The Annals of Probability
1985, Vol. 13, No. 1, 254–268

BRANCHING PROCESSES IN PERIODICALLY VARYING ENVIRONMENT

BY PETER JAGERS AND OLLE NERMAN

Chalmers University of Technology and Gothenburg University

In order to model the diurnal variation of certain cell populations we study general one-type branching processes whose individuals reproduce in a manner that is influenced by time in a periodic fashion. A Malthusian growth rate is established as well as a periodically varying asymptotic composition, over ages e.g.

1. Introduction. Besides exponential growth the asymptotic stable population compositions, and their relation to individual reproductive behaviour, presumably constitute the most important specific contribution of (supercritical) branching processes to the study of actual populations. The known diurnal variation in growth of certain cell populations [cf. 3, 5, 11] raises the question of similar results for processes whose individuals display a reproduction which is time dependent in a periodic manner. Hopper and Brockwell have constructed a model of such phenomena, using random walk ideas [6]; Klein and Macdonald studied Markov branching processes with time periodic death intensity and reproduction law [12]. For general branching processes some heuristic arguments were reported in [8].

This paper establishes the counterpart of exponential growth and the stable population composition for general branching populations in periodically varying environments. For simplicity the period is taken as 1. First, a brief formulation of a model with time dependence is given. A functional relation for the means is deduced, of a generalized convolution type. It is a variant of an equation in the model of [13: Ch. 7]. Positivity and weak compactness arguments are used to find the Malthusian parameter and an appropriate eigenfunction of an operator corresponding to the convolution type transformation (and the Malthusian parameter). These are then applied to reduce the asymptotics of the means of the branching process to those of a sort of periodically state dependent renewal sequence. The latter are caught by a result due to H. Thorisson [18].

Finally the martingale and law-of-large-numbers technique deployed in [14] and [9] can be adapted to investigate the asymptotics of not only means but of the branching process itself and its composition. For simplicity we contend ourselves with a treatment requiring a reproduction variance restriction.

2. The model. With N the positive integers, $N^0 = \{0\}$,

$$I = \cup_{n=0}^{\infty} N^n$$

the set of (conceivable) *individuals*, $(\Omega, \mathscr{A})$ an abstract *life space*, and $\mathscr{B}[0, 1)$

Received July 1983; revised February 1984.
AMS 1980 *subject classifications*. Primary 60J80; secondary 60J85, 92A15.
Key words and phrases. Branching processes, diurnal variation, periodic exponential growth.

the Borel algebra on [0, 1),

$$([0, 1) \times \Omega^I, \mathscr{B}[0, 1) \times \mathscr{A}^I)$$

is the Ulam-Harris population space on which the process is constructed. As usual $0 \in I$ is interpreted as the ancestor and $x = (x_1, \cdots, x_n) \in I$ as the x_nth child of the x_{n-1}th child of $\cdots$ the x_1th child of the ancestor, and the xth coordinate of $(\rho_0, (\omega_x; x \in I))$ describes x's all life, while the first coordinate ρ_0 indicates the phase or *clock* at the ancestor's birth. The life space is thus assumed rich enough for all relevant entities to be defined on it. At least the successive *ages at childbearing*

$$0 \leq \tau(1, \omega) \leq \tau(2, \omega) \leq \cdots \leq \infty$$

should always be defined for $\omega \in \Omega$.

The point process

$$\xi(\omega) = \sum_{k=1}^{\infty} 1_{\{\tau(k,\omega)\}}$$

on R^+ is termed the *reproduction process*. The age of x at her kth childbearing is thus $\tau(k, \omega_x)$ which we denote $\tau_x(k)$ as a function of the basic outcome $(\rho_0, (\omega_x; x \in I))$. Similarly x's reproduction process is

$$\xi_x(\rho_0, (\omega_x; x \in I)) = \xi(\omega_x).$$

The successive *birth times*, σ_x, are defined by induction

$$\sigma_0 = 0$$

$$\sigma_{xk} = \sigma_x + \tau_x(k),$$

where $xy = (x_1, \cdots, x_n, y_1, \cdots, y_m)$ if $x = (x_1, \cdots, x_n)$ and $y = (y_1, \cdots, y_m)$ $(x0 = 0x = x)$. The clock at x's birth, ρ_x, is then of course (∞ mod $1 = 0$)

$$\rho_x = (\sigma_x + \rho_0) \bmod 1.$$

The periodicity in the environment is modelled with a set of *life laws*

$$P(s, \cdot), s \in [0, 1),$$

probability measures on $(\Omega, \mathscr{A})$ for individuals born at s o'clock. All functions

$$s \rightsquigarrow P(s, A), \quad A \in \mathscr{A},$$

and supposed to be measurable.

It is then easy to see that Ionescu Tulcea's theorem [15, page 161] guarantees the existence of unique probability measures $P_s, s \in [0, 1)$, on the basic probability space determined by the starting phase $\rho_0 = s$ and the requirement that for all $x \in I$

$$P_s(\omega_x \in \cdot \mid \omega_y; y \in I \backslash (\{x\} \times I)) = P(\rho_x, \cdot).$$

Now, let S_x, $x \in I$, denote the *ancestor shift* on $[0, 1) \times \Omega^I$, i.e. an operator rendering x an ancestor

$$S_x(\rho_0, (\omega_y; y \in I)) = (\rho_x, (\omega_{xy}; y \in I)).$$

If $\mathscr{A}_n$ is the σ-algebra which is generated by the lives ω_x of all individuals

$x \in \cup_{k=0}^{n} N^k$, then, for any P_s, all *daughter processes* S_x, $x \in N^{n+1}$, are independent, given $\mathscr{A}_n$, and each is conditionally distributed according to the law P_{ρ_x}.

