# AN INFINITE ALLELES VERSION OF THE MARKOV BRANCHING PROCESS 

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#### Abstract

Individuals in a population which grows according to the rules defining the Markov branching process can mutate into novel allelic forms. We obtain some results about the time of the last mutation and the limiting frequency spectrum. In the present context these results refine certain results obtained in the discrete time case and they answer some conjectures still unresolved for the discrete time case.


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## 1. Introduction

Recently Griffiths and Pakes [4] considered a simple branching process in which individuals were classified according to their allelic type and a newly born individual has probability $u$ of mutating to a novel type independently of the previous history of the process. All alleles are selectively neutral in the sense that the offspring distribution is independent of allelic type. Asymptotic results were found for
(i) the number $K_{n}$ of alleles in generation $n$.
(ii) the generation number $L$ of the last mutation event.

[^0](iii) the frequency spectrum $\left(\phi_{i}^{(n)}(j)\right)$, where $\phi_{i}^{(n)}(j)$ is the expected number of alleles represented by $j$ members of the $n$th generation in a process which begins with $i$ individuals carrying the same allele.

A number of questions remain unresolved in the discrete time case. For example, in the subcritical case it was shown that $\left(K_{n}\right)$ has a conditional limiting distribution, but almost nothing is known about the nature of this distribution. Again, if $T$ is the extinction time it was shown in the non-supercritical case that $\left(E_{i}(T-L)\right.$ ) has a limit as $i \rightarrow \infty$, where $E_{i}(\cdot)$ denotes the conditional expectation given the above initial configuration. The situation in the subcritical case is actually quite involved because $i$ must be restricted to certain sub-sequences. It would be of some interest to determine how the limit behaves as a function of the mean number of offspring per individual $m$, even if only for specific examples. However, the limit depends in a complicated way on stationary measures of the process giving the generation sizes and it does not seem possible to gain any insight by purely analytical means. Numerical results were given for the case of a geometric offspring distribution which suggest that when $i$ is large, $E_{i}(T-L)$ increases with $m$.

Finally, when $m<\infty$ it was shown that there is a limiting frequency spectrum $\phi_{i}(j)=\lim _{n \rightarrow \infty} m^{-n} \phi_{i}^{(n)}(j)$. Let $M=m(1-u)$ be the mean number of offspring carrying the parental allele. When $M>1$ the behaviour of $\sum_{k \geq j} \phi_{i}(k)$ as $j \rightarrow \infty$ such that $j M^{-n} \rightarrow c>0$ was determined and a conjecture was made about the behaviour of individual $\phi_{i}(j)$. Obstacles in the way of proving the conjecture were discussed and it was shown to be valid for the fractional linear offspring distribution. A parallel discussion was presented for the case $M=1$ but here no general results are known. The behaviour of $\phi_{i}(j)$ can be determined in the fractional linear case and a conjecture was made on the basis of this example and some other considerations.

Nearly all properties of the simple discrete time branching process have an analogue for the continuous time Markov branching process (M.B.P.) and in many cases the M.B.P. results are more complete and easier to prove. One example, which we will use below, is that the M.B.P. has a unique stationary measure (apart from multiplicative constants) and its generating function has an explicit integral representation. In view of this it seems worthwhile to look at a M.B.P. in which individuals have independently and exponentially distributed life times with mean life-length $a^{-1}$, but otherwise they reproduce and mutate as in the discrete time branching case. It may be hoped that the smoother behaviour of the M.B.P. will lead to a more complete treatment of the problems mentioned above.

Unfortunately it does not seem possible to develop a more complete theory for the number $K_{t}$ of alleles at time $t$. However, we can make some progress with respect to the other problems. For example, in the next section we consider
the non-supercritical case and use $L$ to denote the last time at which a mutation event occurs. We obtain the distribution function (D.F.) of $L$ and some limit theorems for a large initial population. All this is very similar to the discrete time case. One simplification however, is an integral expression for $E_{i}(L)$. We show that the D. F. of $D=T-L$, where we use $T$ to denote the extinction time of the M.B.P., can be explicitly evaluated in terms of the solution of a certain differential equation (equation (2.7) below). This gives more complete results for the limiting behaviour of $D$ as $i \rightarrow \infty$ than are available in the discrete time case. Many of our formulae can be explicitly evaluated for the birth and death process. We use these results to discuss the behaviour of $E_{1}(D)$ and $E_{1}(L)$ under variations of the defining parameters.

In Section 3 we study the frequency spectrum with particular emphasis on the tail behaviour of the limiting frequency spectrum $(\phi(j))$ defined below in Lemma 3.1.3 and (3.1.1). When $M>1$ we argue as in [4] to determine the rate at which $\sum_{k \geq j} \phi(k)$ decreases to zero as $j \rightarrow \infty$. The form of our result, Theorem 3.2.1, is nicer than in [4] because here the limit has a simple form and $j$ is not forced to increase through a lacunary sequence as in the discrete time case. By obtaining a representation of $\phi(j)$ in terms of a renewal sequence we are also able to determine the asymptotic behaviour of $(\phi(j))$; see Theorem 3.2.2 below. This result supports the conjecture in [4].

When $M=1$ and heavy moment conditions are satisfied we are able to obtain the asymptotic behaviour of $(\phi(j))$ (Theorem 3.3 .1 below) and again this supports the conjecture made in [4]. In the M.B.P. case we can express the generating function of $(\phi(j))$ in terms of that of the stationary measure of a critical process (see (3.3.5)). We first prove Theorem 3.3.1 under a special condition which includes the particular case of the birth and death process. This is done because the details are much simpler than in the general case which follows the overall strategy of the special case. In addition we can isolate the main ingredient of the proof of the special case, Theorem 3.3.2, for later use in the general case.

We close this section by introducing some notation. The overall population size at time $t$ is denoted by $Z_{t}$; we assume that $Z_{0}=i$ and that the initial individuals carry the same allele. Expectations conditional on this initial configuration are denoted by $E_{i}(\cdot)$. Let $f(s)=\sum_{j \geq 0} p_{j} s^{j}$ be the probability generating function (p.g.f.) of the offspring distribution, $p_{1}=0, p_{j} \neq 1(j \geq 0)$ and we always assume $m=\sum j p_{j}<\infty$. Let $F_{t}(s)=E_{1}\left(s^{Z_{t}}\right)$, which satisfies the forward and backward equations,

$$
\begin{equation*}
\partial F_{t} / \partial t=b(s) \partial F_{t} / \partial s \quad \text { and } \quad \partial F_{t} / \partial t=b\left(F_{t}\right) . \tag{1.1}
\end{equation*}
$$

respectively, where $b(s)=a(f(s)-s)$.

## 2. The time of last mutation

In this section we will assume $m=f^{\prime}(1-) \leq 1$. The total number $\tau$ of alleles ever to have existed is exactly as it is for the discrete time case since $\tau$ depends only on genealogical aspects of the entire family tree and not on individual life lengths. Then as indicated in [4],

$$
E_{i}\left(s^{\tau}\right)=s[\beta(1-u+u s)]^{i}
$$

where $\beta(s)$ is the p.g.f. of the total number $B$ of births and is the unique solution of the equation

$$
\beta=f(s \beta)
$$

Let $L$ be the time when the last mutation event occurs and $L=0$ if mutation never occurs. Our assumption $m \leq 1$ ensures that the process becomes extinct after finitely many splits and hence $L$ is a well-defined random variable. Let $\delta=\beta(1-u)$. Then clearly

$$
\begin{equation*}
P_{i}(L=0)=P_{i}(\tau=1)=\delta^{i} \tag{2.1}
\end{equation*}
$$

Given $\mathscr{F}_{t}$, the $\sigma$-algebra representing the history of the mutation process up to $t$, then $L \leq t$ if and only if there are no mutations among the descendents of the $Z_{t}$ individuals alive at $t$. This has conditional probability $\delta^{Z_{t}}$, see equation (2.1), and hence

$$
\begin{equation*}
P_{i}(L \leq t)=\left(F_{t}(\delta)\right)^{i} \tag{2.2}
\end{equation*}
$$

which is a precise analogue of the discrete time result in [4, Lemma 3.1]. This distribution function (D.F.) can be evaluated when $\left(Z_{t}\right)$ is a birth and death process. In this case $f(s)=q+p s^{2}$ where $p+q=1$ and then $m=2 p$,

$$
\delta=(2-m) /\left[1+\left(1-(1-u)^{2} m(2-m)\right)^{1 / 2}\right]
$$

and when $m \neq 1$,

$$
F_{t}(s)=\frac{(2-m)(1-s)-(2-m-m s) \exp (a(1-m) t)}{m(1-s)-(2-m-m s) \exp (a(1-m) t)}
$$

and when $m=1$,

$$
F_{t}(s)=\frac{2 s+a t(1-s)}{2+a t(1-s)}
$$

From (2.2) we obtain

$$
E_{i}(L)=\int_{0}^{\infty}\left[1-\left(F_{t}(\delta)\right)^{i}\right] d t
$$

