w_{t+u} \wedge v - w_{t'+u} \wedge v| > \varepsilon'\big) \le 2(v/\varepsilon')K\mathbb{E}_s\left[\sum_{\tau_x > u} \delta_x / z^{\chi}_{\tau_x}\right].$$

Since u can be chosen so as to render the right-hand side arbitrarily small, the convergence in probability follows by completeness and tightness. □

Proof of Corollary 9. As $m(n)\varepsilon(n) = m(n) - m$ and $1 < m \le m(n) \le m(1)$, the equivalence of the two conditions is obvious. Symmetric growth follows by symmetry: let $x \in N^k$ so that $\tau_x = k$ and $\mathcal{G}_x = \mathcal{B}_k$, the σ-algebra generated by the first k generations. With $t = n$

$$\mathbb{E}\big[z^{\chi}_{t-\tau_x}(x)/z^{\chi}_{t} \mid \mathcal{G}_x\big] = \mathbb{E}\big[z_{n-k}(x)/z_n \mid \mathcal{B}_k\big] = 1/z_k,$$

since

$$z_n = \sum_{x \in Z_k} z_{n-k}(x) \text{ and } |Z_k| = z_k$$

if Z_k is the set of realized individuals in the kth generation.

To get hold of $\sum_n \mathbb{E}[\varepsilon(z_{\tau_{X_n}})/z_{\tau_{X_n}}] < \infty$, note that

$$z_{\tau_{X_n}} = z_k \Leftrightarrow y_{k-1} < n \le y_k,$$

where $y_k := \sum_{j=0}^{k} z_j$ is the total population up to k. Thus,

$$\sum_n \varepsilon(z_{\tau_{X_n}})/z_{\tau_{X_n}} = \sum_k z_k \varepsilon(z_k)/z_k,$$

and

$$\sum_n \mathbb{E}\left[\varepsilon(z_{\tau_{X_n}})/z_{\tau_{X_n}}\right] = \sum_k \mathbb{E}[\varepsilon(z_k)] \le \sum_k \varepsilon(\mathbb{E}[z_k]) \le \sum_k \varepsilon\left(m(1)^k\right),$$

which converges precisely if $\sum_n \varepsilon(n)/n < \infty$ by an elementary analytic lemma [cf. Klebaner (1984)]. The same condition yields $\mathbb{E}[w] < \infty$ and hence tightness [Theorem 5 of Klebaner (1984)]. □

And so we turn to the proof of the corollary.

PROOF OF COROLLARY 10. In this case it is the growth of $z_{\tau_{X_n}}$ that is directly mastered, whereas the symmetric growth inequality causes difficulties. Indeed,

$$z_{\tau_{X_1}} = 1, \qquad z_{\tau_{X_2}} = z_{\tau_{X_3}} = 2, \qquad z_{\tau_{X_4}} = z_{\tau_{X_5}} = 3, \dots, z_{\tau_{X_{2n}}} = z_{\tau_{X_{2n+1}}} = n+1$$

on the set where the population does not die out.

For any $x \in I$ with $\tau_x < \infty$ define the set

$$A_x := \{x' \in I;\ \tau_{x'} \le \tau_x \text{ and a daughter of } x' \text{ cycles at } \tau_x\} \cup \{x\}.$$

By the line [Neveu (1986), Jagers (1989)] property of A_x,

$$\sum_{x' \in A_x} z_{t-\tau_{x'}}(x') \le z_t.$$

The inequality comes from the quiescent cells born before those in A_x.