Similarly if $X_1 = 0$, X_2, X_3, $\cdots$ are the individuals numbered in an order not contradicting their appearance

$$0 = \sigma_{X_1} \leq \sigma_{X_2} \leq \cdots,$$

and $\mathscr{L}_n$ is the σ-algebra generated by $\omega_{X_1}, \omega_{X_2}, \cdots, \omega_{X_n}$, then (for any P_s) the distribution of $\omega_{X_{n+1}}$ given $\mathscr{L}_n$ will be $P(\rho_{X_{n+1}}, \cdot)$. Let

$$I(t) = \{xk;\ \sigma_x \leq t < \sigma_{xk} < \infty,\ x \in I,\ k \in N\}$$

denote the *coming generation*, the set of individuals born after t but by mothers who were already then born. Then the *total population* born by t,

$$y_t = \#\{x \in I;\ \sigma_x \leq t\},$$

is a stopping time with respect to $\{\mathscr{L}_n\}$ and the processes S_x, $x \in I(t)$, are conditionally independent given $\mathscr{L}_{y_t}$ each according to the law

$$P_s(S_x \in \cdot \mid \mathscr{L}_{y_t}) = P_{\rho_x}(\cdot).$$

For further discussions of this and similar facts, see [9].

A *random characteristic* $\chi = \{\chi(a);\ a \in R\}$ is a stochastic process on the population space $[0, 1) \times \Omega^I$, here (and usually) taken to be nonnegative and vanishing for $a < 0$. The interpretation is that $\chi(a)$ is the score in some sense of the ancestor at age a, the score of other individuals $x \in I$ being

$$\chi_x(a) = \chi(a) \circ S_x.$$

For examples of random characteristics we refer the reader to [7, 9]. Let it only be pointed out here that this general definition allows the characteristic of an individual to be influenced by the individual's progeny and their characteristics. The *periodic branching process counted by* χ at time t (after the start of the process) is

$$z_t^\chi = \textstyle\sum_{x\in I} \chi_x(t - \sigma_x)$$

and x's χ-*counted daughter process* is

$$z_t^\chi(x) = z_t^\chi \circ S_x = \textstyle\sum_{y\in I} \chi_y \circ S_x(t - \sigma_y \circ S_x) = \sum_{y\in I} \chi_{xy}(t - (\sigma_{xy} - \sigma_x)).$$

This leads to the fundamental decomposition

$$z_{t+u}^\chi = \textstyle\sum_{\sigma_x \leq t} \chi_x(t + u - \sigma_x) + \sum_{x\in I(t)} z_{t+u-\sigma_x}^\chi(x),$$

where the summands in the last term are conditionally independent and distributed as z_v^χ, $v = t + u - \sigma_x$, under P_{ρ_x}, given $\mathscr{L}_{y_t}$. It will be used in Section 5.

3. The expected behaviour of Malthusian processes.

We first consider the expectations

$$m_{s,t}^\chi = E_s[z_t^\chi]$$

with respect to P_s, $s \in [0, 1)$. Denote by

$$\mu(s, t) = E_s[\xi_0(t)] = E_s[\xi_0([0, t])],$$

the *reproduction function* of an individual born at s o'clock, and write

$$g(s, a) = E_s[\chi(a)]$$

for the expected score of an a-aged individual born at the very same s o'clock. Extend the function g periodically so that

$$g(s + n, a) = g(s - n, a) = g(s, a)$$

for $n \in N$, $s \in [0, 1)$, and $a \in R$. For $x \in N^n$ then

$$E_s[\chi_x(t - \sigma_x) \mid \mathscr{A}_{n-1}] = g(s + \sigma_x, t - \sigma_x).$$

Hence, with $n(x) = n \Leftrightarrow x \in N^n$, and $\mathscr{A}_{-1}$ the trivial σ-algebra,

$$\begin{aligned} m^{\chi}_{s,t} &= E_s[\textstyle\sum_{x\in I} \chi_x(t - \sigma_x)] \\ &= \textstyle\sum_{x\in I} E_s[E_s[\chi_x(t - \sigma_x) \mid \mathscr{A}_{n(x)-1}]] \\ &= \textstyle\sum_{x\in I} E_s[g(s + \sigma_x, t - \sigma_x)] \\ &= \int_0^t g(s + u, t - u)E_s[y_{du}]. \end{aligned}$$

But

$$E_s[y_t] = \textstyle\sum_{n=0}^{\infty} E_s[\sum_{x\in N^n} 1_{\{\sigma_x \le t\}}] = \sum_{n=0}^{\infty} \mu_n(s, t) = \nu(s, t),$$

say, where $\mu_0(s, t)$ places mass one at the origin and

$$\mu_n(s, t) = \int_0^t \mu(s + u, t - u)\mu_{n-1}(s, du),$$

for $n \in N$. In conclusion

$$m^{\chi}_{s,t} = \int_0^t g(s + u, t - u)\nu(s, du)$$

and for decent g (i.e. decent χ) the study of $m^{\chi}_{s,t}$ is reduced to that of $\nu(s, t)$.

We assume that we may define operators T_β on $L^\infty[0, 1]$ by

$$T_\beta f(s) = \int_0^\infty f(s + t)e^{-\beta t}\mu(s, dt)$$

at least for β large enough, f periodically continued. If there is a value α such that the spectral radius of T_α is one, then α is the *Malthusian parameter*. The process itself is called *Malthusian* if this spectral radius is also an eigenvalue with a nonnegative and bounded eigenfunction h, vanishing only on a reproduction null set, i.e. such that if $N_0 = \{s; h(s) = 0\}$ then $\mu(s, N_0 - s) = 0$ for all $0 \le s < 1$. The next section gives sufficient conditions for Malthusianness.