Let $y=F_{t}(\delta)$ and use the backward equation (1.1) to obtain the simpler expression

$$
E_{i}(L)=a^{-1} \int_{\delta}^{1} \frac{1-y^{i}}{f(y)-y} d y
$$

Letting $\delta=0$ in this integral gives the well-known formula for $E_{i}(T)$ and in particular we see that these expectations are either both finite or both infinite. In particular $E_{i}(L)$ is finite when $m<1$ and infinite if $m=1$ and $\sum p_{j} j^{2}<\infty$. In the case of the birth and death process

$$
E_{1}(L)=\frac{2}{a m} \log \left(\frac{2-m-m \delta}{2(1-m)}\right)
$$

and numerical calculations indicate that this is an increasing function of $m$. This will be further discussed below. A first order approximation for small $u$ is

$$
E_{1}(L) \simeq m u / a(1-m)^{2}
$$

Equation (2.2) can be used to obtain limit theorems for $L$ in almost exactly the same way as for the discrete time case (op. cit. Theorem 3.1). To state the subcritical ( $m<1$ ) part of this we need the following notation. It is known [9] that $\lim _{t \rightarrow \infty} P_{i}\left(Z_{t}=j \mid Z_{t}>0\right)$ exists as a proper discrete distribution with p.g.f.

$$
Q(s)=1-\exp \left[\lambda \int_{0}^{s} d x / b(x)\right]
$$

where $\lambda=a(m-1)$. When

$$
\begin{equation*}
\sum_{j \geq 1} p_{j} j \log j<\infty \tag{2.3}
\end{equation*}
$$

this limiting conditional distribution has a finite first moment

$$
c=\exp \left[\int_{0}^{1}\left(\frac{1}{1-s}+\frac{\lambda}{b(x)}\right) d x\right]
$$

Finally let $\psi(\cdot)$ be the inverse of the function $1-Q(1-s)$.
THEOREM 2.1.
(i) When $m=1$ and $\gamma=b^{\prime \prime}(1-) / 2<\infty$ then

$$
\lim _{i \rightarrow \infty} P_{i}(L \leq i t)=\exp (-1 / \gamma t)
$$

(ii) When $m<1$ then

$$
\lim _{i \rightarrow \infty} P_{i}\left(i \psi\left(e^{\lambda L}\right) \leq x\right)=1-\exp [-x(1-Q(\delta))]
$$

(iii) If $m<1$ and (2.3) holds then for $-\infty<y<\infty$

$$
\lim _{i \rightarrow \infty} P_{i}(|\lambda| L-\log (i / c) \leq y)=\exp \left[-(1-Q(\delta)) e^{-y}\right]
$$

REMARK. The discrete time analogue of (iii) was not given in [4], although it is easily formulated. A step in proving (ii) is to let $i, t \rightarrow \infty$ such that $i\left(1-F_{t}\right) \rightarrow x$, where $F_{t}=F_{t}(0)$. It follows that

$$
P_{i}(L \leq t) \rightarrow 1-\exp [-x(1-Q(\delta))]
$$

To obtain (iii) we need only use $1-Q\left(F_{t}\right)=e^{\lambda t}$ and $1-Q(s)^{\sim} c(1-s)$ as $s \rightarrow 1^{-}$.
We will now consider the difference $D=T-L$, the time elapsing between the last mutation and extinction. Let $B_{t}$ be the total number of individuals born within $(0, t], \Phi_{t}(s, x)=E_{1}\left(s^{Z_{t}} x^{B_{t}}\right)$ and $G(t)=\Phi_{t}(0,1-u)$.

THEOREM 2.2.

$$
\begin{equation*}
P_{i}(D \leq t)=1-\frac{f[(1-u) G(t)]-G(t)}{f(G(t))-G(t)}\left(1-(G(t))^{i}\right) \tag{2.4}
\end{equation*}
$$

Proof. Observe first that

$$
\begin{align*}
P_{i}(L & =0, T \leq t)=E_{i}\left[P_{i}(L=0 \mid \mathscr{F} t) I(T \leq t)\right] \\
& =E_{i}\left[(1-u)^{B_{t}} ; Z_{t}=0\right]=(G(t))^{i} \tag{2.5}
\end{align*}
$$

Now consider the event $\{v<L<v+d v<T \leq v+t\}$. This occurs if
(i) there is a split in $(v, v+d v)$,
(ii) there are $j \geq 2$ offspring and at least one of these mutates, and
(iii) there are no further mutations amongst the descendents of the $Z_{v}+j-1$ individuals living at $v+d v$ and the process is extinct within a further $t-d v$ units of time. If $Y$ denotes the number of offspring produced by a typical split then

$$
\begin{aligned}
P_{i}(v & <L<v+d v<T \leq v+t) \\
& =E_{i}\left[a Z_{v} d v\left(1-(1-u)^{Y}\right) P_{Z_{v}+Y-1}(L=0, T \leq t) ; Y>0\right]+o(d v) \\
& =E_{i}\left[a Z_{v} d v\left(1-(1-u)^{Y}\right)(G(t))^{Z_{v}+Y-1} ; Y>0\right]+o(d v) \\
& =\left.a[f(G(t))-f((1-u) G(t))] \frac{\partial}{\partial s}\left(F_{v}(s)\right)^{i}\right|_{s=G(t)} d v+o(d v)
\end{aligned}
$$

where we have used (2.5) to get the second equality. The forward equation yields

$$
\frac{\partial}{\partial s}\left(F_{v}(s)\right)^{i}=(1 / b(s)) \frac{\partial}{\partial v}\left(F_{v}(s)\right)^{i}
$$

and integration with respect to $v$ over $(0, \infty)$ yields

$$
P_{i}(L>0, D \leq t)=\frac{f(G(t))-f((1-u) G(t))}{f(G(t))-G(t)}\left(1-(G(t))^{i}\right)
$$

Adding this to (2.5) yields (2.4).
It only remains to check that (2.4) gives a proper D.F. This follows because

$$
\lim _{t \rightarrow \infty} G(t)=E_{1}\left((1-u)^{B}\right)=\delta
$$

and

$$
\lim _{t \rightarrow \infty} f((1-u) G(t))=f((1-u) \delta)=\delta
$$

REMARK. When $m>1$ we may define $D=0$ if $T=\infty$, since the latter event implies $L=\infty$. A simple change in the proof will then give

$$
\begin{equation*}
P_{i}(D \leq t)=1-\frac{f[(1-u) G(t)]-G(t)}{f(G(t))-G(t)}\left(q^{i}-(G(t))^{i}\right) \tag{2.6}
\end{equation*}
$$

a D.F. which has an atom of size $1-q^{i}$ at the origin.
The backward equation satisfied by $\Phi_{t}(s, x)$ yields

$$
\begin{equation*}
G^{\prime}(t)=a[f((1-u) G(t))-G(t)] \tag{2.7}
\end{equation*}
$$

whence

$$
P_{i}(D>t)=\frac{q^{i}-(G(t))^{i}}{b(G(t))} G^{\prime}(t)
$$

Integration over $t$ and a change of variable yields

Theorem 2.3.

$$
E_{i}(D)=a^{-1} \int_{0}^{\delta} \frac{q^{i}-y^{i}}{f(y)-y} d y
$$

Since $\delta<q$ we see that $E_{i}(D)<\infty$ when $p_{0}>0$. If $u=0$ then $\delta=1, L=0$ and we recover the well-known representation for $E_{i}(T)$. If $m \leq 1$ then

$$
\lim _{i \rightarrow \infty} E_{i}(D)=a^{-1} \int_{0}^{\delta} d y /(f(y)-y)
$$

which is always finite.
For the birth and death process with $m \leq 1$ we obtain

$$
E_{1}(D)=\frac{2}{a m} \log \frac{2-m}{2-m-m \delta}
$$

and numerical calculations indicate that this increases as $m$ increases. The behaviour of $E_{1}(D)$ and $E_{1}(L)$ when $a=1$ as functions of $m$ are illustrated in Table 2.1. We note that $E_{1}(L)$ is very much smaller then $E_{1}(D)$ when $m$ is small, or even for quite large $m$ if $u$ is small enough, and $E_{1}(L)$ increases very rapidly when $m \simeq 1$. For this example we have

$$
\begin{gathered}
\lim _{m \rightarrow 0} E_{1}(D)=1 / a \text { and } \lim _{m \rightarrow 0} m^{-1} E_{1}(L)=(2-u) u / a ; \text { and } \\
\lim _{m \rightarrow 1} E_{1}(D)=(2 / a) \log \left[(u(2-u))^{-1 / 2}+1\right] \text { and } \\
E_{1}(L)=(2 / a) \log (1-m)^{-1}-\lim _{m \rightarrow 1} E_{1}(D)+o(1) \quad \text { as } m \rightarrow 1
\end{gathered}
$$

Table 2.1 indicates that when $m<1$ we have $E_{1}(L) \rightarrow 0$ as $u \rightarrow 0$ and it can be shown quite generally that

$$
E_{1}(L) \sim \frac{\operatorname{im} u}{a(1-m)^{2}} \quad(u \rightarrow 0)
$$

