THE DETERMINISTIC EVOLUTION OF GENERAL BRANCHING POPULATIONS

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Probability theory has a strength that extends beyond probabilistic results. The precise formulation of probabilistic models may lead to intuitive arguments that reach further than even sophisticated mathematical analysis of deterministic models. This is well known from the use of Brownian motion in exhibiting solutions of partial differential equations. Another illustration is provided by population dynamics. Branching processes focus on probabilistic problems, and rely on probabilistic methods. But the expected evolution of general branching populations is an interesting topic in its own right, that has much in common with structured deterministic population dynamics. Arguments based on Markov renewal theory demonstrate a remarkable strength as compared to traditional, differential equations based approaches in establishing exponential growth and the ensuing stabilization of population composition of expected populations. This is described in this article, aimed at a broad mathematical readership.

AMS subject classifications: 60J80; 60F25, 92A15..
Keywords and phrases: branching processes, population dynamics..

1 From Galton and Watson to Markov Population Processes

Recall Galton's famous formulation, more than a century ago, of the population extinction problem: "A large nation, of whom we will only concern ourselves with the adult males, N in number, and who each bear separate surnames, colonize a district. Their law of population is such that, in each generation, a_0 per cent of the adult males have no male children who reach adult life; a_1 have one such male child, a_2 have two; and so on up to a_5 who have five. Find (1) what proportion of the surnames will have become extinct after r generations; ..."

Already this historical and pre-exact wording has much of the flavour typical of modern mathematical population dynamics: its starting point is a description of individual behaviour, in this case a probabilistic description of reproduction, and the properties asked for concern the population as a whole - in this case an extinction probability. The latter is typical. In the biologically - not mathematically! - simple Galton-Watson processes that were born

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[1] This work has been supported by the Swedish Natural Sciences Research Council..

out of the surname extinction problem, the investigated population properties always have this probabilistic character. Indeed, the deterministic part of evolution is so simplistic, that it does not warrant any attention.

Not so if the processes evolve in real time, and have a minimal amount of generality: consider the one-type general branching process, *i.e.* a population whose reproduction (in deterministic terms) is determined by a *reproduction function* $\mu(u)$, giving the expected number of children up to (mother's) age u. In demographic and related theory $\mu(u)$ is often given as an integrated product of a survival probability and an age-dependent birth rate, $\int_0^u p(a)b(a)da$.

Then, if the population is started at time 0 from a new-born individual, at time t the total (expected) number of individuals born into the population can be written

$$\sum_{n=0}^{\infty} \mu^{*n}(t).$$

Here

$$\mu^{*0}(t) = \begin{cases} 0 & \text{if } t < 0 \\ 1 & \text{otherwise,} \end{cases}$$

and

$$\mu^{*(n+1)}(t) = \mu^{*n} * \mu(t) = \int_0^t \mu^{*n}(t-u)\mu(du).$$

In this $\mu^{*n}(t)$ clearly stands for the size of the n:th generation of the total population, *i.e.* born by time t.

From an analytic viewpoint, the analysis of the (expected) dynamics of this type of populations is therefore little but the study of sums of convolution powers, a topic well investigated within the framework of renewal theory and integrated into the theory of branching processes since long (*cf.* Harris, 1963).

However, even though these processes are "general" as compared to Galton-Watson processes and much demographic theory, they remain simplistic in assuming all individuals to be of the same type - even though allowing for them to meet with very different fates in life, by chance. During the past decade a general Markov renewal theory has developed - *cf.* the series of papers by Nummelin and coauthors and by Shurenkov - which allows analysis of populations where individuals may not only beget children at any age, and have positions in some state space, but where child-bearing, and individual life evolution in general, may be influenced by some (geno)type inherited from the mother. These are the Markov population processes, or equivalently general branching processes with abstract type spaces, surveyed by Jagers (1991). For a more technical presentation *cf.* Jagers and Nerman (1996).

In this case the reproduction function is replaced by a *reproduction kernel*, describing the (expected) child-bearing of an individual, given her type. Thus, let $(S,\mathcal{S})$ be a measurable space, the *type space*, about which we only assume that the σ-algebra $\mathcal{S}$ is generated by some countable class of sets. Let $\mathcal{B}$ denote the Borel algebra on $\mathbf{R}_+$. The reproduction kernel is denoted $\mu(s, A \times B)$, the (expected) number of B-type children of an s-type mother, while she is in age-interval A, $s \in S, B \in \mathcal{S}$. Note that it is the type at birth that determines the kernel; we shall return to the question of individuals possibly moving in some state space during life. At this junction, let us only note that even though such movement may influence reproduction, the movement itself can be included in the reproduction kernel, which thus remains the entity determining the population dynamics.