Let us note here that if the process is Malthusian and $s \in N_0$, then with h extended periodically

$$0 = \int_0^\infty h(u)e^{-\alpha(u-s)}\mu(s, du - s)$$

implies that (prime for complement)

$$0 = \mu(s, N_0' - s) = \mu(s, N_0' - s) + \mu(s, N_0 - s) = \mu(s, R_+).$$

Hence a process starting at $s \in N_0$ o'clock will exhibit (almost) no births. But also if $s \notin N_0$ $\mu(s, N_0 - s) = 0$, and hence whenever we start (almost) no individuals will be born at times in N_0. In other words we may restrict attention to s such that $h(s) > 0$.

We shall however need an assumption which even forces $\inf h > 0$:

(3.1) The $\mu(s, \cdot)$, $s \in [0, 1)$, have a common Lebesgue continuous component, i.e. for some $0 \leq f \in L^1[0, \infty)$ not a.e. zero, $\mu(s, du) \geq f(u)\, du$ for all s.

If this holds $e^{-\alpha u}\mu_n(s, du - s)$, $s \in [0, 1)$, must also have a common positive Lebesgue component for any n large enough. But, from the eigenvalue property of h:

$$h(s) = \int_0^\infty e^{-\alpha(s+u)} h(u) \mu_n(s, du - s),$$

for any $n \in N$, so that

$$\inf_{0 \leq s < 1} h(s) > 0,$$

as claimed. We can thus define a new kernel

$$\tilde{\mu}(s, du) = h(s + u) e^{-\alpha u} \mu(s, du)/h(s),$$

h extended periodically. It is straight-forward to verify that

$$h(s + u) e^{-\alpha u} \mu_n(s, du)/h(s) = \tilde{\mu}_n(s, du),$$

$\tilde{\mu}_n$ determined from $\tilde{\mu}$ as μ_n from μ. Hence

$$\nu(s, du) = \textstyle\sum_{n=0}^\infty \mu_n(s, du) = \dfrac{h(s)e^{\alpha u}}{h(s + u)} \textstyle\sum_{n=0}^\infty \tilde{\mu}_n(s, du) = \dfrac{h(s)e^{\alpha u}}{h(s + u)} \tilde{\nu}(s, du)$$

in an obvious notation.

But, for each $s \in [0, 1)$, $\tilde{\mu}(s, \cdot)$ is a distribution function on R_+. We extend it in its first argument,

$$\tilde{\mu}(n + s, dt) = \tilde{\mu}(s, dt)$$

and consider an increasing Markov chain $\{M_n\}_0^\infty$ on R_+ with increments

$$M_{n+1} - M_n \mid M_n = s \sim \tilde{\mu}(s, dt).$$

The chain is a sort of renewal sequence, the increments however not i.i.d. By a result due to Thorisson [18] renewal type theorems still hold, under Condition 3.1. Indeed, by Theorem 4 in [18] (or by Harris recurrence arguments) the Markov chain $\{M_n \bmod 1\}$ has a unique invariant distribution, λ say, on $[0, 1)$ which we scale to

$$\pi = \lambda/\gamma,$$

where γ is the expected ergodic step length of $\{M_n\}$,

$$\gamma = \int_0^1 \int_0^\infty (1 - \tilde{\mu}(s, u))\, du\lambda(ds).$$

The measure π is then periodically extended to all R. Provided $\gamma < \infty$, it is then a consequence of [18, Theorem 6] that $\tilde{\nu}(s, n + r - s + \cdot)$ $r \in [0, 1)$, converges towards $\pi(r + \cdot)$, as $n \to \infty$, in the strong sense of convergence in total variation on any finite interval. Hence $e^{-\alpha(n+r-s)}\nu(s, n + r - s + du)$ will tend in the same sense towards

$$h(s)e^{\alpha u}\pi(r + du)/h(r + u).$$

Further the key-renewal-type theorem [18, Theorem 10] (and the facts that $\inf_s h(s) > 0$ and $\sup_s h(s) < \infty$) implies that

$$e^{-\alpha(n+r-s)}m^{\chi}_{s,n+r-s} \to \int_0^\infty g(r - u, u)\, \frac{h(s)e^{-\alpha u}}{h(r - u)}\, \pi(r - du),$$

as $n \to \infty$, provided $\sup_u e^{-\alpha u}g(r - u, u) < \infty$ and $e^{-\alpha u}g(r - u, u) \to 0$, as $u \to \infty$.

For the proofs in Section 5 we shall need some uniformity in these convergences to be guaranteed by the condition:

(3.2) There is a distribution function F on $[0, \infty)$ such that $1 - \tilde{\mu}(s, u) \leq 1 - F(u)$ for all s and u, and such that

$$\int_0^\infty (1 - F(u))\, du < \infty.$$

If this is also satisfied, then the total variation convergence on any fixed interval of $e^{-\alpha(n+r-s)}\nu(s, n + r - s + du)$ towards its limit is indeed uniform in $s \in [0, 1)$ (and also in $r \in [0, 1)$), [18, Theorem 7(a')]. Hence if χ has bounded support and g is bounded the convergence of $e^{-\alpha(n+r-s)}m^{\chi}_{s,n+r-s}$ towards its limit is uniform in $s \in [0, 1)$ (and in $r \in [0, 1)$).

4. Conditions for Malthusianness. Malthusianness as defined is a property of the operators

$$T_\beta f(s) = \int_0^\infty f(s + t)e^{-\beta t}\mu(s, dt) = \int_0^\infty f(t)e^{-\beta(t-s)}\mu(s, dt - s)$$

on $L^\infty[0, 1)$, the integral defined by periodic extension of $f \in L^\infty[0, 1)$. The classical result on the spectral theory of such positive integral operators is Jentzsch's theorem [4, 17]. We shall apply a modern form of it, which makes it possible to relax somewhat the requirements of continuity in s and boundedness of the kernel [17, page 337].

The assumptions we make use of are the following:

(4.1) The process is supercritical in the sense that there is a $\beta > 0$ such that T_β is well defined and its spectral radius $r(T_\beta)$ is finite but not less than one.

