# SOME PROBABILITY DISTRIBUTIONS IN MODELING DNA REPLICATION 

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#### Abstract

By using some quasi-renewal-like equations and functional differential equations, we explicitly compute the Laplace transforms of some random variables introduced by Cowan and Chiu in modeling the mechanism of replication of a DNA molecule [J. Appl. Probab. (1994) 31 301-308]. These Laplace transforms are expressed by means of infinite products arising in the theory of partitions.


1. Introduction. The aim of this paper is to exhibit explicit formulae for the Laplace transforms of some random variables introduced by Cowan and Chiu in modeling the process of replication of a DNA molecule [5, 8]. These Laplace transforms, which are obtained by using some quasi-renewal-like equations and functional differential equations, are expressed by means of infinite products arising in the theory of partitions.
1.1. Description of the biological problem. A DNA is a macro-molecule which has a helical doubled-stranded structure. The strands are antiparallel (they have opposite orientations) and both are made up of nucleotide bases: adenine (A), guanine (G), cytosine (C) and thymine (T). The strands are complementary in the sense that one is determined from the other by the matching rules: the adenine pairs with the guanine and vice versa (purine bases) while the cytosine and the thymine have similar complementarity (pyrimidine bases). Due to this structure, DNA can replicate. The replication process is very complex, it occurs at certain locations on the molecule (origins of separation; see Figure 1) and, according to


Fig. 1. Locations of the eyes of replication along the molecule.

[^0]

FIG. 2. Inside an eye.
the most popular theory (see, e.g., [12] for a detailed description and [4] for a rapid survey), it takes place through several simultaneous stages that we describe now.

Denaturation. The double-stranded structure unwinds from its helical structure and separates into single strands under the action of two enzymes (helicases). Both strands are kept stretched out thanks to single-strand binding proteins (SSBs). They form either a replicating fork at one side of the origin of separation or a pair of replicating forks on both sides of the origin of separation depending on the biological organisms. The forks prevent the molecule from curling up on itself. The part lying within both separated strands is called an "eye" or a "replicon" (Figure 2).

Hybridization. The replication then starts with the help of a DNA polymerase (DNA polymerase III) and proceeds in the direction of the fork, or in two directions, from the origin toward each fork. Since both strands have opposite orientations, the synthesis in each strand is different from the other. Indeed, it always occurs in the sense $5^{\prime} \rightarrow 3^{\prime}$ due to physico-chemical reasons. Now, we assume that we are dealing with, for example, a bidirectional replication (i.e., with a pair of forks).

- The replication along the $3^{\prime} \rightarrow 5^{\prime}$ oriented half-strand (upper strand) which is located on the right of the origin of separation evolves continuously in the direction of the right fork, this is the leading strand. The same holds for the $5^{\prime} \rightarrow 3^{\prime}$ oriented half-strand (lower strand) which is located on the left of the origin of separation [Figure 3(a)].


FIG. 3. (a) Continuous replication over the leading strands. (b) Discontinuous replication over the lagging strands.


FIG. 4. Discontinuous replication over the leading and lagging strands.

- The replication along the $3^{\prime} \rightarrow 5^{\prime}$ oriented half-strand (upper strand) on the left of the origin of separation, as well as the one along the $5^{\prime} \rightarrow 3^{\prime}$ oriented half-strand (lower strand) on the right take place discontinuously, slower in the inverse sense of the separation [Figure 3(b)]. That phenomenon was observed by Okazaki et al. [14] for prokaryotic cells in 1968 and later proved by Huberman and Horwitz [11] for eukaryotic cells in 1971. This yields the lagging strands and the produced fragments are the so-called "Okazaki fragments."
- An alternative theory stipulates that the replications along the leading strands might be also discontinuous (Figure 4); we refer the reader to Callan [3] and Kowalski and Denhardt [13] for an account of that case.

Synthesis of Okazaki fragments. The synthesis of Okazaki fragments forces the template of the lagging strand to make a loop so that the DNA polymerase III can progress simultaneously ensuring the polymerisations of both parental strands (Figure 5). More precisely, an Okazaki fragment joins with a RNA primer which is brought by a RNA polymerase (primase) at a certain locus (primer site) on the molecule. Then, the DNA polymerase III carries out the synthesis until it encounters the previously synthetized fragment. Next, a DNA polymerase I takes


Fig. 5. Detail of the enzymatic complex.


FIG. 6. Synthesis of the Okazaki fragments with the aid of several enzymes.
over from the DNA polymerase III, excises the RNA primer and fill the resulting gap with DNA. Finally, a DNA ligase seals both fragments (Figure 6).
1.2. Stochastically modeling the replicating process. It is quite natural to adopt a stochastic approach in this replicating process for several reasons.

- The replicons seem to be randomly scattered along the molecule. Cowan, Chiu and Holst [9] propose a spatial Poisson model for this scattering distribution (see also [5]).
- The primer sites seem also to be randomly scattered along the molecule. Cowan and Chiu [7, 8] equally introduce a spatial Poisson process for modeling that situation (see also [5]). In addition, one must take into account other factors.
- There is (random) initiating time for the process during which the RNA primer seeks the primer site and then allows the DNA polymerase III to lodge at this locus. It has been considered by Cowan and Chiu [7] and taken to be constant. This time does not affect substantially a posteriori the mathematical analysis and can be omitted.
- There is a sealing time during which the DNA polymerase I excises the RNA primers and fill the resulting gap until sealing two neighboring fragments. This has been also introduced by Cowan and Chiu [7, 8] and taken to be constant. Actually, this time should be random. It can be seen by repeating the arguments of $[7,8]$ that the formulas providing some expected values therein remain valid upon replacing the sealing time by its expectation.
- The case of an entirely discontinuous replication has been also discussed and modeled by Cowan and Chiu [7]. The corresponding study is similar to the case of the semicontinuous replication and will not be considered here.
- The total time of replication inside an eye should be also random since the replicating process is interrupted whenever it meets another fork which is randomly located on the molecule. Actually, two eyes, when meeting, merge into one larger eye. This time is chosen infinite in the model of Cowan and Chiu.