Finally, when $m=1$ and $\gamma=f^{\prime \prime}(1-) / 2<\infty$ the representation of Theorem 2.3 shows that $E_{1}(D) \rightarrow \infty$ as $u \rightarrow 0$ and some algebraic manipulation yields the asymptotic relation

$$
E_{1}(D) \sim(i / 2 \gamma) \log u^{-1} .
$$

|  | $u=0.1$ |  | $u=0.01$ |  | $u=0.001$ |  | $u=0.0001$ |  | $u=0.000001$ |  |  |
| :--- | :---: | ---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $m$ | $E_{1}(D)$ | $E_{1}(L)$ | $E_{1}(D)$ | $E_{1}(L)$ | $E_{1}(D)$ | $E_{1}(L)$ | $E_{1}(D)$ | $E_{1}(L)$ | $E_{1}(D)$ | $E_{1}(L)$ |  |
| .2 | 1.1496 | .02824 | 1.1747 | .003093 | 1.1775 | $3.122 \times 10^{-4}$ | 1.1778 | $3.129 \times 10^{-5}$ | 1.1778 | $3.55 \times 10^{-7}$ |  |
| .4 | 1.3468 | .09161 | 1.4275 | .01088 | 1.4373 | .001109 | 1.4383 | $1.111 \times 10^{-4}$ | 1.4384 | $1.149 \times 10^{-6}$ |  |
| .6 | 1.6113 | .2541 | 1.8297 | .03567 | 1.8617 | .003731 | 1.8650 | $3.748 \times 10^{-4}$ | 1.8654 | $3.790 \times 10^{-6}$ |  |
| .8 | 1.9611 | .7854 | 2.5789 | .1677 | 2.7269 | .01960 | 2.7445 | .001996 | 2.7465 | $1.998 \times 10^{-5}$ |  |
| .9 | 2.1666 | 1.6217 | 3.2438 | .5445 | 3.7048 | .08357 | 3.7794 | .008929 | 3.7882 | $9.000 \times 10^{-5}$ |  |
| .95 | 2.2746 | 2.6757 | 3.6869 | 1.2634 | 4.6530 | .2973 | 4.9134 | .03687 | 4.9499 | $3.800 \times 10^{-4}$ |  |
| .99 | 2.3623 | 5.5609 | 4.0808 | 3.8424 | 5.9203 | 2.0029 |  | 7.3077 | .6155 | 7.9134 | .009826 |
| .999 | 2.3821 | 10.0616 | 4.1710 | 8.2727 | 6.2641 | 6.1795 | 8.4125 | 4.0312 | 11.8207 | .6230 |  |
| 1 | 2.3843 | $\infty$ | 4.1810 | $\infty$ | 6.3026 | $\infty$ | 8.5453 | $\infty$ | 13.1252 | $\infty$ |  |

Table 2.1. Some values of $E_{1}(D)$ and $E_{1}(L)$ for the birth and death process with $a=1$
Results qualitatively similar to those in Table 2.1 are exhibited by the geometric offspring distribution, $f(s)=1 /(1+m-m s)$, for which

$$
\begin{gathered}
\delta=2 /\left[1+m+\left((1+m)^{2}-4 m(1-u)^{2}\right)^{1 / 2}\right], \\
E_{1}(D)=(\delta-\log (1-m \delta)) / a
\end{gathered}
$$

and

$$
E_{1}(L)=[1-\delta-\log ((1-m) /(1-m \delta))] / a .
$$

An immediate consequence of Theorem 2.2 is the following limit theorem.
Theorem 2.4. When $m \leq 1$,

$$
\begin{aligned}
\lim _{i \rightarrow \infty} P_{i}(D \leq t) & =\frac{f(G(t))-f((1-u) G(t))}{f(G(t))-G(t)} \\
& =(b(G(t)))^{-1} G^{\prime}(t)
\end{aligned}
$$

and the limit is a proper D.F.
This limiting D.F. can be evaluated for the birth and death process, as indeed can the full D.F. of Theorem 2.2. In this case we have $f(s)=q+p s^{2}$ and if we set

$$
\varsigma=\left(1-4 p q(1-u)^{2}\right)^{1 / 2}, \quad a_{0}, a_{1}=1 \pm \varsigma \quad \text { and } \quad \sigma(t)=e^{a s t}
$$

then (2.7) can be solved, giving

$$
G(t)=\frac{2 q(\sigma(t)-1)}{a_{0} \sigma(t)-a_{1}} .
$$

Further algebraic manipulation shows that the limit D.F. is

$$
\Delta(t)=\frac{4 \sinh ^{2}(a \varsigma t / 2)}{4 \cosh ^{2}(a \varsigma t / 2)+A}
$$

where $A=(1-4 p q) / p q u(2-u)$. When $m=1, A=0$ and then $\Delta(t)=$ $\tanh ^{2}\left(a_{\varsigma} t / 2\right)$.

## 3. The frequency spectrum

3.1. In this section we let $H(s)=f(u+(1-u) s)$ be the p.g.f. of the distribution of the number of offspring born to a single individual carrying the parental allele and let $r$ denote the extinction probability corresponding to $H(\cdot)$. Let ( $X_{t}: t \geq 0$ ) denote the M.B.P. defined by $H(s)$ and $a, h(s)=a(H(s)-s)$ and

$$
A_{t}^{i}(s)=E_{i}\left(s^{X_{t}}\right)=\sum_{j \geq 0} q_{i j}(t) s^{j}
$$

Now let $\alpha_{t}(j)$ be the number of alleles which are represented by $j$ individuals at time $t$, let $T_{1}, T_{2}, \ldots$ be the successive split times of the process $\left(Z_{t}\right), N_{t}$ be the number of split times in ( $0, t$ ] and $U_{n}$ be the number of offspring produced at time $T_{n}$. Define the indicator functions: $I_{0, j}(t)=1$ if the $i$ ancestors have $j$ like-type representatives alive at time $t$ and for $n, k \geq 1, I_{n, k, j}(t)=1$ if the $k$ th individual born at time $T_{n}$ differs in type to its parent and has $j$ like-type representatives $t$ time units later. It is clear that

$$
\alpha_{t}(j)=I_{0, j}(t)+\sum_{n=1}^{N_{t}} \sum_{k=1}^{U_{n}} I_{n, k, j}\left(t-T_{n}\right) .
$$

For each $n, I_{n, k, j}(t)$ is independent of $U_{n}$ and $T_{n}, E_{i}\left(I_{0, j}(t)\right)=q_{i j}(t)$ and $E\left(I_{n, k, j}(t) \mid U_{n}, T_{n}\right)=u q_{1 j}(t)$. Thus

$$
\Phi_{i, t}(j)=E_{i}\left(\alpha_{t}(j)\right)=q_{i j}(t)+u m E_{i}\left(\sum_{n=1}^{N_{t}} q_{1 j}\left(t-T_{n}\right)\right)
$$

The expectation on the right-hand side can be obtained from the following lemma.

LEMMA 3.1.1. Let $\alpha(t)$ be a bounded continuous function. Then

$$
\beta_{i}(t)=E_{i}\left[\sum_{n=1}^{N_{t}} \alpha\left(t-T_{n}\right)\right]=i a e^{\lambda t} \int_{0}^{t} e^{-\lambda u} \alpha(u) d u
$$

Proof. The independence of family lines implies that $\beta_{i}(t)=i \beta_{1}(t)$ and hence if we let $i=1$ we obtain

$$
E\left(\sum_{n=1}^{N_{t}} \alpha\left(t-T_{n}\right) \mid T_{1}, U_{1}\right)=\alpha\left(t-T_{1}\right)+U_{1} E\left[\sum_{n=1}^{N_{t}^{\prime}} \alpha\left(t-T_{1}-T_{n}^{\prime}\right) \mid T_{1}\right]
$$

where we set $T_{n}^{\prime}=T_{n}-T_{1}$ and $N_{t}^{\prime}$ is the number of split times in ( $\left.T_{1}, t\right]$. It is clear that the conditional expectation on the right-hand side is $\beta_{1}\left(t-T_{1}\right)$, whence removing the conditioning yields

$$
\beta_{1}(t)=a \int_{0}^{t}\left[\alpha(t-u)+m \beta_{1}(t-u)\right] e^{-a u} d u
$$

Rewriting the convolution shows that $\beta_{1}(t)$ is differentiable and satisfies the linear differential equation

$$
\beta_{1}^{\prime}(t)-\lambda \beta_{1}(t)=a \alpha(t)
$$

Solving this subject to the condition $\beta_{1}(0)=0$ gives the assertion.
The number of alleles present at time $t$ is $K_{t}=\sum_{j \geq 1} \alpha_{j}(t)$ and setting $A_{t}=$ $A_{t}(0)$, Lemma 3.1.1 gives

LEMMA 3.1.2. $\phi_{i, t}(j)=q_{i j}(t)_{+} i a m u e^{\lambda t} \int_{0}^{t} e^{-\lambda x} q_{1 j}(x) d x$ and

$$
E_{i}\left(K_{t}\right)=1-A_{t}^{i}+i a m u e^{\lambda t} \int_{0}^{t} e^{-\lambda x}\left(1-A_{x}\right) d x
$$

These expressions are similar in form to those for the discrete time case; see equations (4.1.1) and (2.1.1), respectively in [4]. If $\lambda \leq 0, M=(1-u) m$ and $\bar{\lambda}=a(M-1)$, then $\bar{\lambda}<0$ and $1-A_{t}=O\left(e^{\bar{\lambda} t}\right)$, and the following asymptotic relations follow from Lemma 3.1.2.