(4.2) The convolved $\mu_n(s, \cdot - s)$ are absolutely continuous with respect to some finite measure μ, for $n \geq$ some n_0.

$$\mu_{n_0}(s, du - s) = K(s, u)\mu(du).$$

(For simplicity in the argumentation below we always assume $n_0 = 1$.)

(4.3) The kernel K should be jointly measurable in its two arguments. It should be $L^q[\mu]$ *bounded* for some $q \in (1, \infty]$:

$$\sup_s \int_0^\infty K(s, t)^q \mu(dt) < \infty.$$

By use of weak separability it then follows that T_β^2 is a compact operator [1], [17, p. 337], since by (4.3) and Hölder's inequality T_β maps $L^P[\mu]$ into L^∞, $1/p + 1/q = 1$. Hence [10, page 185], its spectrum may accumulate only in the origin. Since

$$r(T_\beta) \leq \sup_{0 \leq s < 1} \int_0^\infty e^{-\beta(t-s)} \mu(s, dt - s)$$

$$\leq \sup_s \left\{ \int_0^\infty e^{-\beta(t-s)} \mu(dt) \right\}^{1/p} \sup_s \left\{ \int_0^\infty K(s, t)^q \mu(dt) \right\}^{1/q},$$

$\lim_{\beta \to \infty} r(T_\beta) = 0$. Moreover $r(T_\beta)$ does not increase in β and a Hölder argument again applies to show that the map $\beta \curvearrowright T_\beta$ is continuous in the strong operator topology. Hence [10, page 213] the spectrum varies continuously with β and so does the spectral radius. We have proved

LEMMA 4.1. *Under Conditions* (4.1-3) *a Malthusian parameter* $\alpha > 0$ *exists.*

To be meticulously precise about Jentzsch's theorem we should exhibit T_α as an integral operator on $[0, 1)$. Writing

$$\mu_\alpha(dt) = \sum_{n=0}^\infty e^{-\alpha(n+t)} \mu(n + dt)$$

for $t \in [0, 1)$ and

$$\mathscr{K}(s, t) = \sum_{n=0}^\infty e^{-\alpha(n+t-s)} K(s, n + t) \mu(s, n + dt)/\mu_\alpha(dt);$$

in the sense of a Radon-Nikodym derivative, we see however that

$$T_\alpha f(s) = \int_0^\infty f(t) e^{-\alpha(t-s)} \mu(s, dt - s)$$

$$= \int_0^1 f(t) \sum_{n=0}^\infty e^{-\alpha(u+t-s)} \mu(s, n + dt - s)$$

$$= \int_0^1 f(t) \mathscr{K}(s, t) \mu_\alpha(dt).$$

There are then only two conditions to be checked in order to conclude from [17, page 337] that the spectral radius $r(T_\alpha) = 1$ is an eigenvalue with a unique normalized a.e. $[\mu_\alpha]$ strictly positive eigenfunction h, namely that some power of T_α is compact—which we already know—and the following *communication* property: if $S \subset [0, 1)$ and S' denotes its complement in the unit interval, then $\mu_\alpha(S)\mu_\alpha(S') > 0$ implies that

$$\int_S \int_{S'} \mathscr{K}(s, t)\mu_\alpha(ds)\mu_\alpha(dt) > 0,$$

or, in terms of the original measures, that:

if

$$(\textstyle\sum_n \mu(S + n))(\sum_n \mu(S' + n)) > 0$$

(4.4) then also

$$\int_{S'} \mu(s, S + j - s)\mu(ds + k) > 0$$

at least for one pair j, k from N.

Note that this trivially holds if $\mu(s, \cdot)$ have a common Lebesgue continuous component (Condition (3.1)). In conclusion we have proved

THEOREM 4.2. *Under Conditions* (4.1-4) *the process is Malthusian.*

5. Convergence of the processes. In this section we shall consider a periodic Malthusian branching process with parameter $\alpha > 0$ and eigenfunction h. We assume conditions (3.1), (3.2) and

$$\sup_{0\le s<1} \mathrm{Var}_s \left[\int_0^\infty e^{-\alpha u}\xi_0(du)\right] < \infty. \tag{5.1}$$

Recall from Section 3 that $\inf_{0\le s<1} h(s) > 0$ and norm h to satisfy $\sup_{0\le s<1} h(s) = 1$.

With

$$\psi_x = h(\rho_x)e^{-\alpha\sigma_x}, \quad x \in I,$$

$$R_n = \psi_0 + \textstyle\sum_{k=1}^n ((\sum_{j=1}^\infty \psi_{X_kj}) - \psi_{X_k}), \quad n = 0, 1, 2, \cdots$$

turns out to constitute a martingale with respect to $\{\mathscr{G}_n\}$, under any P_s, $s \in [0, 1)$. This is a consequence of the eigenfunction property of h and the fact that conditionally on $\mathscr{G}_n$, $\sigma_{X_{n+1}}$ and $\rho_{X_{n+1}} = (s + \sigma_{X_{n+1}}) \bmod 1$ are both known while the daughter process of X_{n+1} obeys the law $P_{\rho_{X_{n+1}}}$:

$$\begin{aligned} E_s[R_{n+1} - R_n \mid \mathscr{G}_n] &= E_s[\textstyle\sum_{j=1}^\infty \psi_{X_{n+1}j} \mid \mathscr{G}_n] - \psi_{X_{n+1}} \\ &= \int_0^\infty h(s + \sigma_{X_{n+1}} + u)e^{-\alpha(u-\sigma_{X_{n+1}})}\mu(s + \sigma_{X_{n+1}}, du) - \psi_{X_{n+1}} \\ &= e^{-\alpha\sigma}X_{n+1}h(\rho_{X_{n+1}}) - \psi_{X_{n+1}} = 0. \end{aligned}$$

The total population y_t at time t is a stopping time with respect to $\{\mathscr{G}_n\}$ for each fixed t. Thanks to the Optional Sampling Theorem

$$\{w_t\} = \{R_{y_t}\}$$

is therefore a nonnegative supermartingale in continuous time with respect to $\{\mathscr{G}_{y_t}\}$.