It does so much in the same manner as in the case of one-type populations, only convolution has to be replaced by a combination of convolution in age and Markov transition in type: Start the population from one, new-born s-individual at time 0. Her generation, the 0:th, will have a trivial size and type distribution at time t that can be written

$$\mu^0(s,[0,t] \times B) := 1_B(s)1_{\mathbf{R}_+}(t).$$

(As before, we consider the total population, disregarding death for the time being. One with a suffix stands for indicator function.) The next generation, consisting of the ancestor's daughters has the size and type distribution

$$\mu^1(s,[0,t] \times B) := \mu(s,[0,t] \times B),$$

and so it continues:

$$\mu^2(s,[0,t] \times B) := \int_{R_+ \times S} \mu^1(r,[0,t-u] \times B)\mu(s, du \times dr), \ldots$$

$$\mu^{n+1}(s,[0,t] \times B) := \int_{R_+ \times S} \mu^n(r,[0,t-u] \times B)\mu(s, du \times dr), n \in Z_+,$$

the total population size and time distribution at time t thus being

$$U_s(t,B) := U_s([0,t] \times B) := \sum_{n=0}^{\infty} \mu^n(s,[0,t] \times B).$$

We shall allow ourselves to identify non-decreasing functions with measures on $\mathbf{R}_+$, even if the measure is actually defined on $\mathcal{B} \times \mathcal{S}$, as above or in $\mu(s,t,B) := \mu(s,[0,t] \times B)$.

Consider now some property D of an individual, that has a well defined probability, given the individual's type r (at birth) and age a (now). Denote it by $p_D(r,a)$. The property D could be 'being in some specified subset of a geographical or general state space'; it could simply mean 'being alive' so that if L_r denotes the distribution function of the life span of an r-type individual, then $p_D(r,a) = 1 - L_r(a)$. Actually D might also refer to the progeny of an individual, like the number of granddaughters. Here we shall assume that it can not refer backwards to progenitors. However, if a property refers only finitely many generations backward that can be remedied by the simple trick of moving the property backwards to the last common ancestor of those concerned, *cf.* Jagers and Nerman (1984) where also other cases are discussed. In the present paper we assume throughout that $p_D(r,a) = 0$ for $a < 0$.

A simple classical example of this kind is

$$p_{D_u}(r,a) = 1_{[0,u]}(a)(1 - L_r(a)),$$

D_u meaning that the individual has been born ($a \geq 0$), is not above age u, and is still alive at age a. Other examples would be the probability of being in mitosis, or having a specified DNA-content or size. A particularly popular model is to let the individual be born at some starting position (note that this need not at all be the type of the individual, even though information about birthplace may be included in the latter) and then let it diffuse to other positions.

The important matter, in our context, is that once D has been fixed, and p_D is measurable, then the (expected) number of individuals having the property D at time t will be given by

$$(1) \qquad M_s(t,D) := \int_{\mathbf{R}_+ \times S} p_D(r, t-u) U_s(du \times dr).$$

The study of (the deterministic part of) population evolution can thus be described as the analysis of the functions $M_s(\cdot, D)$ of time, for $s \in S$ and various D.

The results that follow have the form

$$(2) \qquad M_s(t,D) \sim h(s) e^{\alpha t} \hat{p}_D(\alpha)/\alpha\beta,$$

as $t \to \infty$ - with a slight modification in the so called lattice case, where the population dynamics display some inherent periodicities. Here, $h : S \to \mathbf{R}_+$ is a reproductive value function: it decribes the fitness of the types. Mathematically it arises as an eigenfunction. The α is the famous Malthusian growth parameter and β a time scaler, meaning the average age at childbearing, in a certain sense. As indicated by the notation, $\hat{p}_D(\alpha)$ is a Laplace transform evaluated at the Malthusian parameter:

$$\hat{p}_D(\alpha) := \int_{\mathbf{R}_+ \times S} p_D(r,t) \alpha e^{-\alpha t} dt \pi(dr),$$

where π is a *stable type distribution*, mathematically appearing as an eigenmeasure, as we shall see in the next section.