But the $z_u(x')$ do not decrease in u whereas $p(s)$ does not increase in s:

$$1 \ge \sum_{x' \in A_x} \mathbb{E}\left[z_{t-\tau_{x'}}(x')/z_t \mid \mathscr{G}_x\right] \ge |A_x| \mathbb{E}\left[z_{t-\tau_x}(x)/z_t \mid \mathscr{G}_x\right].$$

But $|A_x|$ must be greater than or equal to $c_{\tau_x}/2$. It is clear from the proof of the theorem that now it only remains to prove that

$$\sum_n \mathbb{E}\left[\varepsilon(n)/c_{\tau_{X_n}}\right] < \infty.$$

But

$$\mathbb{E}\left[\varepsilon(n)/c_{\tau_{X_n}}\right] \sim \varepsilon(n)/n\mathbb{E}\left[z_{\tau_{X_n}}/c_{\tau_{X_n}}\right] \sim \varepsilon(n)/n$$

by the assumption of a strictly positive growth factor. □

7. Another tumor model. An alternative to age-dependent tumor models is provided by Bell–Anderson type cell-size dependent approaches. Here the idea [cf. Diekmann, Heijmans and Thieme (1984)] is that cells grow according to a differential equation, and split according to a cell-size determined intensity, daughter cells sharing their mother's mass equally.

Hence, there is a splitting intensity $b(s) \ge 0$, s standing for individual cell size. Similarly there may be a death intensity $\delta(s) \ge 0$. Individual cell growth is usually taken to be deterministic in the model, that is, the same for all cells with given birth size, $s' = g(s)$, $s(0) =$ size at birth, $g > 0$.

The growth equation yields $dt = ds/g(s)$ and the distribution function for the size r at death or division of a cell with birth size s is

$$1 - \exp\left\{ -\int_s^r (b(q) + \delta(q)) \frac{dq}{g(q)} \right\}.$$

To obtain r-sized daughter cells the mother must herself attain size $2r$ and the expected number of r-sized daughters becomes

$$2b(2r)\exp\left(-\int_s^{2r} (b(q) + \delta(q)) \frac{dq}{g(q)} \right).$$

Once r has been fixed, the age u at division is determined by

$$\int_s^{2r} \frac{dq}{g(q)} = u.$$

In the notation

$$f(s) := \int_0^s (b(q) + \delta(q)) \frac{dq}{g(q)}, \qquad c(s) := \int_0^s \frac{dq}{g(q)},$$

we can thus write the reproduction kernel

$$\mu(s, dr \times du) = 4\frac{b(2r)}{g(2r)} \exp(-(f(2r) - f(s))) 1_{\{c(2r) - c(s)\}}(du)\, dr, \qquad 2r \geq s,$$

so that

$$\mu(s, \mathbb{R}_+) = 2e^{f(s)} \int_{s/2}^{\infty} \frac{b(r)}{g(r)} e^{-f(r)}\, dr.$$

(It is usually assumed that there are maximal and minimal cell sizes, and integration is restricted to the interval between those.)

Gyllenberg and Webb (1990) introduced population size into this as above, by a probability $\rho(z, s) = 1 - p(z, s)$ that a newborn cell turns quiescent, arguing that this usually occurs directly after mitosis, if ever. Clearly, one could also consider population-size dependent splitting intensities, either $b(z, s)$, $\delta(z, s)$, where z is the tumor size at the birth of the individual, or with instantaneous feedback, z and s then denoting the tumor and cell sizes at the time considered.

In the first case

$$m(z, s) = 2p(z, s) e^{f(s)} \int_{s/2}^{\infty} \frac{b(r)}{g(r)} e^{-f(r)}\, dr$$

and we recover the conditions

$$\sum_n \sup_s \{ p(n, s) - p(s) \} < \infty$$

or (under further conditions, cf. Corollary 10)

$$\sum_n \sup_s \{ p(n, s) - p(s) \} / n < \infty$$

for Malthusianness to transfer, under weak requirements on the underlying intensities and growth function. Similarly, it is a matter of straightforward analytic technicalities to formulate and check suitable conditions on intensities for the latter two models.

Acknowledgments. Thanks to the never ending departmental corridor seminar for elucidating discussions on the uniform integrability conditions and to an Associate Editor in charge for caring to point out a score of linguistic and typographic slips.

REFERENCES

BREIMAN, L. (1968). *Probability*. Addison-Wesley, Reading, MA.