Lemma 3.1.3. As $t \rightarrow \infty$,

$$
e^{-\lambda t} \phi_{i, t}(j) \rightarrow i a m u G_{j}(\lambda)
$$

where $G_{j}(\lambda)=\int_{0}^{\infty} e^{-\lambda t} q_{1 j}(t) d t$, and $e^{-\lambda t} E_{i}\left(K_{t}\right) \rightarrow i a m u \int_{0}^{\infty} e^{-\lambda x}\left(1-A_{x}\right) d x$.
These may be compared with the second assertion in Theorem 4.1.1 and Lemma 2.1.1, respectively, in [4]. Let

$$
\begin{equation*}
\phi(j)=a m u G_{j}(\lambda) \tag{3.1.1}
\end{equation*}
$$

which we interpret as a kind of limiting frequency spectrum, cf. the discussion following Theorem 4.1.1 in [4]. The $G_{j}(\lambda)$ are a kind of exponentially weighted Green's function. In the following subsections we will be concerned with the case $M \geq 1$, whence $\lambda>0$. Quantities similar to these, but with $\lambda<0$, have
been studied by Pakes [8]. In the next subsection we will use the approach in [4] to obtain the asymptotic behaviour of $\sum_{k \geq j} \phi(k)$, as $j \rightarrow \infty$, when $M>1$. The details are similar but the result is a lot "nicer" than the discrete time case. Then we use an approach similar to that in [8] to obtain the asymptotic behaviour of $\phi(j)$ (Theorem 3.2.2 below). This result corresponds to Conjecture 4.2.1 in [4].

We end this subsection with a couple of general observations. First, observe that

$$
\sum_{j \geq 1} G_{j}(\lambda)=\int_{0}^{\infty} e^{-\lambda t}\left(1-A_{t}\right) d t
$$

and when $m>1$ we can define $C=\lambda \int_{0}^{\infty} e^{-\lambda t} A_{t} d t<1$ and write the last relation as

$$
\begin{equation*}
\lambda \sum_{j \geq 1} G_{j}(\lambda)=1-C \tag{3.1.2}
\end{equation*}
$$

Secondly,

$$
\sum j G_{j}(\lambda)=\int_{0}^{\infty} e^{-\lambda t} E_{1}\left(X_{t}\right) d t=1 / a m u
$$

and hence for all parameter values $j G_{j}(\lambda) \rightarrow 0$ as $j \rightarrow \infty$.
3.2. Throughout this subsection we assume $M>1$ and $\sum_{j \geq 1} p_{j} j \log j<\infty$. When $X_{0}=1, e^{-\bar{\lambda} t} X_{t} \rightarrow W$ (a.s.) and $W$ has a D.F. $V(\cdot)$ satisfying

$$
V(x)=r+\int_{0}^{x} v(y) d y
$$

where $v(x)>0$ for each $x>0$. Let

$$
\nu=(m-1) /(M-1)
$$

and note that $\nu>1$. The moment condition $\sum p_{j} j^{\nu}<\infty$ is obviously necessary for the finititude of the limit in our first main result, but the proof used here requires a slightly stronger condition. Let $\mu_{\nu}=E\left(W^{\nu}\right)$.

THEOREM 3.2.1. Let $M>1$ and $\sum p_{j} j^{\nu+\varepsilon}<\infty$ for some $\varepsilon>0$. Then

$$
\lim _{j \rightarrow \infty} j^{\nu} \sum_{k \geq j} \phi(k)=\frac{m u}{m-1} \mu_{\nu}<\infty
$$

Proof. Observe first that the moment condition implies that $E_{1}\left(X_{t}^{\nu+\varepsilon}\right)<\infty$ ([2], page 153) and then that Theorem 5 in [3] applied to the discrete skeleton $\left(X_{n h}\right)$ shows that $\mu_{\nu}<\infty$.

Now

$$
\sum_{k \geq j} G_{k}(\lambda)=\int_{0}^{\infty} e^{-\lambda v} P_{1}\left(X_{v} \geq j\right) d v
$$

Choose $t$ so that $j e^{-\bar{\lambda} t}=1$ and $t^{\prime}>0$. Observing that $\nu \bar{\lambda}=\lambda$, we have

$$
\begin{aligned}
j^{\nu} \int_{t-t^{\prime}}^{\infty} e^{-\lambda v} P_{1}\left(X_{v} \geq j\right) d v & =\int_{-t^{\prime}}^{\infty} e^{-\lambda y} P_{1}\left(e^{-\bar{\lambda}(t+y)} X_{t+y} \geq e^{-\bar{\lambda} y}\right) d y \\
& \rightarrow \int_{-t^{\prime}}^{\infty} e^{-\lambda y}\left(1-V\left(e^{-\bar{\lambda} y}\right)\right) d y
\end{aligned}
$$

and we have used the dominated convergence theorem.
Markov's inequality yields

$$
\begin{aligned}
j^{\nu} \int_{0}^{t-t^{\prime}} e^{-\lambda v} P_{1}\left(X_{v} \geq j\right) d v & \leq j^{-\varepsilon} \int_{0}^{t-t^{\prime}} e^{-\nu \bar{\lambda} v} E_{1}\left(X_{v}^{\nu+\varepsilon}\right) d v \\
& =O\left(j^{-\varepsilon} \int_{0}^{t-t^{\prime}} e^{-\nu \bar{\lambda} v+(\nu+\varepsilon) \bar{\lambda} v} d v\right) \\
& =O\left(e^{-\bar{\lambda} \varepsilon t^{\prime}}\right)
\end{aligned}
$$

It follows that

$$
\begin{aligned}
\int_{-t^{\prime}}^{\infty} e^{-\lambda y}\left(1-V\left(e^{-\bar{\lambda} y}\right)\right) d y & \leq \liminf _{j \rightarrow \infty} j^{\nu} \sum_{k \geq j} \phi(k) \\
& \leq \limsup _{j \rightarrow \infty} j^{\nu} \sum_{k \geq j} \phi(k) \\
& \leq \int_{-t^{\prime}}^{\infty} e^{-\lambda y}\left(1-V\left(e^{-\bar{\lambda} y}\right)\right) d y+O\left(e^{-\bar{\lambda} \varepsilon t^{\prime}}\right)
\end{aligned}
$$

Now let $t^{\prime} \rightarrow \infty$ to obtain

$$
j^{\nu} \sum_{k \geq j} G_{k}(\lambda) \rightarrow \int_{-\infty}^{\infty} e^{-\lambda y}\left(1-V\left(e^{-\bar{\lambda} y}\right)\right) d y
$$

even if the integral is infinite. Making the substitution $x=e^{-\bar{\lambda} y}$ reduces the integral to

$$
\bar{\lambda}^{-1} \int_{0}^{\infty} x^{\nu-1}(1-V(x)) d x=(\nu \bar{\lambda})^{-1} \mu_{\nu}
$$

and the theorem follows.
We now prove the local analogue of Theorem 3.2.1.
THEOREM 3.2.2. Under the conditions of Theorem 3.2.1,

$$
\lim _{j \rightarrow \infty} j^{1+\nu} \phi(j)=\frac{m u}{m-1} \mu_{\nu}
$$

Proof. We begin by finding a representation for $j G_{j}(\lambda)$. Let $G(s, \lambda)=$ $\sum_{j \geq 1} G_{j}(\lambda) s^{j}$. By using the forward and backward equations for $A_{t}(s)$ (see
equation (1.1)) we obtain

$$
\begin{aligned}
G(s, \lambda) & =\int_{0}^{\infty} e^{-\lambda t} \int_{0}^{s} \frac{\partial A_{t}(x)}{\partial x} d x d t \\
& =\int_{0}^{s}(h(x))^{-1} \int_{0}^{\infty} e^{-\lambda t} \frac{\partial A_{t}(x)}{\partial t} d t d x \\
& =\int_{0}^{s}(h(x))^{-1}\left(-x+\lambda \int_{0}^{\infty} e^{-\lambda t} A_{t}(x) d t\right) d x
\end{aligned}
$$

whence

$$
\begin{equation*}
\partial G(s, \lambda) / \partial s=(h(s))^{-1}(\lambda G(s, \lambda)+C-s) . \tag{3.2.1}
\end{equation*}
$$