Actually, by making the possible choices of sets D precise (Jagers and Nerman 1984 and 1996), one can see that the class of all $\hat{p}_D(\alpha)$ defines a measure on a grand, doubly infinite pedigree space, centered around a typical individual. This measure determines the *stable population composition*, aspects of which - like the stable age distribution - have played such an important role in the development of population dynamics. It gives not only the probabilities of properties of the typical individual's own life, like her type or state at various ages but also the probability distribution of her progeny, and of her past ancestry and their history.

2 Some Markov Renewal Theory

Once the basic Relation (1) has been established, the mathematical analysis leading to (2), is a straightforward application of Markov renewal theory. We shall use the terminology and results by Shurenkov (1984 and later). With slight changes we could instead have relied upon Niemi and Nummelin (1986).

First some terminology: Let $K(s, A), s \in S, A \in \mathcal{S}$ be any non-negative kernel on $(S, \mathcal{S})$, *i.e.* such that for any $s, K(s, \cdot)$ is a non-negative measure and for any $A, K(\cdot, A)$ is a measurable function. By integration K defines two linear maps:

$$Kf(s) := \int_S f(r)K(s, dr),$$

of non-negative measurable functions, and

$$mK(A) := \int_S K(s, A)m(ds),$$

of non-negative measures, into themselves. Defining the product of kernels the obvious way,

$$KL(s, A) := \int_S L(r, A)K(s, dr),$$

we may consider iterated kernels K^n. Here $K^0(s, A)$ and K^1 are given the conventional meanings of $1_A(s)$ and K, respectively, and $K^{n+1} = KK^n$. The *Perron root* ρ of K is defined by

$$1/\rho := \sup\{t \in \mathbf{R}_+; \sum_{n=0}^{\infty} t^n K^n(s, \cdot) \text{ is } \sigma\text{-finite for each } s \in S\}.$$

If the Perron root is finite and positive and if the kernel satisfies some further communication conditions (*cf.* Nummelin, 1984, or Shurenkov, 1989), then an abstract Perron-Frobenius theorem holds: There exist a unique (up to multiplication by constants) σ-finite measure π on $(S, \mathcal{S})$ and a unique (in the same sense and a.e. π) positive and finite (π-a.e.) function h such that

$$\pi K = \rho\pi \text{ and } Kh = \rho h.$$

The communication conditions mentioned are two:

1. positivity: There should exist a non-trivial σ-finite measure m on $(S, \mathcal{S})$ such that $\sum K^n(s, A) > 0$ for all $s \in S$, as soon as $m(A) > 0$.
2. recurrence: For m as above and any measurable $f > 0$,

$$\sum_n \int_{S\times S} f(s)K^n(r, ds)m(dr)/\rho^n = \infty.$$

Returning now to population dynamics, we define the Laplace transform $\hat{\mu}_\lambda$ of the reproduction kernel by

$$\hat{\mu}_\lambda(s, B) := \int_0^\infty e^{-\lambda t}\mu(s, dt \times B),$$

Under broad conditions it is possible to choose α so as to render the Perron root of $\hat{\mu}_\alpha$ one, *cf.* Jagers (1983), Ney and Nummelin (1987), and Shurenkov (1992). By definition, this α is the *Malthusian parameter.* For the interpretation it is nice if eigenfunction h and eigenmeasure π from the Perron-Frobenius theorem are such that they can be chosen to satisfy

$$\pi(S) = \int_S h(s)\pi(ds) = 1.$$

With this specification they are unique and referred to as the ***reproductive value*** and ***stable type distribution***, respectively. Actually, for the treatment of the stochastic evolution this assumption, and that $\inf h > 0$, and further that

$$\sup_s \mu(s, [0, \epsilon] \times S) < 1$$

for some $\epsilon > 0$ are needed. Since we restrain ourselves to the expected evolution, we can refrain from these requirements. Only so called strong or positive α-recurrence,

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

is needed. (This entity might be interpreted as the stable age at childbearing, though some care has to be exercised about this in the multi-type case, *cf.* Jagers (1991).)