COHN, H. and KLEBANER, F. (1986). Geometric rate of growth in Markov chains with applications to population size dependent models with dependent offspring. *Stochastic Anal. Appl.* **4** 283–308.

DIEKMANN, O., HEIJMANS, H. J. A. M. and THIEME, H. R. (1984). On the stability of the cell size distribution. *J. Math. Biol.* **19** 227–248.

GYLLENBERG, M. and WEBB, G. F. (1990). A nonlinear structured cell population model of tumor growth with quiescence. *J. Math. Biol.* **28** 671–694.

GYLLENBERG, M. and WEBB, G. F. (1992). Asynchronous exponential growth of semigroups of nonlinear operators. *J. Math. Anal. Appl.* **167** 443–467.

JAGERS, P. (1975). *Branching Processes with Biological Applications*. Wiley, Chichester.

JAGERS, P. (1989). General branching processes as Markov fields. *Stochastic Process. Appl.* **32** 183–212.

JAGERS, P. (1996). Towards dependence in general branching processes. In *Classical and Modern Branching Processes* (K. Athreya and P. Jagers, eds.). Springer, New York.

KELLER, G., KERSTING, G. and RÖSLER, U. (1987). On the asymptotic behaviour of discrete time stochastic growth processes. *Ann. Probab.* **15** 305–343.

KERSTING, G. (1986). On recurrence and transience of growth models. *J. Appl. Probab.* **23** 614–625.

KLEBANER, F. (1984). Geometric rate of growth in population size dependent branching processes. *J. Appl. Probab.* **21** 40–49.

KLEBANER, F. (1985). A limit theorem for population size dependent branching processes. *J. Appl. Probab.* **22** 48–57.

KLEBANER, F. (1989). Geometric growth in near-supercritical population size dependent multitype Galton–Watson processes. *Ann. Probab.* **17** 1466–1477.

KLEBANER, F. (1994). Asymptotic behaviour of Markov population processes with asymptotically linear rate of change. *J. Appl. Probab.* **31** 614–625.

KÜSTER, P. (1983). Generalized Markov branching processes with state dependent offspring distribution. *Z. Wahrsch. Verw. Gebiete* **64** 475–503.

KÜSTER, P. (1985). Asymptotic growth of controlled Galton–Watson processes. *Ann. Probab.* **13** 1157–1178.

LINDVALL, T. (1992). *Lectures on the Coupling Method*. Wiley, Chichester.

NERMAN, O. (1981). On the convergence of super-critical general (C-M-J) branching processes. *Z. Wahrsch. Verw. Gebiete* **57** 365–395.

NEVEU, J. (1986). Arbres et processus de Galton–Watson. *Ann. Inst. H. Poincaré* **22** 199–207.

NIEMI, S. and NUMMELIN, E. (1986). On nonsingular renewal kernels with an application to a semigroup of transition kernels. *Stochastic Processes Appl.* **22** 177–202.

NUMMELIN, E. (1984). *General Irreducible Markov Chains and Nonnegative Operators*. Cambridge Univ. Press.

OLOFSSON, P. (1994). General branching processes with local dependencies. Ph.D. dissertation, Dept. Mathematics, Chalmers and Gothenburg Univ.

OLOFSSON, P. (1996). Branching processes with local dependencies. *Ann. Appl. Probab.* **6** 238–268.

RITTGEN, W. (1986). Über das qualitative Verhalten populationsabhängiger Markoffscher Verzweigungsprozesse. Fachbereich Mathematik der Johannes-Gutenberg-Univ., Mainz.

SEVASTYANOV, B. A. and ZUBKOV, A. M. (1974). Controlled branching processes. *Teor. Veroyatnast. Primen.* **19** 15–25.

SHURENKOV, V. M. (1989). *Ergodičeskie Processy Markova* (*Ergodic Markov Processes*). Nauka, Moscow. (In Russian.)

YURACHKOVSKII, A. P. (1987). Convergence of nonhomogeneous asymptotically critical branching processes in a series scheme to processes of diffusion type. *Theory Probab. Math. Statist.* **36** 143–151.

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