The derivative in this equation is well-defined for $0 \leq s \leq 1$ and since $h(r)=0$ we conclude that

$$
\begin{equation*}
C=r-\lambda G(r, \lambda) \tag{3.2.2}
\end{equation*}
$$

Let $W(s)=(H(s)-r) /(s-r)$, a p.g.f., and for $0 \leq s \leq 1$ let

$$
U(s)=\sum_{j=0}^{\infty} u_{j} s^{j}=(1-W(s))^{-1}
$$

The form of $H(s)$ shows that it generates an aperiodic distribution and we can conclude that ( $u_{j} / u_{0}$ ) is an aperiodic renewal sequence. Invoking the Erdös-Feller-Pollard theorem yields

$$
\begin{equation*}
u_{j} \rightarrow u_{\infty}=\frac{1-r}{M-1} \tag{3.2.3}
\end{equation*}
$$

By using (3.2.2) and the definition of $U(s)$ we can express (3.2.1) as

$$
\begin{equation*}
\partial G(s, \lambda) / \partial s=a^{-1} U(s)\left(1-\frac{\lambda(G(r, \lambda)-G(s, \lambda))}{r-s}\right) \tag{3.2.4}
\end{equation*}
$$

Let $g_{j}=\lambda \sum_{k \geq 0} G_{j+k}(\lambda) r^{k}(j \geq 0)$. It has been observed by Pakes [8] that the generating function of the $g_{j}$ is the subtracted term in (3.2.4). Equating coefficients of $s^{j}$ in (3.2.4) gives the representation

$$
(j+1) G_{j+1}(\lambda)=a^{-1}\left(u_{j}-\sum_{k \geq 0}^{j} u_{j-k} g_{k}\right)
$$

It follows from (3.1.1) and (3.2.2) that $\sum_{j \geq 0} g_{j}=1$ and hence we can re-arrange the previous expression into the desired representation

$$
\begin{equation*}
(j+1) G_{j+1}(\lambda)=a^{-1}\left(u_{j} \sum_{k>j} g_{k}+\sum_{k=0}^{j}\left(u_{j}-u_{j-k}\right) g_{k}\right) \tag{3.2.5}
\end{equation*}
$$

We now set about estimating the rate of convergence to zero of each of the two components on the right. Letting $\gamma_{j}=\lambda \sum_{k \geq j} G_{k}(\lambda)$ we obtain

$$
\beta_{j}=\sum_{k \geq j} g_{k}=\sum_{k \geq 0} \gamma_{j+k} r^{k}
$$

and using the dominated convergence theorem and the result $j^{\nu} \gamma_{j} \rightarrow \mu_{\nu}$, which in essence is the result proved in Theorem 3.2.1, we obtain $j^{\nu} \beta_{j} \rightarrow \mu_{\nu} /(1-r)$. It follows from this that $j^{\nu} g_{j} \rightarrow 0$ and hence from (3.2.3),

$$
\lim _{j \rightarrow \infty} a^{-1} j^{\nu} u_{j} \beta_{j}=\frac{\mu_{\nu}}{a(M-1)}
$$

This will give the assertion of the theorem once we show that the convolution-like sum in (3.2.5) is $o\left(j^{-\nu}\right)$.

To see this first observe that

$$
\left|\sum_{k \leq j / 2}\left(u_{j}-u_{j-k}\right) g_{k}\right| \leq\left|u_{\infty}-u_{j}\right| \sum_{k \geq 0} g_{k}+\sum_{k \leq j / 2}\left|u_{\infty}-u_{j-k}\right| g_{k}
$$

The recurrence distribution generating the renewal sequence $\left\{u_{j} / u_{0}\right\}$ has a finite moment of order $\nu$, whence Proposition 2 of Lindvall [6] yields $u_{\infty}-u_{j}=o\left(j^{-\nu}\right)$ and since $\sum g_{j}=1$ we conclude that the above sum is $o\left(j^{-\nu}\right)$.

The remaining component is

$$
\begin{aligned}
\left|\sum_{j / 2<k \leq j}\left(u_{j}-u_{j-k}\right) g_{k}\right|= & \left|\sum_{j / 2<k \leq j} \sum_{l=j-k+1}^{j}\left(u_{l}-u_{l-1}\right)\left(\beta_{k}-\beta_{k+1}\right)\right| \\
\leq & \sum_{j / 2<l \leq j}\left|u_{l}-u_{l-1}\right| \sum_{j / 2<k \leq j}\left(\beta_{k}-\beta_{k+1}\right) \\
& +\sum_{1 \leq l \leq j / 2}\left|u_{l}-u_{l-1}\right| \sum_{k=j-l+1}^{j}\left(\beta_{k}-\beta_{k+1}\right) .
\end{aligned}
$$

The first double sum on the right is at most

$$
\left(\beta_{[j / 2]}-\beta_{j}\right) \sum_{l>j / 2}\left|u_{l}-u_{l-1}\right|=o\left(j^{-\nu}\right)
$$

since the series converges. The second double sum is

$$
\begin{gathered}
\sum_{1 \leq l \leq j / 2}\left|u_{l}-u_{l-1}\right|\left(\beta_{j-l+1}-\beta_{j+1}\right) \\
\sup _{j \leq 1} j^{\nu}\left(\beta_{[j / 2]}-\beta_{j}\right)<\infty \quad \text { and } \quad j^{\nu}\left(\beta_{j-l+1}-\beta_{j+1}\right) \rightarrow 0 .
\end{gathered}
$$

In view of these, the dominated convergence theorem can be used to show that the above sum is $o\left(j^{-\nu}\right)$, and the proof is complete.
3.3. In this subsection we assume $M=1$ and begin by finding some alternative expressions for $G(s, \lambda)$. Let

$$
\pi(s)=\int_{0}^{s} d x / h(x)
$$

be the generating function of the invariant measure ( $\pi_{j}: j \geq 1$ ) which satisfies $\pi_{j}=\sum_{i \geq 1} \pi_{i} q_{i j}(t)$ for $j \geq 1$. The generating function form of these equations is

$$
\begin{equation*}
\pi(s)=\pi\left(A_{t}(s)\right)-\pi\left(A_{t}\right) \tag{3.3.1}
\end{equation*}
$$

Letting $s=A_{\tau}$ in this equation yields $\pi\left(A_{t+\tau}\right)=\pi\left(A_{t}\right)+\pi\left(A_{\tau}\right)$ which has the solution

$$
\begin{equation*}
\pi\left(A_{t}\right)=\delta t \tag{3.3.2}
\end{equation*}
$$

for some positive constant $\delta$. However, $\pi^{\prime}(0)=1 / h(0)=\left(a \tilde{p}_{0}\right)^{-1}$, where $\tilde{p}_{0}=$ $f(u)$, and (3.3.2) yields

$$
\begin{equation*}
\delta=\frac{\partial A_{t}}{\partial t} \pi^{\prime}\left(A_{t}\right)=\left.h\left(A_{t}\right) \pi^{\prime}\left(A_{t}\right)\right|_{t=0}=a \tilde{p}_{0} / a \tilde{p}_{0}=1 \tag{3.3.3}
\end{equation*}
$$

The function $\pi(\cdot)$ has an inverse $\gamma(\cdot)$ defined on $[0, \infty]$ and satisfying $\gamma(0)=0$ and $\gamma(\infty)=1$. Equations (3.3.1)-(3.3.3) yield

$$
A_{t}(s)=\gamma(t+\pi(s))
$$

whence

$$
\begin{equation*}
G(s, \lambda)=\int_{0}^{\infty} e^{-\lambda t}(\gamma(t+\pi(s))-\gamma(t)) d t \tag{3.3.4}
\end{equation*}
$$

This representation has a number of alternative forms. For example, letting $t=\pi(v)$ gives

$$
G(s, \lambda)=\int_{0}^{1}[\gamma(\pi(v)+\pi(s))-v][V(v) / h(v)] d v
$$

where $V(s)=\exp (-\lambda \pi(s))$. Alternatively, differentiation of (3.3.4) with respect to $s$ yields

$$
G^{\prime}(s, \lambda)=\pi^{\prime}(s) \int_{0}^{\infty} e^{-\lambda t} \gamma^{\prime}(t+\pi(s)) d t
$$

However, $1=\gamma^{\prime}(x) \pi^{\prime}(\gamma(x))=\gamma^{\prime}(x) / h(\gamma(x))$ and hence

$$
G^{\prime}(s, \lambda)=\pi^{\prime}(s) \int_{0}^{\infty} e^{-\lambda t} h(\gamma(t+\pi(s))) d t
$$

Now let $y=\gamma(t+\pi(s))$, that is, $t=\pi(y)-\pi(s)$. The integration interval $\mathbf{R}_{+}$is mapped into $[s, 1]$ and $d t=d y / h(y)$. Thus we obtain our principal representation

$$
\begin{equation*}
G^{\prime}(s, \lambda)=\pi^{\prime}(s) \int_{s}^{1} \exp [-\lambda(\pi(y)-\pi(s))] d y \tag{3.3.5}
\end{equation*}
$$

The integral in this expression can be "evaluated" in the case of the critical birth-death process where $h(s)=a(1-s)^{2} / 2$ and $\pi(s)=2 / a(1-s)$. If we let $c=2 \lambda / a=2(m-1)$ and make the change of variables $v=(1-y)^{-1}-(1-s)^{-1}$ the resulting integral can be evaluated in terms of the exponential integral $E_{1}(x)=$ $\int_{x}^{\infty} e^{-v} d v / v$ as

$$
G^{\prime}(s, \lambda)=\frac{2}{a(1-s)}\left[1-s-\left(c \exp \left(\frac{c}{1-s}\right)\right) E_{1}\left(\frac{c}{1-s}\right)\right] .
$$

The integral giving this expression can be expressed as a power series in $s$ which yields

$$
G_{j}(\lambda)=\frac{2}{a} \int_{0}^{\infty} e^{-c v}\left(\frac{v}{1+v}\right)^{j-1} \frac{d v}{(1+v)^{2}} .
$$

This integral arose as an approximant in the discrete time case and its asymptotic behaviour was determined using a naive version of Laplace's method. An integral similar to this arises in the general case and we apply Laplace's method more carefully. First we state the main result.