The periodicity problems, already hinted at, are made precise in the following manner: the reproduction kernel (or the whole population) is said to be d-*lattice*, $d > 0$, if for some $c : S \to [0, d)$, and $L_{dc}(s) := \{(t, r); t \in \mathbf{R}_+, r \in S, t = c(r) - c(s) + nd, \text{ for some } n = 0, 1, \ldots\}$

$$\pi(\{s; \mu(s, \mathbf{R}_+ \times S) > \mu(s, L_{dc}(s))\}) = 0,$$

d being the maximal such number. This has the meaning that there is a stepping time unit for reproduction, independent of both mother's and child's type, but a shift which may depend on both. We call c the *shift*. If the kernel is d-lattice for some d, it is called lattice, and otherwise non-lattice.

Finally, we need the notion of direct Riemann integrability, which is due to Shurenkov (1989) *pp.* 80 *ff.*, in this general context. A measurable function $g : S \times \mathbf{R}_+ \to \mathbf{R}$ is *directly Riemann integrable* (π) if for any $\epsilon > 0$ we can find $\delta > 0$ and functions g^- and g^+ both in $L^1[\pi \times dt]$ such that for π-almost all r, $g^-(r, \cdot) \leq g(r, \cdot) \leq g^+(r, \cdot)$, $g^{\pm}(r, t) = g^{\pm}(r, n\delta)$ for $n\delta \leq t < (n + 1)\delta$, and the $L^1[\pi \times dt]$-distance between g^+ and g^- is less than ϵ. We also need the concept of being spread-out: For fixed $r \in S$ and a Borel set B, the reproduction kernel $\mu(r, B \times \cdot)$ is absolutely continuous with respect to $\hat{\mu}(r, \cdot)$. It is possible to choose a regular version of the Radon-Nikodym derivative, $F(r, dt, s)$, which is a measure on $\mathbf{R}_+$ in its middle coordinate. *Spread-outness* means that, for almost all r, s with respect to $\pi(dr)\hat{\mu}(r, ds)$, this measure is non-singular with respect to Lebesgue measure.

Theorem 2.1 *Consider a non-lattice reproduction kernel* μ *such that the Malthusian parameter* α *exists,* $\beta < \infty$*,* $\hat{\mu}_\alpha$ *satisfies the two communication conditions, and such that* $\sup_t e^{-\alpha t} U_s(t, S) < \infty$. *Let* D *be a property such that the function* $e^{-\alpha t} p_D(r, t)$ *is directly Riemann integrable* (π). *Then, for* π*-almost all* s*,*

$$\lim_{t \to \infty} e^{-\alpha t} M_s(t, D) = h(s) \hat{p}_D(\alpha)/\alpha\beta.$$

If the population is as above and some μ^n *is, further, spread-out, then for* π*-almost all* $s \in S$ *the convergence holds uniformly in all* D *with* $\hat{p}_D(\alpha) \leq 1$ *(without any requirement of Riemann integrability or finite* $\sup_t e^{-\alpha t} U_s(t, S)$*).*

Note that in the supercritical case ($\alpha > 0$), the direct Riemann integrability requirement disappears and $\hat{p}_D(\alpha) \leq 1$ trivially. The $\sup_t e^{-\alpha t} U_s(t, S) < \infty$ condition is stronger than needed, presumably it can be discarded altogether, *cf.* Shurenkov (1989), *p.* 122. The already mentioned condition $\sup_s \mu(s, [0, \epsilon] \times S) =: m < 1$, for some $\epsilon > 0$ suffices to establish it:

$$1 = \int_{\mathbf{R}_+ \times S} (1 - \mu(r, t - u, S) U_s(du \times ds) \geq$$

$$\geq (1 - m)(U_s(t, S) - U_s(t - \epsilon, S)).$$

Since the same inequality holds also when t is replaced by $t - k\epsilon, k = 1, \ldots [t/\epsilon]$,

$$U_s(t, S) \leq (t/\epsilon + 1)/(1 - m),$$

so that $U_s(t, S)$ can grow at most linearly in t.