In this paper, we focus our attention on the random distribution of the primer sites on the lagging strand in the context of the unidirectional semicontinuous replication corresponding to the model of Cowan and Chiu [8] that we briefly review below.
1.3. The model of Cowan and Chiu. One of both strands-corresponding to the line $(-\infty,+\infty)$ say, in a linear approach though a folded structureis progressively separated from the other from the origin of separation, 0 say. The replication along the negative half-line $(-\infty, 0)$ is continuous and is not considered here. Contrarily, the discontinuous replication along the positive half-line $[0,+\infty)$ is of interest to us. The corresponding half single strand is progressively separated from left-to-right from the other at a speed $r$. The copying operation takes place in the opposite direction from right-to-left at a speed $c \leq r$ from the primer sites whenever such a site is uncovered providing some fragments of DNA. In the probabilistic model of Cowan and Chiu [8], the primer sites are located along $[0,+\infty)$ according to a spatial Poisson process of intensity $\mu$ and their appearances in time is then a temporal Poisson process of intensity $\lambda=r \mu$. Although the strands have a discrete composition of bases, on the scale of fork movements, a continuous stochastic process is appropriate for that analysis. Eventually, the fragments join each together. There is a time, $\delta$ say, for sealing each pair of neighboring extremities. The newly replicated DNA comprises two parts (Figure 7):

- a single strand (the "mainland") obtained by concatenation, from the origin, of those segments for which the left extremity joins the nearest right neighboring extremity. The mainland is connected to the origin;


FIG. 7. Okazaki fragments along the lagging strand.

- the remaining segments that are not yet connected to the origin; they are the Okazaki fragments (or "islands"). The interstices between them are called "oceans." Any fragment which becomes connected to the mainland is no longer called Okazaki fragment.

Cowan and Chiu [8] introduced several quantitative random variables:
(i) $N_{t}$ denotes the number of extant Okazaki fragments at time $t$;
(ii) $P_{t}$ denotes the cumulative length of all copying up until to time $t$ (including the mainland);
(iii) $L_{t}$ denotes the cumulative length of extant Okazaki fragments at time $t$;
(iv) $D_{t}$ denotes the distance between the frontier of the action (the location where both strands are separated) and the nearest end of the mainland at time $t$.
Let us introduce also $\tilde{P}_{t}=r t-P_{t}$. The quantity $\tilde{P}_{t}$ is the cumulative length of the interstices between Okazaki fragments at time $t$. The following relationship between the foregoing quantities holds:

$$
D_{t}+P_{t}=L_{t}+r t
$$

Cowan and Chiu [8] computed the asymptotical mean length of Okazaki fragments $n=\lim _{t \rightarrow+\infty} \mathbb{E}\left(N_{t}\right)$, the asymptotical mean length of interstices $\tilde{p}=$ $\lim _{t \rightarrow+\infty} \mathbb{E}\left(\tilde{P}_{t}\right)$ by using renewal theory. They wrote out an integral equation for the mean distance $\mathbb{E}\left(D_{t}\right)$ which lies in the general context of the quasi-renewal equations that were introduced and studied by Piau [15, 16]. In particular, the latter derived an expression for the asymptotical mean distance $d=\lim _{t \rightarrow+\infty} \mathbb{E}\left(D_{t}\right)$. Cowan and Chiu also gave an estimate for the unknown parameter $\mu$ (the inverse of the mean inter-primer sites distance) by numerically evaluating the limiting ratio $\lim _{t \rightarrow+\infty}\left[\mathbb{E}\left(L_{t}\right) / \mathbb{E}\left(N_{t}\right)\right]$ for which some biological data are available under the assumption $\delta=0$. Recently, Cowan [6] proposed a way for writing the asymptotical distribution of $N_{t}$ as $t$ goes to infinity in the case $\delta=0$ (actually, this condition is not restrictive) and he obtained the asymptotical generating function of $N_{t}, \phi(s)=\lim _{t \rightarrow+\infty} \mathbb{E}\left(s^{N_{t}}\right)$.

We now recall the main results derived by the quoted authors. Put $a=c /(c+r)$ and $b=1-a$. Let $\sigma_{0}(n)$ denote the number of divisors of the integer $n$. We shall use the notation $Q_{n}(b)=\prod_{k=1}^{n}\left(1-b^{k}\right)$ and adopt the convention $\prod_{k=1}^{0}=1$ throughout this paper.