We will assume that $H(s)$ is holomorphic at $s=1$. Let $g_{n}=H^{(n)}(1) / n!$ and $\gamma_{n}=a g_{n}$. It is known that under this condition $\pi(\cdot)$ can be expressed in the following form

$$
\begin{equation*}
\pi(s)=\gamma_{2}^{-1}\left[(1-s)^{-1}-\left(\gamma_{3} / \gamma_{2}\right) \log (1-s)+\psi(s)\right] \tag{3.3.6}
\end{equation*}
$$

where $\psi(s)$ is holomorphic at $s=1$; see [5, equation (36)]. Let

$$
c=(m-1) / g_{2}=u /(1-u) g_{2} \quad \text { and } \quad B=\lambda g_{3} / g_{2}^{2}=g_{3} u /(1-u) g_{2}^{2} .
$$

The function $\mathscr{A}(s)=\exp (c \psi(s))$ is holomorphic at $s=1$ and non-zero in its region of holomorphy. The same is true for $\mathscr{B}(s)=1 / \mathscr{A}(s)$. With this notation we state

THEOREM 3.3.1. Let $M=1$ and $H(s)$ be holomorphic at $s=1$. Then as $j \rightarrow \infty$

$$
\begin{equation*}
\phi(j)^{\sim} M j^{B / 2-3 / 4} \exp \left(-2(c j)^{1 / 2}\right) \tag{3.37}
\end{equation*}
$$

where

$$
M=\pi^{1 / 2} c^{B / 2+5 / 4} e^{c / 2}(\mathscr{B}(1))^{-1} \sum_{n=0}^{\infty} \frac{c^{n} \mathscr{B}(n)(1)}{n!\Gamma(n+B+2)} .
$$

Remark. The form of $M$ suggests that the analagous discrete time result is much more complicated than envisaged in [4].

For expository purposes it is convenient to consider the special case of (3.3.6) where $\psi(s)$ is a constant function, the value of which is irrelevant. This choice gives

$$
H(s)=\sum_{j \geq 0} h_{j} s^{j}=s+\frac{g_{2}^{2}(1-s)^{2}}{g_{2}+g_{3}(1-s)}
$$

which is the p.g.f. of a critical offspring distribution having geometric weights on $\{2,3, \ldots\}$. Indeed if $\alpha=g_{3} /\left(g_{2}+g_{3}\right)$ then

$$
h_{0}=g_{2} \alpha, \quad h_{0}+h_{1}=1-g_{2}^{2} \alpha \quad \text { and } \quad h_{j}=h_{0}(1-\alpha)^{2} \alpha^{j-2} \quad(j \geq 2) .
$$

The case $g_{3}=0$ arises when we start with a linear birth and death process, that is, $f(s)=q+p s^{2}$.

Substitution into (3.3.5) gives

$$
G^{\prime}(s, \lambda)=\pi^{\prime}(s) \int_{s}^{1}\left[\exp \left(-c\left((1-y)^{-1}-(1-s)^{-1}\right)\right)\right]\left(\frac{1-y}{1-s}\right)^{B} d y
$$

The substitution $x=(1-y)^{-1}-(1-s)^{-1}$ reduces this to

$$
\begin{equation*}
G^{\prime}(s, \lambda)=\gamma_{2}^{-1}\left[1+\left(g_{3} / g_{2}\right)(1-s)\right] \int_{0}^{\infty} e^{-c x}(1+x(1-s))^{-B-2} d x \tag{3.3.8}
\end{equation*}
$$

and the binomial theorem applied to the integrand yields the "explicit" expression

$$
\begin{equation*}
j G_{j}(\lambda)=\gamma_{2}^{-1} F_{j-1}+\left(\gamma_{3} / \gamma_{2}^{2}\right)\left(F_{j-1}-F_{j-2}\right) \tag{3.3.9}
\end{equation*}
$$

where

$$
F_{j}=\binom{j+B+1}{j} I(j, B, c)
$$

and

$$
\begin{equation*}
I(j, B, c)=\int_{0}^{\infty} e^{-c x} x^{j}(1+x)^{-j-B-2} d x \tag{3.3.10}
\end{equation*}
$$

We obtain a more compact expression for $F_{j}$ as follows. The integral can be expressed in terms of a confluent hypergeometric function:

$$
I(j, B, c)=j!U(j+1,-B, c)
$$

see [1, equation (13.1.3)]. Kummer's transformation (op. cit. (13.1.29)) applied to this hypergeometric function is

$$
U(j+1,-B, c)=e^{B+1} U(j+B+2, B+2, c)
$$

and this yields

$$
\begin{equation*}
I(j, B, c)=\left(c^{B+1} j!/ \Gamma(j+B+2)\right) i(j+B+1, B, c) \tag{3.3.11}
\end{equation*}
$$

where

$$
i(j, B, c)=\int_{0}^{\infty} e^{-c x} x^{j}(1+x)^{B-j} d x
$$

In particular, we obtain

$$
F_{j}=\left(c^{B+1} / \Gamma(B+2)\right) i(j+B+1, B, c)
$$

The next theorem gives asymptotic results for $i(j, B, c)$.

THEOREM 3.3.2. As $j \rightarrow \infty$,

$$
\begin{equation*}
i(j, B, c) \sim \pi^{1 / 2} e^{c / 2} c^{-B / 2-3 / 4} j^{B / 2+1 / 4} \exp \left(-2(c j)^{1 / 2}\right) \tag{3.3.12}
\end{equation*}
$$

and if $A>0$,

$$
\begin{equation*}
i(j+A, B, c) / i(j, B, c) \rightarrow 1 \tag{3.3.13}
\end{equation*}
$$

Proof. Let $\theta=j^{1 / 2}$ and make the substitution $v=\theta /(1+x)$ to obtain the representation

$$
i(j, B, c)=\theta^{B+1} e^{c} \int_{0}^{\theta} e^{-c \theta / v}(1-v / \theta)^{j} v^{-B-2} d v
$$

Now

$$
(1-y)^{j}=\exp \left[-j \sum_{n \geq 1} y^{n} / n\right] \leq \exp \left[-j\left(y+y^{2} / 2\right)\right]
$$

whence

$$
\begin{aligned}
i(j, B, c) & \leq \theta^{B+1} e^{c} \int_{0}^{\infty} v^{-B-2} \exp \left[-\left(c \theta / v+\theta v+v^{2} / 2\right)\right] d v \\
& =\theta^{B+1} e^{c} \int_{0}^{\infty} q(v) e^{-\theta p(v)} d v
\end{aligned}
$$

where

$$
p(v)=c / v+v \text { and } q(v)=v^{-B-2} \exp \left(-v^{2} / 2\right)
$$

Obviously $p^{\prime}(v)=-c / v^{2}+1$ has exactly one zero in $[0, \infty)$, namely $v=c^{1 / 2}$, and as $x \rightarrow 0$ we have

$$
p\left(c^{1 / 2}+x\right)-p\left(c^{1 / 2}\right)=c /\left(c^{1 / 2}+x\right)-c^{1 / 2}+x \sim x^{2} c^{-1 / 2}
$$

and

$$
q\left(c^{1 / 2}+x\right) \rightarrow c^{-B / 2-1} e^{-c / 2}
$$

It is evident that all the conditions for Laplace's method adumbrated by Olver [7, page 81] are satisfied and in his notation we have

$$
\mu=2, \quad P=c^{-1 / 2}, \quad \lambda=1 \quad \text { and } \quad Q=c^{-B / 2-1} e^{-c / 2}
$$

It follows that $(i(j, B, c))$ is bounded above by a sequence having the asymptoic form given in (3.3.12).