Like the spread-out case, the lattice form of the theorem can do without any boundedness condition on U_s:

Theorem 2.2 *Consider a d-lattice reproduction kernel μ such that the Malthusian parameter α exists, $\beta < \infty$, and $\hat{\mu}_\alpha$ satisfies the two communication conditions. Denote the shift by c, and consider a property D, such that for any $u > 0$*

$$\int_S \pi(dr) \sum_{k=0}^{\infty} e^{-\alpha(kd+c(r))} p_D(r, kd + c(r) + u) < \infty,$$

(obviously the case if $\alpha > 0$ and $\pi(S) = 1$). Then, for π-almost all s,

$$\lim_{n\to\infty} e^{-\alpha(nd+c(s))} M_s(nd + c(s) + u, D) =$$

$$= dh(s) \int_S \pi(dr) \sum_{k=0}^{\infty} e^{-\alpha(kd+c(r))} p_D(r, kd + c(r) + u)/\alpha\beta.$$

These two results (cf. Jagers, 1989) establish exponential growth, and also the stable asymptotic composition in quite broad generality. Thus, they are the expected branching process form of what is recently being called asynchronous exponential growth within structured population dynamics, Gyllenberg and Webb (1992), adapting to cell kinetical terminology. (But, of course, our results concern only the "linear" case.) To get hold of the stable composition, define E just to be the property of being born and no further restriction, so that $p_E(r, t) \equiv 1$ if and if only $t > 0$. Then, $\hat{p}_E(\alpha) = 1$ and hence

$$M_s(t, D)/M_s(t, E) \to \hat{p}_D(\alpha), \text{ as } t \to \infty$$

(in the non-lattice formulation). In order to catch the composition within the live population, replace E by the property A of being alive, and obtain

$$\hat{p}_A(\alpha) = \int_{\mathbf{R}_+ \times S} \alpha e^{-\alpha t}(1 - L_r(t))\pi(dr)dt = 1 - \hat{L}(\alpha),$$

if $L(t) := \int_S L_s(t)\pi(ds)$ denotes the life span distribution of an individual whose type follows the stable type distribution. Ultimately,

$$M_s(t, D \cap A)/M_s(t, A) \to \hat{p}_{D\cap A}(\alpha)/(1 - \hat{L}(\alpha)), \text{ as } t \to \infty,$$

again in the non-lattice case.

As already pointed out, this discussion has been very imprecise about the possible choices of properties D. For technical treatment we refer to Jagers and Nerman (1996). The point is that D may refer not only to a typical individual and its progeny but also backwards, say n generations. In this way we obtain convergence theorems, and in the spread-out case even uniform convergence theorems, for the approach of the (expected) composition towards a stable asymptotic composition, which gives not only the probability that a typical individual has some property of her own but also describes her history and future, i.e. her progenitors and progeny.

3 Branching Processes and Structured Population Dynamics

Branching processes have developed towards generality, starting from the simple schemes of independent and identically distributed random variables that constitute (the reproduction of) Galton-Watson processes. In a parallel way, structured population dynamics has evolved out of crude classical differential equations for population growth. The pride and glory of branching processes are not the deterministic results surveyed here, but rather the corresponding stochastic results: in the supercritical case not only expectations display 'asynchronous exponential growth' but so do the underlying stochastic population processes themselves, under natural supplementary conditions. Structured population dynamics also arrives at results like our Theorems 1 and 2, but similarly its thrust nowadays is elsewhere, into the evasive feedback from the population as a whole onto individual behaviour, generally and in detailed special models.

This is an area that has been very difficult even to formulate in branching processes, since the very concept of *population* dynamics as it were indicates an individual reproduction initiative, and as a consequence naturally leads to individuals being thought of as acting independently. In a full-fledged stochastic model you would like the feedback to come from the actual, stochastic population size and not from its expectation, which is hard to feel for the individual. In deterministic models such difficulties can be surpassed — or concealed.

However, in a sequence of papers Klebaner (1989, 1991, 1994, and others) has demonstrated exponential growth of population-size dependent simple branching processes, of the Galton-Watson or Markov branching kind. By use of a coupling device ("imaginary abortions") these results were partly extended to general branching processes (Jagers, 1997b) and quite recently a complete generalization has been obtained for age-dependent, population size influenced branching processes (Jagers and Klebaner, 1998). A simplified formulation runs as follows: Let $m_n \geq m > 1$ be the expected number of children if the population has size n. Then $\sum(m_n - m)/n < \infty$ is essentially necessary and sufficient for the process to grow as if reproduction were independent of population size, always with expectation m. It is interesting to note that the mentioned coupling approach leads to the sufficient condition $\sum m_n - m < \infty$.