Theorem A (Cowan, Cowan and Chiu, Piau).

$$
\begin{aligned}
& n=\lambda \delta+\frac{r}{c}, \quad \tilde{p}=\frac{r}{\lambda a}, \\
& d=r \delta+\frac{r}{\lambda b} \sum_{n=1}^{\infty}\left[1-\prod_{k=n}^{\infty}\left(1-b^{k}\right)\right]=r \delta+\frac{r}{\lambda b} \sum_{n=1}^{\infty} \sigma_{0}(n) b^{n} .
\end{aligned}
$$

If $\delta=0$,

$$
\begin{equation*}
\phi(s)=\prod_{n=1}^{\infty}\left[1-(1-s) b^{n}\right] . \tag{1}
\end{equation*}
$$

In this work, we calculate the Laplace transforms of the random variables $N_{t}$ and $D_{t}$, that is $\mathbb{E}\left(e^{-\alpha N_{t}}\right)$ and $\mathbb{E}\left(e^{-\alpha D_{t}}\right)$, and deduce their limiting Laplace transforms as $t$ goes to infinity by using quasi-renewal equations as in [15] together with quasi-renewal-like equations and functional differential equations. We also evaluate $\lim _{t \rightarrow+\infty} \mathbb{E}\left(e^{-\alpha \tilde{P}_{t}}\right)$ and propose a way for finding $\lim _{t \rightarrow+\infty} \mathbb{E}\left(e^{-\alpha L_{t}}\right)$. The results are expressed by mean of infinite products providing a decomposition for the limiting random variables $N_{\infty}=\lim _{t \rightarrow+\infty} N_{t}, \tilde{P}_{\infty}=\lim _{t \rightarrow+\infty} \tilde{P}_{t}$ and $D_{\infty}=\lim _{t \rightarrow+\infty} D_{t}$ as a series of independent random variables (Bernoulli, Poisson and exponentially distributed).

As in [8], we suppose that the sealing time $\delta$ is constant. It should be reasonable to consider a random time instead. As we previously mentioned, it is possible by repeating the arguments of Cowan and Chiu to see that the formulas for $n$ and $d$ in Theorem A hold if $\delta$ is now the expected sealing time. Our analysis is done under the assumption that $\delta$ is constant and would be much more difficult to carry out with a random time. Nevertherless, we hope it should give an insight into the matter.

Finally, we would like to mention that the infinite products involved arise in the theory of partitions (related to the so-called " $q$-series"; see, e.g., [1]) and are used also in other probabilistic applications [2, 10].
2. The results. Set $\varphi(\alpha, t)=\mathbb{E}\left(e^{-\alpha N_{t}}\right), \psi(\alpha, t)=\mathbb{E}\left(e^{-\alpha \tilde{P}_{t}}\right)$ and $\chi(\alpha, t)=$ $\mathbb{E}\left(e^{-\alpha D_{t}}\right)$. Our results are stated in the three theorems below.

THEOREM 1. We have the following explicit expressions for $\varphi$ and $\chi$ :

$$
\begin{gather*}
\varphi(\alpha, t)=\left\{\begin{array}{lr}
e^{-\lambda\left(1-e^{-\alpha}\right) t}, & \text { if } 0 \leq t \leq \delta, \\
e^{-\lambda \delta\left(1-e^{-\alpha}\right)} \sum_{n=0}^{\infty} \prod_{k=1}^{n}\left[1-\left(1-e^{-\alpha}\right) b^{k}\right] e^{-\lambda(t-\delta)} \frac{[\lambda(t-\delta)]^{n}}{n!}, \\
\text { if } t \geq \delta,
\end{array}\right.  \tag{2}\\
\chi(\alpha, t)= \begin{cases}e^{-r \alpha t}, & \text { if } 0 \leq t \leq \delta, \\
e^{-r \delta \alpha} \sum_{n=0}^{\infty}\left[\sum_{k=0}^{n} \frac{Q_{n}(b)}{Q_{k}(b)}\left(b-\frac{r \alpha}{\lambda}\right)^{k}\right] e^{-\lambda(t-\delta)} \frac{[\lambda(t-\delta)]^{n}}{n!}, \\
\text { if } t \geq \delta .\end{cases}
\end{gather*}
$$

THEOREM 2. The following asymptotics hold:

$$
\begin{align*}
& \lim _{t \rightarrow+\infty} \varphi(\alpha, t)=e^{-\lambda \delta\left(1-e^{-\alpha}\right)} \prod_{n=1}^{\infty}\left[1-\left(1-e^{-\alpha}\right) b^{n}\right]  \tag{4}\\
& \lim _{t \rightarrow+\infty} \psi(\alpha, t)=\prod_{n=0}^{\infty}\left[1+\frac{r \alpha}{\lambda} b^{n}\right]^{-1}  \tag{5}\\
& \lim _{t \rightarrow+\infty} \chi(\alpha, t)=e^{-r \delta \alpha} \prod_{n=1}^{\infty}\left[1+\frac{r \alpha}{\lambda} \frac{b^{n-1}}{1-b^{n}}\right]^{-1} . \tag{6}
\end{align*}
$$

Identity (4) coincides with the expression (1) for the generating function of Cowan ([6], formula 19) in the case $\delta=0$ as it is easily seen by replacing $e^{-\alpha}$ by $s$. Actually we employ an alternative method for establishing (4). On the other hand, we recognize within each of the products in (2) and (4)-(6) the Laplace transforms of Bernoulli and exponentially distributed random variables. Moreover, the first exponential in (4) is the Laplace transform of a Poisson random variable. These remarks imply the decompositions for the random variables $N_{t}, N_{\infty}, \tilde{P}_{\infty}$ and $D_{\infty}$ that are displayed in the following theorem.