We now obtain a family of lower bounds for $(i(j, B, c))$ which are amenable to Laplace's method as follows. For $0 \leq y<1$ let $R(y)=\sum_{n \geq 3} y^{n} / n$ and observe that as $\theta \rightarrow \infty$,

$$
j R(\theta / v)=\sum_{n \geq 3} v^{n} / n \theta^{n-2} \rightarrow 0
$$

Let $A$ be a fixed constant exceeding $2 c^{1 / 2}$ and observe that if $\theta>A$ then with $R_{A}(v)=\sum_{n \geq 3} v^{n} / n A^{n-2}$ we have

$$
i(j, B, c) \geq \theta^{B+1} e^{c} \int_{0}^{2 c^{1 / 2}} Q(v) \exp (-\theta p(v)) d v
$$

where

$$
Q(v)=v^{-B-2} \exp \left[-\left(v^{2} / 2+R_{A}(v)\right)\right]
$$

Laplace's method can be applied as above to the lower bound with the sole change that now

$$
Q=c^{-B / 2-1} \exp \left[-\left(c / 2+R_{A}\left(c^{1 / 2}\right)\right)\right]
$$

We conclude that

$$
\begin{aligned}
\exp \left(-R_{A}\left(c^{1 / 2}\right)\right) & \leq \liminf _{j \rightarrow \infty} \pi^{-1 / 2} e^{-c / 2} c^{B / 2+3 / 4} j^{-B / 2-1 / 4} e^{2 \sqrt{c j}} i(j, B, c) \\
& \leq \limsup _{j \rightarrow \infty}(\cdot) \leq 1
\end{aligned}
$$

Now let $A \rightarrow \infty$ and observe that $R_{A}\left(c^{1 / 2}\right) \rightarrow 0$. This completes the proof of (3.3.12).

Equation (3.3.13) follows from (3.3.12) and

$$
\exp \left[2 c^{1 / 2}\left((j+A)^{1 / 2}-j^{1 / 2}\right)\right]=\exp \left[2 A c^{1 / 2} /\left((j+A)^{1 / 2}+j^{1 / 2}\right)\right] \rightarrow 1
$$

It follows from Theorem 3.3.2 that

$$
\begin{equation*}
F_{j} \sim\left[\pi^{1 / 2} e^{c / 2} c^{B / 2+1 / 4} / \Gamma(B+2)\right] j^{B / 2+1 / 4} \exp \left(-2(c j)^{1 / 2}\right) \tag{3.3.14}
\end{equation*}
$$

and in addition we infer from (3.3.13) that $F_{j-1} / F_{j-2} \rightarrow 1$. It follows that the first term on the right-hand side of (3.3.9) dominates the second term and hence (3.1.1), (3.3.9) and the above results yield the assertion of Theorem 3.3.1 for this special case, that is, (3.3.7) holds with

$$
M=\pi^{1 / 2}(m-1) e^{c / 2} c^{B / 2+1 / 4} / g_{2} \Gamma(B+2)
$$

For the birth and death case we have $B=0$.
We now consider the general case (3.3.6) and try to follow the above development. The steps leading to (3.3.8) now yield

$$
\begin{aligned}
G^{\prime}(s, \lambda)= & \gamma_{2}^{-1} \mathscr{A}(s)\left[1+\left(g_{2} / g_{3}\right)(1-s)+(1-s)^{2} \psi(s)\right] \\
& \times \int_{0}^{\infty} e^{-c x}(1+x(1-s))^{-B-2} \mathscr{B}\left(1-\frac{1-s}{1+x(1-s)}\right) d x
\end{aligned}
$$

The main task in the proof is to obtain the asymptotic behaviour of the coefficient of $s^{j}$ in the power series expansion of the integral. We anticipate that this coefficient, $I_{j}$, is proportional to $\gamma_{j}=j^{\alpha} \exp \left(-2(c j)^{1 / 2}\right)$ for some $\alpha$. Writing $\mathscr{A}(s)=\sum a_{j} s^{j}$, holomorphy of $\mathscr{A}(\cdot)$ implies that $\left|a_{j}\right|=O\left(\rho^{j}\right)$ for some $\rho<1$. The leading contribution to $j G_{j}(\lambda)$ will arise from the convolution of $\left(a_{j}\right)$ and $\left(I_{j}\right)$. The behaviour of this convolution is given in the next lemma, in which we assume the result anticipated above.

Lemma 3.3.1.

$$
\lim _{j \rightarrow \infty} I_{j}^{-1} \sum_{i=0}^{j} a_{i} I_{j-i}=\mathscr{A}(1)
$$

Proof. Let $\delta(j)=K j^{1 / 2}$ where $K>0$ is a constant. For all sufficiently large $j$ we can replace $I_{j}$ by $\gamma_{j}$. Dealing first with small subscripts we observe that $\left(I_{j}\right)$ is a bounded sequence whence

$$
\sum_{\delta(j) \leq i \leq j} a_{i} I_{j-i}=O\left(\sum_{\delta(j) \leq i<j} \rho^{i}\right)=O\left(\rho^{K \sqrt{j}}\right)
$$

By choosing $K$ so large that $K \log \rho^{-1}>2 c^{1 / 2}$ we can ensure that $\rho^{\delta(j)} / \gamma_{j} \rightarrow 0$.
Next, observe that

$$
\sup _{i \leq \delta(j)}\left(\gamma_{j-1} / \gamma_{j}\right)=M_{j} \exp \left[2 c^{1 / 2}\left(j^{1 / 2}-(j-\delta(j))^{1 / 2}\right)\right]
$$

where $M_{j}=1$ if $\alpha \geq 0$ and $M_{j}=(1-\delta(j) / j)^{\alpha}$ if $\alpha<0$. In either case $\sup _{j} M_{j}<\infty$. Since the above exponent $\rightarrow 0$ as $j \rightarrow \infty$ we see that the domainated convergence theorem can be applied to give $\gamma_{j}^{-1} \sum_{i \leq \delta(j)} a_{i} \gamma_{j-i} \rightarrow$ $\sum a_{i}$, and the proof is complete.

Let

$$
t(x, s)=(1-s) /(1+x-x s)
$$

The function $\mathscr{B}(1-t(x, s))$ is a holomorphic function of $s$ in a disc centered at the origin and radius exceeding unity and hence it has a power series representation, $\sum_{j \geq 0} K_{j}(x) s^{j}$ say. Using the binomial expansion $(1-z)^{-B-2}=$ $\sum_{i=0}^{\infty}\binom{i+B+1}{i} z^{i}$, the coefficient, $I_{j}$, of $s^{j}$ in the integral of (3.3.15) is

$$
\begin{equation*}
I_{j}=\sum_{i=0}^{j}\binom{i+B+1}{i} \int_{0}^{\infty} e^{-c x} x^{i}(1+x)^{-i-B-2} K_{j-i}(x) d x \tag{3.3.16}
\end{equation*}
$$

The contribution of the $i=j$ term is

$$
I_{j}^{(j)}=\binom{j+B+1}{j} \int_{0}^{\infty} e^{-c x} x^{j}(1+x)^{-j-B-2} \mathscr{B}\left(\frac{x}{1+x}\right) d x
$$

and this differs from $F_{j}$ only by the presence of $\mathscr{B}(\cdot)$ in the integrand. $A$ consideration of the proof of Theorem 3.3 .2 shows that the main contribution to $I_{j}^{(j)}$ arises from the region where $x$ is large and it is apparent that as $j \rightarrow \infty$,

$$
\begin{equation*}
I_{j}^{(j)} \sim \mathscr{B}(1) F_{j} . \tag{3.3.17}
\end{equation*}
$$

Let $I_{j}^{*}=I_{j}-I_{j}^{(j)}$. Our next task is to obtain a compact representation for $I_{j}^{*}$. The next lemma gives an explicit expression for $K_{j}(x)$.

LEMMA 3.3.2. Let $B_{i}=\mathscr{B}^{(i)}(1)$. Then for $j \geq 1$,

$$
K_{j}(x)=\sum_{i=1}^{j} x^{j-i}(1+x)^{-j-i} d_{i j} B_{i}
$$

where

$$
\begin{equation*}
d_{i j}=(i!)^{-1}\binom{j-1}{i-1} \quad(1 \leq i \leq j) \tag{3.3.18}
\end{equation*}
$$

Proof. Observe that $\partial t(x, s) / \partial s=-(1+x-x s)^{-2}$ and

$$
(\partial / \partial s) \mathscr{B}(1-t(x, s))=(1+x-x s)^{-2} \mathscr{B}^{\prime}(1-t(x, s))
$$

By using these to calculate the second and third derivative it is a reasonable guess that

$$
\left(\partial^{j} / \partial s^{j}\right) \mathscr{B}(1-t(x, s))=\sum_{i=1}^{j} x^{j-i}(1+x-x s)^{-j-i} c_{i j} \mathscr{B}^{(i)}(1-t(x, s))
$$

where $c_{1 j}=j$ ! and $c_{j j}=1$. This expansion can be verified by induction and the proof yields the recursion

$$
c_{i, j+1}=(j+i) c_{i j}+c_{i-1, j} \quad(2 \leq i \leq j)
$$

The form of the asserted formula for $K_{j}(x)$ follows by setting $s=0$ in the above expansion and defining $d_{i j}=(j!)^{-1} c_{i j}$. This gives the recursion

$$
d_{i, j+1}=\left((j+i) d_{i j}+d_{i-1, j}\right) /(j+1)
$$

with boundary conditions $d_{1 j}=1$ and $d_{j j}=1 / j$ !, and the validity of (3.3.18) can be verified by induction on $j$.