Now recall the definition of $I(t)$, the coming generation at t. It is directly verified that

$$w_t = \textstyle\sum_{x\in I(t)} \psi_x.$$

Observe also that on $\{y_t \nrightarrow \infty\}$ R_n and w_t both eventually vanish, so that almost surely the limits

$$R_\infty = \lim_{n\to\infty} R_n$$

and

$$w_\infty = \lim_{t\to\infty} w_t$$

must be equal.

THEOREM 5.1. *For any P_s, $s \in [0, 1)$, $\{w_t\}$ is an L^2-convergent martingale, $\{w_\infty > 0\} = \{y_t \to \infty\}$ a.s. and $P_s(w_\infty > 0) = P_s(y_t \to \infty) > 0$.*

PROOF. The first part of the theorem follows from the L^2-convergence of $\{R_n\}$ which in its turn is a consequence of

$$\lim_{n\to\infty} \mathrm{Var}_s[R_n] < \infty,$$

to be shown now:

$$\begin{aligned}\mathrm{Var}_s[R_n] &= E_s[\textstyle\sum_{j=0}^{n-1} \mathrm{Var}_s[R_{j+1} - R_j \mid \mathscr{G}_j]]\\ &= E_s[\textstyle\sum_{j=0}^{n-1} e^{-2\alpha\sigma_{X_{j+1}}} v(s + \sigma_{X_{j+1}})],\end{aligned}$$

where

$$v(s) = \mathrm{Var}_s\left[\int_0^\infty h(s+u)e^{-\alpha u}\xi_0(du)\right].$$

Hence

$$\lim_{n\to\infty} \mathrm{Var}_s[R_n] = E_s\left[\int_0^\infty e^{-2\alpha u} v(s+u) y_{du}\right] = \int_0^\infty e^{-2\alpha u} v(s+u)\nu(s, du),$$

which due to (5.1) is convergent together with

$$\int_0^\infty e^{-2\alpha u}\nu(s, du),$$

since h is bounded.

But from the asymptotics of $\nu(s, \cdot)$ (Section 3) and $\inf h(s) > 0$

$$\sup_t e^{-\alpha t}\nu(s, t) < \infty.$$

Consider now the second claim of the theorem. By the definitions of $\{w_t\}$ and $\{y_t\}$ obviously

$$\{w_\infty > 0\} \subseteq \{y_t \to \infty\}.$$

Denote by $w_\infty(x) = \lim_{t\to\infty} w_t \circ S_x$, $x \in I$, the limit of the "daughter martingale" of x, and observe that, on $\{y_t \to \infty\}$,

$$w_\infty > w_\infty(X_n)e^{-\alpha\sigma x_n}$$

for all n. Hence

$$P_s(\{w_\infty > 0\} \cup \{y_t \nrightarrow \infty\} \mid \mathscr{L}_n) \geq P_s(w_\infty(X_{n+1}) > 0 \mid \mathscr{L}_n)$$
$$= E_s[P_{\rho X_{n+1}}(w_\infty > 0)] \geq \inf_s P_s(w_\infty > 0).$$

But by Levy's theorem the first of these terms must tend to the indicator function of $\{w_\infty > 0\} \cup \{y_t \nrightarrow \infty\}$. Therefore if we can prove that $\inf_s P_s(w_\infty > 0) > 0$, it follows that

$$P_s(w_\infty > 0 \quad \text{or} \quad y_t \nrightarrow \infty) = 1$$

and consequently that $\{w_\infty > 0\} = \{y_t \to \infty\}$ a.s., as claimed.

To prove that $\inf_{0\leq s<1} P_s(w_\infty > 0)$ is not zero we need

LEMMA 5.2. *For some $\varepsilon > 0$ and $n \in N$ there exists to each $s \in [0, 1)$ an $i_s \in \{1, \cdots, n\}$ such that the distribution of ρ_{i_s} under $P(s, \cdot)$ has an absolutely continuous component with density at least ε, on a set B_s with Lebesgue measure at least ε.*

PROOF OF THE LEMMA. By (3.1) there is an $\varepsilon > 0$ and a set A with positive Lebesgue measure, say $\delta > 0$, such that, for all $s \in [0, 1)$, $\mu(s, du) \geq \varepsilon\, 1_A(u)\, du$. This A can be chosen bounded. Let c be an upper bound of A.

The Malthusianess of the process implies that

$$\sup_{0\leq s<1} \int_0^\infty e^{-\alpha u}\mu(s, du) < \infty$$

and hence that $\sup_s \mu(s, c) < \infty$. Condition (5.1) yields—in the notation $\xi(c) = \xi([0, c])$—that

$$\sup_{0\leq s<1} E_s[\xi^2(c)] < \infty.$$

Since

$$\xi(c) = \textstyle\sum_{i=1}^\infty 1_{[0,c]}(\tau(i)),$$

and $1_{[0,c]}(\tau(i)) = 0$ if $\xi(c) < i$, it holds for any $n \in N$ and $s \in [0, 1)$ that

$$E_s[\textstyle\sum_{i>n} 1_{[0,c]}(\tau(i))] = E_s[\sum_{i>n} 1_{[0,c]}(\tau(i));\ \xi(c) > n]$$
$$\leq E_s[\xi(s);\ \xi(s) > n] \leq \sup_{0\leq r<1} E_r[\xi^2(c)]/n.$$

Thus we can choose n to render

$$E_s[\sum_{i>n} 1_{[0,c]}(\tau(i))] < \varepsilon\delta/2$$

for all s.