THEOREM 3. The random variables $N_{t}, \tilde{P}_{t}$ and $D_{t}$ converge in distribution as $t$ goes to infinity respectively to the random variables $N_{\infty}, \tilde{P}_{\infty}$ and $D_{\infty}$ given by

$$
N_{\infty}=\sum_{n=0}^{\infty} X_{n}, \quad \tilde{P}_{\infty}=\sum_{n=0}^{\infty} Y_{n} \quad \text { and } \quad D_{\infty}=r \delta+\sum_{n=1}^{\infty} Z_{n}
$$

where
(i) $X_{0}$ is a Poisson random variable with parameter $\lambda \delta,\left(X_{n}\right)_{n \geq 1}$ is a sequence of independent Bernoulli random variables of parameters $b^{n}, n \geq 1$, which are independent of $X_{0}$;
(ii) $\left(Y_{n}\right)_{n \geq 0}$ is a sequence of independent exponentially distributed random variables with parameters $\lambda /\left(r b^{n}\right), n \geq 0$;
(iii) $\left(Z_{n}\right)_{n \geq 1}$ is a sequence of independent exponentially distributed random variables with parameters $(\lambda b / r) \times\left(1 / b^{n}-1\right), n \geq 1$.
We also have the following decomposition at a finite time $t$ :

$$
N_{t} \stackrel{\text { law }}{=} \begin{cases}\tilde{X}_{0}, & \text { if } 0 \leq t<\delta,  \tag{7}\\ v_{t} & X_{n=0}, \\ \sum_{n=0} X_{n} \geq \delta,\end{cases}
$$

where $\tilde{X}_{0}$ is a Poisson random variable of parameter $\lambda t$ and $v_{t}$ is a Poisson random variable of parameter $\lambda(t-\delta)$ which is independent of the sequence $\left(X_{n}\right)_{n \geq 0}$.

The means and variances of $N_{\infty}$ and $\tilde{P}_{\infty}$ can be easily derived from these representations:

$$
\begin{aligned}
\mathbb{E}\left(N_{\infty}\right) & =\lambda \delta+\sum_{n=1}^{\infty} b^{n}=\lambda \delta+\frac{r}{c} \\
\operatorname{var}\left(N_{\infty}\right) & =\lambda \delta+\sum_{n=1}^{\infty} b^{n}\left(1-b^{n}\right)=\lambda \delta+\frac{r(r+c)}{c(2 r+c)} \\
\mathbb{E}\left(\tilde{P}_{\infty}\right) & =\frac{r}{\lambda} \sum_{n=0}^{\infty} b^{n}=\frac{r(r+c)}{\lambda c}, \\
\operatorname{var}\left(\tilde{P}_{\infty}\right) & =\sum_{n=0}^{\infty}\left(\frac{r}{\lambda}\right)^{2} b^{2 n}=\frac{r^{2}(r+c)^{2}}{\lambda^{2} c(2 r+c)}
\end{aligned}
$$

The moments of $\tilde{P}_{\infty}$ may be computed with the aid of an alternative form of (5) thanks to (A.1):

$$
\lim _{t \rightarrow+\infty} \psi(\alpha, t)=\sum_{n=0}^{\infty} \frac{1}{Q_{n}(b)}\left(-\frac{r \alpha}{\lambda}\right)^{n}
$$

The successive derivatives can be easily evaluated at $\alpha=0$ from that expression and we get

$$
\mathbb{E}\left(\tilde{P}_{\infty}^{n}\right)=\frac{n!}{Q_{n}(b)}\left(\frac{r}{\lambda}\right)^{n}
$$

On the other hand, concerning the mean and variance of $D_{\infty}$, we have

$$
\begin{aligned}
\mathbb{E}\left(D_{\infty}\right) & =r \delta+\frac{r}{\lambda b} \sum_{n=1}^{\infty} \frac{b^{n}}{1-b^{n}} \\
\operatorname{var}\left(D_{\infty}\right) & =\left(\frac{r}{\lambda b}\right)^{2} \sum_{n=1}^{\infty}\left(\frac{b^{n}}{1-b^{n}}\right)^{2}
\end{aligned}
$$

To evaluate the foregoing quantities, we calculate

$$
\sum_{n=1}^{\infty} \frac{b^{n}}{1-b^{n}}=\sum_{n=1}^{\infty} b^{n} \sum_{m=0}^{\infty} b^{m n}=\sum_{m, n \geq 1} b^{m n}=\sum_{p=1}^{\infty} \sigma_{0}(p) b^{p}
$$

where $\sigma_{0}(p)=\#\{k: k \mid p\}$, and similarly

$$
\begin{aligned}
\sum_{n=1}^{\infty}\left(\frac{b^{n}}{1-b^{n}}\right)^{2} & =\sum_{n=1}^{\infty} b^{2 n} \sum_{m=0}^{\infty}(m+1) b^{m n} \\
& =\sum_{m, n \geq 1}(m-1) b^{m n}=\sum_{p=1}^{\infty}\left[\sigma_{1}(p)-\sigma_{0}(p)\right] b^{p}
\end{aligned}
$$

where $\sigma_{1}(p)=\sum_{k \mid p} k$. Hence, we obtain

$$
\begin{aligned}
\mathbb{E}\left(D_{\infty}\right) & =r \delta+\frac{r}{\lambda b} \sum_{n=1}^{\infty} \sigma_{0}(n) b^{n} \\
\operatorname{var}\left(D_{\infty}\right) & =\left(\frac{r}{\lambda b}\right)^{2} \sum_{n=1}^{\infty}\left[\sigma_{1}(n)-\sigma_{0}(n)\right] b^{n} .
\end{aligned}
$$

The means of $N_{\infty}$ and $\tilde{P}_{\infty}$ together with the variance of $N_{\infty}$ were evaluated by Cowan and Chiu [8] and Cowan [6] and the mean of $D_{\infty}$ by Piau [15, 16]. It is also possible to derive the mean and the variance of $N_{t}$ by using (7).