Substituting the results of Lemma 3.3.2 and (3.3.16), reversing the order of summation and using the notation of (3.3.10) yields

$$
\begin{equation*}
I_{j}^{*}=\sum_{n=1}^{j}\left(B_{n} / n!\right) \sigma(j, n, B) I(j-n, B+2 n, c) \tag{3.3.19}
\end{equation*}
$$

where

$$
\sigma(j, n, B)=\sum_{i=0}^{j-n}\binom{i+B+1}{i}\binom{j-i-1}{n-1} \quad(1 \leq n \leq j)
$$

We compute this quantity in the next lemma.

Lemma 3.3.3.

$$
\sigma(j, n, B)=\binom{j+B+1}{j-n}
$$

Proof. By using the decomposition

$$
\binom{i+B+1}{i}=\binom{i+B+2}{i}-\binom{i+B+1}{i-1}
$$

it is easily seen that the assertion is true for $n=1$. Using the identities

$$
\binom{j}{i}=\frac{j}{i}\binom{j-1}{i-1} \quad \text { and } \quad\binom{i+j}{i}=\frac{j+1}{i}\binom{i+j}{i-1}
$$

we obtain

$$
\begin{aligned}
& \sigma(j, n+1, B)=\sum_{i=0}^{j-n-1}\binom{i+B+1}{i}\left(\frac{j-i-1}{n}\right)\binom{j-i-2}{n-1} \\
& \quad=\frac{j-1}{n} \sigma(j-1, n, B)-\frac{B+2}{n} \sum_{i=1}^{j-n-1}\binom{i+B+1}{i-1}\binom{j-i-2}{n-1} \\
& \quad=\frac{j-1}{n} \sigma(j-1, n, B)-\frac{B+2}{n} \sum_{k=0}^{j-2-n}\binom{k+(B+1)+1}{k}\binom{(j-2)-k-1}{n-1} \\
& =\frac{j-1}{n} \sigma(j-1, n, B)-\frac{B+2}{n} \sigma(j-2, n, B+1) .
\end{aligned}
$$

The assertion can now be proved using this identity and an induction argument.
Let $F(j, n)=\sigma(j, n, B) I(j-n, B+2 n, c)$, whence $F(j, 0)=F_{j}$. The transformation (3.3.11) yields

$$
F(j, n)=\frac{c^{B+2 n-1} \Gamma(j+B+2)}{\Gamma(n+B+2) \Gamma(j+n+B+2)} i(j+n+B+1,2 n+B, c)
$$

and Theorem 3.3.2 and the asymptotic relation $\Gamma(x+\alpha) / \Gamma(x+\beta) \sim x^{\alpha-\beta}$ $(x \rightarrow \infty)$ yields

$$
F(j, n) / F_{j} \rightarrow \frac{\Gamma(B+2)}{\Gamma(n+B+2)} c^{n}
$$

as $j \rightarrow \infty$ for each fixed $n$. Then provided it is permissable to take a limit inside the sum representing $I_{j}^{*} / F_{j}$, see (3.3.19), we will obtain

$$
\begin{equation*}
\lim _{j \rightarrow \infty} I_{j}^{*} / F_{j}=\Gamma(B+2) \sum_{n=1}^{\infty} \frac{B_{n} c^{n}}{n!\Gamma(n+B+2)} \tag{3.3.20}
\end{equation*}
$$

Without going into complete detail, the validity of this interchange can be seen as follows.

As remarked above, the $B_{n}$ tend to zero geometrically fast. Choose $j^{\prime}$ so large that $\left|B_{n}\right|<\delta^{n}$ for some $\delta<1$ whenever $n>j^{\prime}$. Thus the sum defining $I_{j}^{*} / F_{j}$ can be split into two parts, a sum over $\left\{1, \ldots, j^{\prime}\right\}$, and the complimentary sum which is bounded in modulus by

$$
R\left(j, j^{\prime}\right)=\delta^{j^{\prime}} \sum_{n=1}^{\infty} F(j, n) / n!F_{j}
$$

It suffices to show that $F(j, n) / F_{j}=O\left(K^{n}\right)$ for some positive number $K$ and that the bound is independent of $j$. This is done using the bound

$$
\begin{aligned}
i(j+n+B+1 & , 2 n+B, c) \\
& \leq e^{c} \theta^{2 n+B+1} \int_{0}^{\theta} v^{-2 n-B-2} \exp \left[-\theta(c / v+v)-v^{2} / 2\right] d v
\end{aligned}
$$

where $\theta=(j+n+B+1)^{1 / 2}$, obtained from the proof of Theorem 3.3.2. The required uniform bounds are obtained by splitting the range of integration into three parts, namely, $J_{1}=\left[0, c^{1 / 2} /(1+\varepsilon)\right], J_{2}=\left[c^{1 / 2} /(1-\varepsilon), \theta\right]$ and $[0, \theta] \backslash\left(J_{1} \cup J_{2}\right)$. The main contribution arises from the last components and modifications to the details of applying Laplace's method to this integral will give the required bound.

The change of variable $z=c^{1 / 2} v^{-1}-1$ shows that the contribution of $J_{1}$, $i_{1}(j, n)$ say, satisfies

$$
\begin{aligned}
& i_{1}(j, n) \theta^{2 n+B+1} \exp \left(2(c j)^{1 / 2}\right. \\
& \quad \leq c^{n+B / 2} \int_{\varepsilon}^{\infty}(1+z)^{2 n+B} \exp \left[-\theta c^{1 / 2} \frac{z^{2}}{1+z}\right] d z \\
& \quad \leq c^{n+B / 2}\left(1+\varepsilon^{-1}\right)^{2 n+B} \int_{0}^{\infty} z^{2 n+B} \exp \left(-\theta \varepsilon c^{1 / 2} z\right) d z
\end{aligned}
$$

and hence for some $K>0$,

$$
i_{1}(j, n)=O\left(K^{n} \Gamma(n+B+1) \exp \left(-2(c j)^{1 / 2}\right)\right.
$$

where, here and below, the implicit constant is independent of $j$ and $n$. It follows that the corresponding contribution to $F(j, n) / F_{j}$ is

$$
\begin{gathered}
O\left\{(c K)^{n} \frac{\Gamma(2 n+B+1) \Gamma(j+B+2)}{\Gamma(j+n+B+2) \Gamma(n+B+2)} j^{-B / 2-1 / 4}\right\} \\
=O\left\{(c K)^{n} j^{-B / 2-1 / 4} \prod_{1=n}^{j} \frac{i+B+1}{i+n+B+1}\right\}
\end{gathered}
$$

which more than adequately fulfills our requirements. The contribution of $J_{2}$ is handled in a similar manner. Equation (3.3.20) now follows by letting $j \rightarrow \infty$ and then $j^{\prime} \rightarrow \infty$.

We have shown that $I_{j}$ is asymptotically proportional to

$$
j^{B / 2+1 / 4} \exp \left(-2(c j)^{1 / 2}\right)
$$

as required for Lemma 3.3.1. It is also apparent now that the contributions to $j G_{j}(\lambda)$ arising from the second and third terms within the square brackets in (3.3.15) are negligible compared to the first term. It follows that

$$
G_{j}(\lambda)^{\sim} \mathscr{A}(1) I_{j} / j \gamma_{2}
$$

and Theorem 3.3.1 now follows from (3.1.1), (3.3.14), (3.3.17) and (3.3.20).

## References

[1] M. Abramowitz and I. A. Stegun, Handbook of mathematical functions (National Bureau of Standards, Washington, D. C. 1964).
[2] K. B. Athreya and P. E. Ney, Branching processes (Springer-Verlag, Berlin, 1972).
[3] N. H. Bingham and R. A. Doney, 'Asymptotic properties of supercritical branching processes I: The Galton-Watson process', Adv. in Appl. Probab. 4 (1976), 711-731.
[4] R. C. Griffiths and A. G. Pakes, 'An infinite alleles version of the simple branching process', Adv. in Appl. Probab., to appear.
[5] S. Karlin and J. McGregor, 'On the spectral representation of branching processes with mean one', J. Math Anal. Appl. 21 (1968), 485-495.
[6] T. Lindvall, 'On coupling of discrete renewal processes', Z. Wahrsch. Verw. Gebiete 48 (1979), 57-70.
[7] F. W. J. Olver, Asymptotics and special functions, (Academic Press, New York, 1974).
[8] A. G. Pakes, 'The age of a Markov process', Stochastic Process Appl. 8 (1979), 277-303.
[9] V. M. Zolotarev, 'More exact statements of several theorems in the theory of branching processes', Theor. Probab. Appl. 2 (1957), 245-253.

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