But here we treat the common ground of classical theory, independent individuals from a stochastic viewpoint, the "linear" case in differential equations jargon. (Note, however that "linearity" may harbour quite complicated dependencies, locally in the pedigree, cf. Jagers, 1997a). The similarity on that common ground has become more evident by recent developments in structured population dynamics, shifting focus from differential equations to expected offspring operators and using generation representations, *cf.* Diekmann, Gyllenberg, Metz, and Thieme (1993), Diekmann (1993) and Thieme (1992).

Indeed, Diekmann (1993) even takes as his starting point the expected number $B(\tau, \xi, \eta)$ of offspring with state ξ at birth, produced per unit of time by an individual of age τ, which was born in state η. This defines a next generation operator K by

$$(K\phi)(\xi) := \int_\Omega (\int_0^\infty B(\tau, \xi, \eta) d\tau) \phi(\eta) d\eta,$$

and more generally for $\lambda \geq 0$

$$(K_\lambda\phi)(\xi) := \int_\Omega (\int_0^\infty B(\tau, \xi, \eta) e^{-\lambda\tau} d\tau) \phi(\eta) d\eta.$$

The only difference, besides notation, is that the state (in this case = type) space $\Omega (= S)$ is taken as Euclidean and that the reproduction kernel here is assumed to be absolutly continuous with respect to Lebesgue measure. The continued analysis of K, viewed firsthand as an operator on $L^1(\Omega)$, is in terms of the spectral radius $R_0 := \lim_{n \to \infty} \| K^n \|^{1/n}$. How does this compare to the Perron root, playing the corresponding role in Markov renewal theory?

By Cauchy-Hadamard clearly $\rho \leq R_0$. A simple example where the inequality is strict is provided by the random walk on the integers, $W\phi(x) := p\phi(x+1) + (1-p)\phi(x-1), x \in \mathbf{Z}_+, 0 < p < 1$. This operator on the bounded functions has spectral radius $R_0 = 1$, whereas a check of the binomial expression that describes W^n yields convergence of $\sum t^n W^n(x, \{y\})$ precisely when $t < 1/2\sqrt{p(1-p)}$ so that $\rho = 2\sqrt{p(1-p)} < 1 = R_0$, if $p \neq 1/2$. However, if S is a compact metric space equipped with its Borel σ-algebra, K an operator that maps continuous functions into themeselves, and is topologically irreducible in the sense that for each $s \in S$ and open $G \subset S$ there is an n such that $K^n(s, G) > 0$, then $\rho = R_0$ (Shurenkov, 1992).

Diekmann, Gyllenberg, Metz and Thieme (1993) translate the abstract p.d.e. problems that constitute classical structured population dynamics into abstract convolution equations. It would be tempting to translate those further into our terminology, but on the general level only notational matters remain after the translation already performed in *op. cit.* Therefore it may be more instructive to have a glance at how Markov renewal theory in the form of Theorems 1 and 2 would work in a precise model, which has been thoroughly analyzed within the structured populations framework. We take a look at cells with size-dependent (as opposed to age-dependent) individual behaviour, the Bell-Anderson model, *cf.* Diekmann, Heijmans, and Thieme (1984) or Diekmann's paper in Metz and Diekmann (1986). *Cf.* also Arino and Kimmel (1993).

The basic assumption is that there is a splitting intensity $b(x) \geq 0$, x standing for the individual cell size. Similarly there is a death intensity $\delta(x) \geq 0$, death meaning the cell disappearing without giving birth to daughter cells. When a cell splits, its mass is assumed to be equally divided between the daughters. Individual cell growth is deterministic *i. e.* the same for all cells with given birth size, $x' = g(x), x(0) =$ size at birth, $g > 0$. Assume that there is a minimal and a maximal cell size a and $4a$ so that $0 < a \leq x(0) \leq 2a$, and no cell, smaller than $2a$, can divide. (The following argument is not correct without some such condition, absent from a first version of this paper, as noted by Alexandersson (1998).)