The proofs of Theorems 1 and 2 rely on quasi-renewal-like equations for the functions $\varphi, \psi$ and $\chi$. We shall put $\varphi(\alpha, t)=\varphi(t), \psi(\alpha, t)=\psi(t)$ and $\chi(\alpha, t)=$ $\chi(t)$ for simplicity when no confusion is possible.
3. Some integral equations. In this section we write out some integral equations for the functions $\varphi, \psi$ and $\chi$.

Proposition 4. The functions $\varphi, \psi$ and $\chi$ satisfy the following quasi-renewal-like equations:

$$
\begin{align*}
\varphi(t)= & \lambda e^{-\alpha} \int_{0}^{t} \varphi(t-s) e^{-\lambda s} d s  \tag{8}\\
& +\lambda\left(1-e^{-\alpha}\right) \int_{0}^{a(t-\delta)^{+}} \varphi(t-s) e^{-\lambda s} d s+e^{-\lambda t}, \\
\psi(t)= & \lambda \int_{0}^{a t} \psi(t-s) e^{-\lambda s} d s  \tag{9}\\
& +\lambda e^{c \alpha t} \int_{a t}^{t} \psi(t-s) e^{-(\lambda+r \alpha / b) s} d s+e^{-(\lambda+r \alpha) t}, \\
\chi(t)= & \lambda \int_{0}^{a(t-\delta)^{+}} \chi(t-s) e^{-\lambda s} d s+e^{-\lambda a(t-\delta)^{+}-r \alpha t} . \tag{10}
\end{align*}
$$

Proof. We make use of a method of Cowan and Chiu [8] based on introducing the instant $T_{1}$ when the first primer site is uncovered and next conditioning on the event $T_{1}=s, s \geq 0$.

Time $T_{1}$ is exponentially distributed with parameter $\lambda$. Set $\varphi(t \mid s)=$ $\mathbb{E}\left(e^{-\alpha N_{t}} \mid T_{1}=s\right), \psi(t \mid s)=\mathbb{E}\left(e^{-\alpha \tilde{P}_{t}} \mid T_{1}=s\right)$ and $\chi(t \mid s)=\mathbb{E}\left(e^{-\alpha D_{t}} \mid T_{1}=s\right)$. We then have $\varphi(t)=\lambda \int_{0}^{\infty} \varphi(t \mid s) e^{-\lambda s} d s, \psi(t)=\lambda \int_{0}^{\infty} \psi(t \mid s) e^{-\lambda s} d s$ and $\chi(t)=$ $\lambda \int_{0}^{\infty} \chi(t \mid s) e^{-\lambda s} d s$. Conditioning on the event $T_{1}=s$, the first fragment is uncovered at time $s$, its location is then at the distance $r s$ from the origin. Denote for the moment $N_{s, t}, D_{s, t}, P_{s, t}$ the quantities, which are similar to $N_{t}, D_{t}, P_{t}$, associated with the replication process observed since time $s$. Between times $s$ and $t$,
since the replication occurs leftward at a speed $c$, the corresponding covered distance is $c(t-s)$. At time $t$, the position of the left extremity of that fragment is $r s-c(t-s)=(r+c) s-c t$ and the fragment will be connected to the origin, when reaching it, after duration $\delta$. Thus the condition $(r+c) s-c t>-c \delta$, or $s>a(t-\delta)$, says that the fragment has not yet joined the origin: $N_{t}=N_{s, t}+1$ and $D_{t}=r t$; the condition $s \leq a(t-\delta)$ says that the fragment is connected to the origin so forming the mainland, it is not an Okazaki fragment any longer and $N_{t}=N_{s, t}$ as well as $D_{t}=D_{s, t}$. Likewise, at time $t$, the length of the first fragment is $c(t-s) \wedge r s$. Therefore, if $c(t-s)<r s$, or $s>a t$, then $P_{t}=P_{s, t}+c(t-s)$ and if $s \leq a t, P_{t}=P_{s, t}+r s$. Because of the regenerative character of the Poisson process, the quantities $N_{s, t}, D_{s, t}, P_{s, t}$ and $N_{t-s}, D_{t-s}, P_{t-s}$ are respectively equally distributed.

The foregoing discussion provides then the three families of relations below.