Let $f_i(s, u)$ denote the density of the Lebesgue continuous part of the distribution of $\tau(i)$ under $P(s, \cdot)$, $i \in N$ and $s \in [0, 1)$. Then for $u \in A$

$$\sum_{i=1}^{\infty} f_i(s, u) \geq \varepsilon$$

and so

$$\varepsilon\delta/2 > E_s[\sum_{i>n} 1_{[0,c]}(\tau(i))]$$
$$\geq \int_0^{\infty} \sum_{i>n} f_i(s, u)\, du \geq \int_A (\varepsilon - \sum_{i=1}^{n} f_i(s, u))^+ du.$$

If now ℓ_s is the Lebesgue measure of

$$\{u \in A;\ \sum_{i=1}^{n} f_i(s, u) \leq \varepsilon/3\}$$

it follows that $\ell_s < 3\delta/4$. In other words

$$A_s = \{u \in A;\ \sum_{i=1}^{n} f_i(s, u) > \varepsilon/3\}$$

must have a Lebesgue measure at least $\delta/4$. But

$$A_s \subseteq \cup_{i=1}^{n} \{u \in A;\ f_i(s, u) > \varepsilon/3n\}$$

so that at least one of the sets in this union has Lebesgue measure not less than $\delta/4n$. The short final step from bearing age to clock is left to the reader. □

The proof of the theorem is now completed by

$$P_s(w_\infty > 0) \geq P_s(w_\infty(i_s) > 0,\ \sigma_{i_s} < \infty) = E_s[P_{\rho_{i_s}}(w_\infty > 0);\ \sigma_{i_s} < \infty]$$
$$\geq \varepsilon \int_{B_s} P_u(w_\infty > 0)\, du.$$

But, by the L^2-convergence of $\{w_t\}$, $P_s(w_\infty > 0) > 0$ for all $0 \leq s < 1$. Since B_s has Lebesgue measure $\geq \varepsilon$ the integrals must have a strictly positive lower bound. □

THEOREM 5.3. *Suppose that χ is a characteristic such that*

$$\sup_{s,a} E_s[\chi(a)] < \infty,$$

and

$$\sup_s E_s[\chi(a)] \to 0,$$

as $a \to \infty$. Then, for $r, s \in [0, 1)$,

$$e^{-\alpha(n+r-s)} z_{n+r-s}^{\chi} \to w_\infty \int_0^{\infty} E_{r-u}[\chi(u)] e^{-\alpha u} \pi(r - du)/h(r - u)$$

in $L^1(P_s)$, as $n \to \infty$.

Before the proof we give a consequence of this and Theorem 5.1 on the composition of the total population

COROLLARY 5.4. *If χ satisfies the conditions of Theorem 5.3, then, for r, $s \in [0, 1)$,*

$$\frac{z^{\chi}_{n+r-s}}{y_{n+r-s}} \to \frac{\int_0^\infty E_{r-u}[\chi(u)]e^{-\alpha u}\pi(r-du)/h(r-u)}{\int_0^\infty e^{-\alpha u}\pi(r-du)/h(r-u)}$$

in P_s-probability on $\{y_t \to \infty\}$, as $n \to \infty$.

PROOF OF THE THEOREM. Fix s and $r \in [0, 1)$. Let

$$\chi^c(a) = (\chi(a) \wedge c)1_{[0,c]}(a),$$

where $0 < c < \infty$. From Section 3 we know that

$$\begin{aligned}\lim_{n\to\infty} E_s[\,|\,e^{-\alpha(n+r-s)}z^{\chi}_{n+r-s} - e^{-\alpha(n+r-s)}z^{\chi^c}_{n+r-s}\,|\,]\\ = \lim_{n\to\infty} e^{-\alpha(n+r-s)}m^{\chi}_{s,n+r-s} - \lim_{n\to\infty} e^{-\alpha(n+r-s)}m^{\chi^c}_{s,n+r-s}\\ = \int_0^\infty E_{r-u}[\chi(u) - (\chi(u) \wedge c)1_{[0,c]}(u)]h(s)e^{-\alpha u}\pi(r-du)/h(r-u).\end{aligned}$$

This is also the expected absolute difference between the suggested limits of $e^{-\alpha(n+r-s)}z^{\chi}_{n+r-s}$ and $e^{-\alpha(n+r-s)}z^{\chi^c}_{n+r-s}$. Since it can be made arbitrarily small by choice of c large, it is enough to prove the proposed convergence for all $e^{-\alpha(n+r-s)}z^{\chi^c}_{n+r-s,c} < \infty$.

By the already shown common Lebesgue component of $\tilde{\mu}(s, \cdot)$ $0 \le s < 1$, it is straightforward to dominate $\tilde{\nu}$:

$$\tilde{\nu}(s, t) \le U(t), \quad 0 \le s < 1, \quad t > 0,$$

where $U(t)$ is the renewal function of a renewal sequence with increments distributed as a mixture of an atom at zero and the common Lebesgue component of $\tilde{\mu}(s, \cdot)$. Hence it follows that

$$\sup_s E_s[y_t] = \sup_s \nu(s, t) < \infty,$$

for any fixed $t < \infty$.

Arguing as in the proof of Theorem 3.2 in [9] one can prove that

$$\mathrm{Var}_s[y_t] = \int_0^t v(s+u, t-u)\nu(s, du)$$

where

$$v(s, t) = \mathrm{Var}_s\left[\int_0^t \nu(s+u, t-u)\xi_0(du)\right].$$

But then, since $\nu(s+u, t-u) \le \nu(s+u, t)$,

$$\begin{aligned}\mathrm{Var}_s[y_t] &= \int_0^t (\sup_{s'}\nu(s', t))^2 \mathrm{Var}_s[\xi_0(t)]\nu(s, du)\\ &\le (\sup_{s'}\nu(s', t))^3 \sup_{s'}\mathrm{Var}_{s'}[\xi_0(t)] < \infty,\end{aligned}$$

as a consequence of (5.1) and the fact that $\sup_{0\le s<1}\nu(s, t) < \infty$. Hence

$\sup_{0\le s<1} E_s[y_t^2] < \infty$, and accordingly also

$$\sup_{u\le t}\sup_{0\le s<1}\mathrm{Var}_s[z_u^{\chi^c}] \le c^2 \sup_{0\le s<1} E_s[y_t^2] < \infty,$$

for all $t < \infty$.