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

$$1 - exp(-\int_x^y (b(\xi) + \delta(\xi))\frac{d\xi}{g(\xi)}.$$

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

$$2b(2y)exp(-\int_x^{2y} (b(\xi) + \delta(\xi))\frac{d\xi}{g(\xi)}dy.$$

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

$$\int_x^{2y} \frac{d\xi}{g(\xi)} = u.$$

In the notation

$$f(x) := \int_a^x (b(\xi) + \delta(\xi))\frac{d\xi}{g(\xi)}, c(x) := \int_a^x \frac{d\xi}{g(\xi)},$$

we can thus write the reproduction kernel

$$\mu(x, du \times dy) = 4\frac{b(2y)}{g(2y)}e^{-(f(2y)-f(x))}1_{\{c(2y)-c(x)\}}(du)dy, a \leq x, y \leq 2a.$$

It follows that

$$\hat{\mu}_\lambda(x, dy) = 4\frac{b(2y)}{g(2y)} e^{-(f(2y)-f(x))-\lambda(c(2y)-c(x))} dy.$$

Iterating this, we see that

$$\hat{\mu}^2_\lambda(x, dy) = \int_0^\infty \hat{\mu}_\lambda(\xi, dy)\mu_\lambda(x, d\xi)$$

$$= 4\frac{b(2y)}{g(2y)} \int_a^{2a} e^{-(f(2y)-f(\xi))-\lambda(c(2y)-c(\xi))} 4\frac{b(2\xi)}{g(2\xi)} e^{-(f(2\xi)-f(x))-\lambda(c(2\xi)-c(x))} d\xi$$

$$= 4^2\frac{b(2y)}{g(2y)} e^{-(f(2y)-f(x))-\lambda(c(2y)-c(x))} \int_a^{2a} \frac{b(2\xi)}{g(2\xi)} e^{-(f(2\xi)-f(\xi))-\lambda(c(2\xi)-c(\xi))} d\xi$$

$$= 4^2 \hat{\mu}_\lambda(x, dy) I(\lambda),$$

where $I(\lambda)$ denotes the integral. Generally

$$\hat{\mu}^n_\lambda(x, dy) = 4^n \hat{\mu}_\lambda(x, dy) I^{n-1}(\lambda).$$

Since I is a non increasing function, easily stated conditions yield a unique α such that $I(\alpha) = 1/4$ (which will be > 0 if $I(0) > 1/4$). Returning to the definition of the Perron root we see that

$$\sum_{n=0}^{\infty} t^n \hat{\mu}^n_\alpha(x, dy)$$

converges/diverges for $t <$ or ≥ 1. Thus α is the Malthusian parameter, and the kernel is recurrent. It is easy to formulate conditions for the kernel to be positive with respect to Lebesgue measure (on some interval) and for the strong recurrence condition $0 < \beta < \infty$. The condition that $\sup_s \mu(s, [0, \epsilon] \times S) < 1$ for some $\epsilon > 0$ is clearly satisfied. Moreover, for x, y given, $\mu(x, dt \times dy)$ gives mass only to the age point $c(2y) - c(x)$. From the definition of d-lattices, we know that we are in the lattice case if and only if all splits occur at ages $c(y) - c(x) + nd, n \in \mathbf{Z}_+$, *i.e.* iff $c(2y) = c(y) + d$ - by the continuity of c, d can only appear once. Since

$$c(y) = \int_a^y \frac{d\xi}{g(\xi)},$$

it is direct to check that this is the case precisely when $g(2y) = 2g(y)$, as shown in Metz and Diekmann (1986). We see that we have asynchronous exponential growth if this is not the case, and a periodic behaviour otherwise, by applying Theorems 1 and 2, respectively. It is also easy to guess how slight changes in the model, *e.g.* the introduction of a quiescent period will destroy the lattice properties, and thus salvage the pure asynchronous exponential growth.

Acknowledgements. I thank Ziad Taib for timely and helpful reading of this manuscript.

REFERENCES

Alexandersson, M. (1998). *Branching Processes and Cell Populations.* Licentiate Thesis, Dep. Mathematics, Chalmers U. Tech. and Göteborg U.

Arino, A. and Kimmel, M. (1993). Comparison of approaches to modelling of cell population dynamics. *SIAM Journal of Applied Mathematics* **53**, 1480-1504.

Diekmann, O. (1993). An invitation to structured (meta)population models. In: Levin, S. A., Powell, T., and Steele, J. (eds.) *Patch Dynamics.* Springer-Verlag, New York

Diekmann, O., Gyllenberg, M., Metz, J. A. J., and Thieme, H. R. (1993). The "cumulative" formulation of (physiologically) structured population models. In: Ph. Clement and G. Lumer (eds.), *Evolution Equations, Control Theory and Biomathematics*, Marcel Dekker, New York, 145-154.