1. For the random variable $N_{t}$ we have:
(i) for $0 \leq t<\delta$,

$$
\left(N_{t} \mid T_{1}=s\right) \stackrel{\operatorname{law}}{=} \begin{cases}N_{t-s}+1, & \text { if } 0 \leq s \leq t, \\ 0, & \text { if } s>t,\end{cases}
$$

and then

$$
\varphi(t \mid s)= \begin{cases}e^{-\alpha} \varphi(t-s), & \text { if } 0 \leq s \leq t \\ 1, & \text { if } s>t\end{cases}
$$

(ii) for $t \geq \delta$,

$$
\left(N_{t} \mid T_{1}=s\right) \stackrel{\text { law }}{=} \begin{cases}N_{t-s}, & \text { if } 0 \leq s \leq a(t-\delta) \\ N_{t-s}+1, & \text { if } a(t-\delta)<s \leq t \\ 0, & \text { if } s>t,\end{cases}
$$

and then

$$
\varphi(t \mid s)= \begin{cases}\varphi(t-s), & \text { if } 0 \leq s \leq a(t-\delta) \\ e^{-\alpha} \varphi(t-s), & \text { if } a(t-\delta)<s \leq t \\ 1, & \text { if } s>t\end{cases}
$$

Therefore (8) holds.
2. For $\tilde{P}_{t}$ we see that

$$
\left(P_{t} \mid T_{1}=s\right) \stackrel{\text { law }}{=} \begin{cases}P_{t-s}+r s, & \text { if } 0 \leq s \leq a t \\ P_{t-s}+c(t-s), & \text { if } a t<s \leq t, \\ 0, & \text { if } s>t\end{cases}
$$

This in turn implies that

$$
\left(\tilde{P}_{t} \mid T_{1}=s\right) \stackrel{\text { law }}{=} \begin{cases}\tilde{P}_{t-s}, & \text { if } 0 \leq s \leq a t \\ (r+c) s-c t-\tilde{P}_{t-s}, & \text { if } a t<s \leq t \\ r t, & \text { if } s>t\end{cases}
$$

and then

$$
\psi(t \mid s)= \begin{cases}\psi(t-s), & \text { if } 0 \leq s \leq a t \\ e^{-(r \alpha / b) s-c \alpha t} \psi(t-s), & \text { if } a t<s \leq t \\ e^{-r \alpha t}, & \text { if } s>t\end{cases}
$$

We immediately get (9).
3. Finally, we obtain for $D_{t}$ :
(i) for $0 \leq t<\delta, D_{t}=r t$ and so $\chi(t \mid s)=e^{-r \alpha t}$,
(ii) for $t \geq \delta$,

$$
\left(D_{t} \mid T_{1}=s\right) \stackrel{\text { law }}{=} \begin{cases}r t, & \text { if } s>a(t-\delta), \\ D_{t-s}, & \text { if } 0 \leq s \leq a(t-\delta),\end{cases}
$$

and then

$$
\chi(t \mid s)= \begin{cases}e^{-r \alpha t}, & \text { if } s>a(t-\delta), \\ \chi(t-s), & \text { if } 0 \leq s \leq a(t-\delta)\end{cases}
$$

Thus (10) is validated.

## 4. Proof of Theorem 1.

4.1. The random variable $N_{t}$. Solving (8) boils down to solving, first, an ordinary renewal equation on the interval $[0, \delta]$, and second, a functional differential equation for the function $\tilde{\varphi}$ defined as $\tilde{\varphi}(t)=e^{\lambda t} \varphi(t+\delta)$ for any $t \geq 0$.

Indeed, (8) reads for $0 \leq t<\delta$ as

$$
\begin{equation*}
\varphi(t)=\lambda e^{-\alpha} \int_{0}^{t} \varphi(t-s) e^{-\lambda s} d s+e^{-\lambda t} \tag{11}
\end{equation*}
$$

This is a classical renewal equation, the solution of which being accessible by successive iterations:

$$
\varphi=e_{\lambda}+\sum_{n=1}^{\infty} e^{-n \alpha} e_{\lambda} \star F_{\lambda}^{\star n}
$$

In our settings $e_{\lambda}$ is the function $e_{\lambda}(t)=e^{-\lambda t}, F_{\lambda}$ is the distribution function defined by $F_{\lambda}(d t)=\lambda e^{-\lambda t} \mathbb{1}_{[0, \infty)}(t) d t$ and $\star$ denotes the convolution of a function by a measure. The $n$th iterated convolution of $F_{\lambda}$ is the Erlang distribution

$$
F_{\lambda}^{\star n}(d t)=\frac{\lambda^{n} t^{n-1}}{(n-1)!} e^{-\lambda t} \mathbb{1}_{[0, \infty)}(t) d t
$$

Then it is easy to see that the solution of (11) is

$$
\begin{equation*}
\varphi(t)=e^{-\lambda\left(1-e^{-\alpha}\right) t} \quad \text { for } 0 \leq t<\delta \tag{12}
\end{equation*}
$$

Next we study (8) over the interval $[\delta, \infty$ ) with the aid of the result below.

Proposition 5. The function $\tilde{\varphi}$ satisfies the following functional differential equation:

$$
\begin{equation*}
\frac{d \tilde{\varphi}}{d t}(t)-\lambda \tilde{\varphi}(t)+\lambda \nu b \tilde{\varphi}(b t)=0 \tag{13}
\end{equation*}
$$

where $\nu=1-e^{-\alpha}$, together with the initial condition $\tilde{\varphi}(0)=e^{-\lambda \delta \nu}$.
Proof. Equation (8) reads in terms of the function $\tilde{\varphi}$ as

$$
\begin{align*}
\tilde{\varphi}(t)= & e^{-\lambda \delta}\left[\lambda e^{-\alpha} \int_{0}^{\delta} \varphi(s) e^{\lambda s} d s+1\right]  \tag{14}\\
& +\lambda\left[e^{-\alpha} \int_{0}^{t} \tilde{\varphi}(s) d s+\left(1-e^{-\alpha}\right) \int_{b t}^{t} \tilde{\varphi}(s) d s\right]
\end{align*}
$$

The term within the first pair of brackets equals $e^{\lambda \delta e^{-\alpha}}$ by virtue of (12). Therefore, $\tilde{\varphi}(0)=e^{-\lambda \delta \nu}$. Performing next an easy differentiation in (14) leads to (13).