Recall the fundamental decomposition given in Section 2. For χ^c and $u > c$ it takes the form

$$z_{t+u}^{\chi^c} = \textstyle\sum_{x;\sigma_x\le t} \chi_x^c(t+u-\sigma_x) + \sum_{x\in I(t)} z_{t+u-\sigma_x}^{\chi^c}(x) = \sum_{x\in I(t)} z_{t+u-\sigma_x}^{\chi^c}(x),$$

since $\chi^c(a) = 0$ for $a > c$. Hence, u still $> c$,

$$\begin{aligned}\mathrm{Var}_s[e^{-\alpha(t+u)} z_{t+u}^{\chi^c} \mid \mathscr{G}_{y_t}] &= \textstyle\sum_{x\in I(t),\sigma_x\le t+u} e^{-2\alpha(t+u)}\mathrm{Var}_s[z_{t+u-\sigma_x}^{\chi^c}(x) \mid \mathscr{G}_{y_t}] \\ &\le \textstyle\sum_{x\in I(t),\sigma_x\le t+u} e^{-2\alpha(t+u)} \sup_{0\le u'\le u, 0\le s<1}\mathrm{Var}_s[z_{u'}^{\chi^c}] \\ &\le e^{-\alpha(t+u)} \textstyle\sum_{x\in I(t),\sigma_x\le t+u} e^{-\alpha(t+u-\sigma_x)} h(\rho_x) e^{-\alpha\sigma_x} \\ &\quad \cdot \sup_{0\le u'\le u, 0\le s<1}\mathrm{Var}_s[z_u^{\chi^c}]/\inf_{0\le s'<1} h(s') \\ &\le e^{-\alpha(t+u)} w_t \sup_{0\le u'\le u, 0\le s<1}\mathrm{Var}_s[z_{u'}^{\chi^c}]/\inf_{0\le s'<1} h(s').\end{aligned}$$

Further

$$E_s[z_{t+u}^{\chi^c} \mid \mathscr{G}_{y_t}] = \textstyle\sum_{x\in I(t)} m_{\rho_x, t+u-\sigma_x}^{\chi^c}$$

so that we can conclude that

$$E_s[(e^{-\alpha(t+u)} z_{t+u}^{\chi^c} - \textstyle\sum_{x\in I(t)} m_{\rho_x,t+u-\sigma_x}^{\chi^c})^2] = E_s[\mathrm{Var}_s[e^{-\alpha(t+u)} z_t^{\chi^c} \mid \mathscr{G}_{y_t}]] \to 0,$$

as $t \to \infty$.

By this our task has been reduced to proving

$$\begin{aligned}&\lim_{j\to\infty} \lim_{n\to\infty} E_s[\,|\, e^{-\alpha(n+j+r-s)} \textstyle\sum_{x\in I(n)} m_{\rho_x, n+j+r-s-\sigma_x}^{\chi^c} \\ &\quad - w_n \displaystyle\int_0^\infty E_{r-u}[\chi^c(u)] e^{-\alpha u}\pi(r-du)/h(r-u)\,|\,] = 0.\end{aligned}$$

We write κ_r for the coefficient of w_n here and recall from Section 3 (the remark at the end) that the convergence

$$e^{-\alpha(n+j+r-s-\sigma_x)} m_{\rho_x,n+j+r-s-\sigma_x}^{\chi^c}/h(\rho_x) \to \kappa_r$$

is uniform in s, as $n + j + r - s - \sigma_x \to \infty$. Hence in

$$\begin{aligned}&e^{-\alpha(n+j+r-s)} \textstyle\sum_{x\in I(n)} m_{\rho_x,n+j+r-s-\sigma_x}^{\chi^c} - \kappa_r w_n \\ &\quad = \textstyle\sum_{x\in I(n),\sigma_x\le n+j/2} e^{-\alpha\sigma_x} h(\rho_x)\{e^{-\alpha(n+j+r-s-\sigma_x)} m_{\rho_x,n+j+r-s-\sigma_x}^{\chi^c}/h(\rho_x) - \kappa_r\} \\ &\qquad + \textstyle\sum_{x\in I(n),\sigma_x> n+j/2} e^{-\alpha\sigma_x} h(\rho_x)\{e^{-\alpha(n+j+r-s-\sigma_x)} m_{\rho_x,n+j+r-s-\sigma_x}^{\chi^c}/h(\rho_x) - \kappa_r\},\end{aligned}$$

for any $\varepsilon > 0$, the first sum can be made smaller than $\varepsilon\, w_n$ by choice of j large, whereas the second is smaller than some constant times

$$\textstyle\sum_{x\in I(n),\sigma_x> n+j/2} e^{-\alpha\sigma_x} h(\rho_x).$$

Since $E_s[w_n] = h(s)$ remains bounded, it is enough to show that the expectation of the latter sum tends to a limit, as $n \to \infty$, which then decreases to zero, as

$j \to \infty$. But

$$\textstyle\sum_{x \in I(n), \sigma_x > n+j/2} e^{-\alpha \sigma_x} h(\rho_x) = e^{-\alpha n} z_n^{\varphi_j},$$

where φ_j is the characteristic

$$\varphi_j(a) = e^{\alpha a} \int_{a+j/2}^{\infty} e^{-\alpha u} h(\rho_0 + u) \xi_0(du).$$