Diekmann, O., Heijmans, H. J. A. M., and Thieme, H. R. (1984). On the stability of the cell size distribution. *J. Math. Biology* **19** 227-248.

Gyllenberg, M. and Webb, G. F. (1992). Asynchronous exponential growth of semigroups of non-linear operators. *Journal of Mathematical Analysis and Applications* **167** 443-467.

Harris, T. E. (1963). *The Theory of Branching Processes.* Springer-Verlag, Berlin. New ed. by Dover, New York, 1989.

Jagers, P. (1975). *Branching Processes with Biological Applications.* J. Wiley & Sons, Chichester etc.

Jagers, P. (1983). On the Malthusianness of general branching processes in abstract type spaces. In: Gut, A. and Holst, L. (eds.) *Probalitity and Mathematical Statistics. Essays in Honour of Carl-Gustav Esseen.* Dep. Mathematics, Uppsala University.

Jagers, P. (1989). General branching processes as Markov fields. *Stochastic Processes and their Applications* **32** 183-242.

Jagers, P. (1991). The growth and stabilization of populations. *Statistical Science* **6** 269-283.

Jagers, P. (1997a). Towards dependence in general branching processes. In: Athreya, K. B. and Jagers, P.(eds.), *Classical and Modern Branching Processes.* Springer, New York.

Jagers, P. (1997b). Coupling and population dependence in branching processes. *Annals of Applied Probability* **7**, 281-298.

Jagers, P. and Klebaner F. (1998) *Population-size-dependent and age-dependent branching processes.* Preprint, Dep. Mathematics, Chalmers U. Tech. and Göteborg U. 1998:56.

Jagers, P. and Nerman, O. (1984). The growth and composition of branching populations. *Advances in Applied Probability* **16** 221-259.

Jagers, P. and Nerman, O. (1996). The asymptotic composition of supercritical multi-type branching populations. In: J. Azéma, M. Emery and M. Yor (eds.) *Séminaire de Probabilités XXX.* Lecture Notes in Mathematics **1626**, Springer-Verlag.

Klebaner, F. C. (1989). Geometric growth in near-super-critical population size dependent Galton-Watson processes. *Annals of Probability* **17** 1466-1477.

Klebaner F. C. (1991). Asymptotic behaviour of near-critical multitype branching processes. *Journal of Applied Probability* **28** 512-519.

Klebaner, F. C. (1994). Asymptotic behaviour of Markov population processes with asymptotically linear rate of change. *Journal of Applied Probability* **31**, 614-625.

Metz, J. A. J. and Diekmann, O. (eds.) (1986). *The Dynamics of Physiologically Structured Populations.* Lecture Notes in Biomathematics **68**. Springer-Verlag, Berlin.

Ney, P. and Nummelin E. (1984). Markov additive processes I. Eigenvalue properties and limit theorems. *Annals of Probability* **15** 561-592.

Niemi, S. and Nummelin, E. (1986). On non-singular renewal kernels with an application to a semigroup of transition kernels. *Stochastic Processes and their Applications* **22** 177-202.

Nummelin, E. (1984). *General Irreducible Markov Chains and Non-negative Operators.* Cambridge University Press, Cambridge.

Shurenkov, V. M. (1984). On the theory of Markov renewal. *Theory of Probability and its Applications* **29** 247-265.

Shurenkov, V. M. (1989). *Ergodicheskie protsessy Markova.* Nauka, Moscow.

Shurenkov, V. M. (1992). *On the relationship between spectral radii and Perron roots.* Dep. Mathematics, Chalmers U. Tech. and Göteborg U. Preprint.

Shurenkov, V. M. (1992). *On the existence of a Malthusian parameter.* Dep. Mathematics, Chalmers U. Tech. and Göteborg U. Preprint.

Thieme, H. R. (1992). Analysis of structured population models by nonlinear perturbations of semigroups and evolutionary systems. *3rd International Conference on Mathematical Population Dynamics.*

Webb, G. F. (1985). *Theory of Nonlinear Age-Dependent Population Dynamics.* Marcel Dekker, New York.

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