Now, we can expand $\tilde{\varphi}$ into a Taylor series as follows.
PROPOSITION 6. The function $\tilde{\varphi}$ admits a Taylor expansion $\tilde{\varphi}(t)=$ $\sum_{n=0}^{\infty} \varphi_{n} t^{n} /(n!)$ where

$$
\begin{equation*}
\varphi_{n}=\lambda^{n} e^{-\lambda \delta v} \prod_{k=1}^{n}\left(1-v b^{k}\right) \tag{15}
\end{equation*}
$$

Proof. By differentiating (13) $n$ times we get the following recursion:

$$
\frac{d^{n+1} \tilde{\varphi}}{d t^{n+1}}(t)=\lambda \frac{d^{n} \tilde{\varphi}}{d t^{n}}(t)-\lambda \nu b^{n+1} \frac{d^{n} \tilde{\varphi}}{d t^{n}}(b t)
$$

Evaluating this relation at time $t=0$ obviously yields the coefficients by induction according to

$$
\varphi_{0}=e^{-\lambda \delta \nu} \quad \text { and } \quad \varphi_{n+1}=\lambda\left(1-v b^{n+1}\right) \varphi_{n}, \quad n \geq 0
$$

from which (15) ensues.
Due to the estimate $0 \leq \varphi_{n} \leq \lambda^{n} e^{-\lambda \delta \nu}$, we can assert that the Taylor expansion of $\tilde{\varphi}$ has an infinite radius of convergence, thus proving Proposition 6 .

Expression (2) now follows and the limiting result (4) is easily deduced from (2) by using the following elementary fact: if $\left(u_{n}\right)_{n \geq 0}$ is a sequence converging toward $u_{\infty}$, then

$$
\begin{equation*}
e^{-x} \sum_{n=0}^{\infty} u_{n} \frac{x^{n}}{n!} \underset{x \rightarrow+\infty}{\longrightarrow} u_{\infty} \tag{16}
\end{equation*}
$$

4.2. The random variable $\tilde{P}_{\infty}$. We are now looking for the $\operatorname{limit}^{\lim } \lim _{t \rightarrow+} \psi(t)$ by using an argument similar to one of Piau [15]. To this end, we introduce the Laplace transform with respect to the $t$-argument of $\psi$ :

$$
L \psi(p)=\int_{0}^{\infty} e^{-p t} \psi(t) d t
$$

It is classical that the asymptotical behaviors of $\psi$ and $L \psi$ are connected together by

$$
\begin{equation*}
\lim _{t \rightarrow+\infty} \psi(t)=\lim _{p \rightarrow 0^{+}} p L \psi(p) \tag{17}
\end{equation*}
$$

whenever $\psi$ is a monotonic function for instance. Our aim is to calculate the righthand side of (17). This will be done in several stages:
(i) the first step consists of writing down another integral equation satisfied by $\psi$ (Proposition 7);
(ii) second, we derive an integro-differential equation that $\psi$ solves (Proposition 8) from which the function $\psi$ will be seen to be decreasing and then the limiting result (17) applies;
(iii) next, we show that $L \psi$ solves a functional equation (Proposition 9);
(iv) ultimately, we evaluate $L \psi(p)$ at the particular value $p=\lambda a / b$ (Proposition 10); indeed, it will be seen that the explicit value $L \psi(\lambda a / b)$ yields the limiting result we are looking for.

## PROPOSITION 7. The function $\psi$ solves the following integral equation:

$$
\begin{equation*}
\psi(t)=1-r \alpha \int_{0}^{b t} \psi(s) e^{-(\lambda a / b) s} d s-r \alpha e^{-\lambda t} \int_{b t}^{t} \psi(s) e^{\lambda s} d s \tag{18}
\end{equation*}
$$

Proof. We begin by rewriting (9) as

$$
\begin{align*}
\psi(t)= & \lambda e^{-(\lambda+r \alpha) t} \int_{0}^{b t} \psi(s) e^{(\lambda+r \alpha / b) s} d s  \tag{19}\\
& +\lambda e^{-\lambda t} \int_{b t}^{t} \psi(s) e^{\lambda s} d s+e^{-(\lambda+r \alpha) t}
\end{align*}
$$

and compute $\int_{0}^{t} \psi(s) d s$ as follows:

$$
\begin{aligned}
\int_{0}^{t} \psi(s) d s= & \lambda \int_{0}^{t} e^{-\lambda u} d u \int_{b u}^{u} \psi(s) e^{\lambda s} d s \\
& +\lambda \int_{0}^{t} e^{-(\lambda+r \alpha) u} d u \int_{0}^{b u} \psi(s) e^{(\lambda+r \alpha / b) s} d s+\int_{0}^{t} e^{-(\lambda+r \alpha) u} d u \\
= & \int_{0}^{t} \psi(s) e^{\lambda s}\left[e^{-\lambda s}-e^{-\lambda[t \wedge(s / b)]}\right] d s
\end{aligned}
$$