From Section 3

$$\begin{aligned}
&E_s[e^{-\alpha n} z_n^{\varphi_j}] \\
&\quad \to \int_0^{\infty} E_{s-a}[\varphi_j(a)] h(s) e^{-\alpha a} \pi(s - da)/h(s - a) \\
&\quad = \int_0^{\infty} \left(\int_{a+j/2}^{\infty} e^{-\alpha u} h(s - a + u) \mu(s - a, du) \right) h(s) \pi(s - da)/h(s - a) \\
&\quad = h(s) \int_0^{\infty} \left(\int_{a+j/2}^{\infty} \tilde{\mu}(s - a, du) \right) \pi(s - du) \\
&\quad = h(s) \int_0^{\infty} (1 - \tilde{\mu}(s - a, a + j/2)) \pi(s - da),
\end{aligned}$$

as $n \to \infty$. Since

$$h(s) = E_s[w_n] = E_s[z_n^{\varphi_\infty}] = h(s) \int_0^{\infty} (a - \tilde{\mu}(s - a, a)) \pi(s - da)$$

dominated convergence, as $j \to \infty$, yields the required convergence to zero. □

6. A remark on application. We have found that the asymptotic size of a χ-counted population as compared to the total population born is

$$\frac{\int_0^\infty e^{-\alpha u} g(r - u, u) \pi(r - du)/h(r - u)}{\int_0^\infty e^{-\alpha u} \pi(r - du)/h(r - u)}$$

at r o'clock, $g(s, u) = E_s[\chi(u)]$. But π and h may be difficult to estimate. Let us instead assume that the total population has been followed for some time and known to be of the form $e^{\alpha t} \varphi(t)$ at large times t and t mod 1 o'clock, say. Then

$$e^{\alpha t} \varphi(t) \approx w_\infty e^{\alpha t} \int_0^{\infty} e^{-\alpha u} \pi(t - du)/h(t - u) = w_\infty \int_{-\infty}^{t} e^{\alpha v} \pi(dv)/h(v).$$

Assuming that φ is differentiable implies that

$$(\alpha \varphi(t) + \varphi'(t))\, dt \approx w_\infty \pi(dt)/h(t),$$

which yields the approximate expression

$$\frac{\int_0^\infty e^{-\alpha u} g(r - u, u)(\alpha \varphi(r - u) + \varphi'(r - u))\, du}{\int_0^\infty e^{-\alpha u}(\alpha \varphi(r - u) + \varphi'(r - u))\, du}$$

for the ratio considered. This is given in [8] together with some cell kinetic illustrations.

REFERENCES

[1] DUNFORD, N. and SCHWARTZ, J. (1958). *Linear Operators. I.* Interscience, New York.
[2] FELLER, W. (1971). *An Introduction to Probability Theory and its Applications II.* Wiley, New York.
[3] HALBERG, F., HANS, E. and SCHEVING, L. E. (1978). Sampling of biologic rhythms, chronocytokinetics and experimental oncology. In: *Biomathematics and Cell Kinetics.* (Valleron, A.-J. and Macdonald, P.D.M., eds) 175–190. North Holland, Amsterdam.
[4] HARRIS, T. E. (1963). *The Theory of Branching Processes.* Springer, Berlin.
[5] HARTMANN, N. R. and MØLLER, U. (1978). A compartment theory in cell kinetics including considerations on circadian variations. In: *Biomathematics and Cell Kinetics* (Valleron, A.-J. and Macdonald, P.D.M., eds), North Holland, Amsterdam.
[6] HOPPER, J. L. and BROCKWELL, P. J. (1978). A stochastic model for cell populations with circadian rhythms. *Cell Tissue Kinet.* **11** 205–225.
[7] JAGERS, P. (1975). *Branching Processes with Biological Applications.* Wiley, London.
[8] JAGERS, P. (1983). Stochastic models for cell kinetics. *Bull. Math. Biol.* **45** 507–519.
[9] JAGERS, P. and NERMAN, O. (1984). The growth and composition of branching populations. *Adv. Appl. Probab.* **16** 221–259.
[10] KATO, T. (1976). *Perturbation Theory for Linear Operators, 2nd ed.* Springer-Verlag, Berlin.
[11] KEIDING, N., HARTMANN, N. R. and MØLLER, U. (1982). Circadian variation in influx and transition intensities in the S phase of hamster cheek pouch epithelium cells. Statistical Research Unit, Copenhagen.
[12] KLEIN, B. and MACDONALD, P. D. M. (1980). The multitype continuous-time Markov branching process in a periodic environment. *Adv. Appl. Probab.* **12** 81–93.
[13] MODE, C. J. (1971). *Multitype Branching Processes.* Elsevier, New York.
[14] NERMAN, O. (1981). On the convergence of supercritical general (C-M-J) branching processes. *Z. Wahrsch. verw. Gebiete* **57** 365–395.
[15] NEVEU, J. (1965). *Mathematical Foundations of the Calculus of Probability.* Holden-Day, San Francisco.
[16] RIESZ, F. and NAGY-SZ, B. (1955). Leçons sur analyse fonctionelle. *Akadémiai Kiadó*, Budapest.
[17] SCHAEFER, H. H. (1974). *Banach Lattices and Positive Operators.* Springer-Verlag, Berlin.
[18] THORISSON, H. (1983). Periodic renewal theory. Report 1983-5, Dept. Mathematics, Chalmers U. Tech. and U. Göteborg.
[19] MACDONALD, P. D. M. (1981). Measuring circadian rhythms in cell populations. In: *The Mathematical Theory of the Dynamics of Biological Populations II.* (Hiorns, R. W. and Cooke, D., eds.), Academic, London 281–306.

DEPARTMENT OF MATHEMATICS
CHALMERS UNIVERSITY OF TECHNOLOGY
AND UNIVERSITY OF GÖTEBORG
S-412 96 GÖTEBORG, SWEDEN.