$$
\begin{aligned}
&+\frac{\lambda}{\lambda+r \alpha} \int_{0}^{b t} \psi(s) e^{(\lambda+r \alpha / b) s}\left[e^{-(\lambda+r \alpha) s / b}-e^{-(\lambda+r \alpha) t}\right] d s \\
&+\frac{1}{\lambda+r \alpha}\left[1-e^{-(\lambda+r \alpha) t}\right] \\
&= \int_{0}^{t} \psi(s) d s-\frac{r \alpha}{\lambda+r \alpha} \int_{0}^{b t} \psi(s) e^{-(\lambda a / b) s} d s-e^{-\lambda t} \int_{b t}^{t} \psi(s) e^{\lambda s} d s \\
&-\frac{\lambda}{\lambda+r \alpha} e^{-(\lambda+r \alpha) t} \int_{0}^{b t} \psi(s) e^{(\lambda+r \alpha / b) s} d s \\
&+\frac{1}{\lambda+r \alpha}\left[1-e^{-(\lambda+r \alpha) t}\right] \\
&= \int_{0}^{t} \psi(s) d s-\frac{1}{\lambda+r \alpha}\left[\lambda e^{-(\lambda+r \alpha) t} \int_{0}^{b t} \psi(s) e^{(\lambda+r \alpha / b) s} d s\right. \\
&\left.\quad+\lambda e^{-\lambda t} \int_{b t}^{t} \psi(s) e^{\lambda s} d s+e^{-(\lambda+r \alpha) t}\right] \\
&-\frac{1}{\lambda+r \alpha}\left[r \alpha \int_{0}^{b t} \psi(s) e^{-(\lambda a / b) s} d s+r \alpha e^{-\lambda t} \int_{b t}^{t} \psi(s) e^{\lambda s} d s-1\right] .
\end{aligned}
$$

Consequently, using (19) to replace the term within the first pair of brackets in the last displayed equality by $\psi(t)$ and eliminating $\int_{0}^{t} \psi(s) d s$ yields (18).

Proposition 8. The function $\psi$ solves the integro-differential equation:

$$
\begin{equation*}
\frac{d \psi}{d t}(t)+(\lambda+r \alpha) \psi(t)+\lambda r \alpha \int_{0}^{b t} \psi(s) e^{-(\lambda a / b) s} d s=\lambda \tag{20}
\end{equation*}
$$

Proof. Differentiating (18) gives

$$
\begin{equation*}
\psi^{\prime}(t)=\lambda r \alpha e^{-\lambda t} \int_{b t}^{t} \psi(s) e^{\lambda s} d s-r \alpha \psi(t) \tag{21}
\end{equation*}
$$

By virtue of (18), we can see that

$$
r \alpha e^{-\lambda t} \int_{b t}^{t} \psi(s) e^{\lambda s} d s=1-\psi(t)-r \alpha \int_{0}^{b t} \psi(s) e^{-(\lambda a / b) s} d s
$$

Inserting this expression in (21) immediately gives (20).

Since $\psi$ is positive, we see from (20) that $\psi^{\prime}(0)=-r \alpha$ and that $\psi^{\prime}(t)+(\lambda+$ $r \alpha) \psi(t)$ has a negative derivative. This implies that the function $t \mapsto e^{(\lambda+r \alpha) t} \psi^{\prime}(t)$ is decreasing and then $\psi^{\prime}(t) \leq-r \alpha e^{-(\lambda+r \alpha) t}<0$. As a result, $\psi$ is decreasing and (17) is now validated.

Proposition 9. The Laplace transform of the function $\psi$ satisfies the following relation:

$$
\begin{equation*}
L \psi(p)=\frac{p+\lambda}{p(p+\lambda+r \alpha)}-\frac{\lambda r \alpha}{p(p+\lambda+r \alpha)} L \psi\left(\frac{p+\lambda a}{b}\right) . \tag{22}
\end{equation*}
$$

Proof. Applying the Laplace transformation to (19) together with Fubini's theorem we obtain

$$
\begin{aligned}
L \psi(p)= & \lambda \int_{0}^{\infty} e^{-(p+\lambda+r \alpha) t} d t \int_{0}^{b t} \psi(s) e^{(\lambda+r \alpha / b) s} d s \\
& +\lambda \int_{0}^{\infty} e^{-(p+\lambda) t} d t \int_{b t}^{t} \psi(s) e^{\lambda s} d s+\int_{0}^{\infty} e^{-(p+\lambda+r \alpha) t} d t \\
= & \frac{\lambda}{p+\lambda+r \alpha} \int_{0}^{\infty} \psi(s) e^{(\lambda+r \alpha / b) s} e^{-(p+\lambda+r \alpha) s / b} d s \\
& +\frac{\lambda}{p+\lambda} \int_{0}^{\infty} \psi(s) e^{\lambda s}\left[e^{-(p+\lambda) s}-e^{-(p+\lambda) s / b}\right] d s+\frac{1}{p+\lambda+r \alpha} \\
= & \frac{\lambda}{p+\lambda} L \psi(p)-\frac{\lambda r \alpha}{(p+\lambda)(p+\lambda+r \alpha)} L \psi\left(\frac{p+\lambda a}{b}\right)+\frac{1}{p+\lambda+r \alpha} .
\end{aligned}
$$

Relation (22) now ensues.
Then we deduce from (17) and (22) that

$$
\begin{equation*}
\lim _{t \rightarrow+\infty} \psi(t)=\frac{\lambda}{\lambda+r \alpha}[1-r \alpha L \psi(\lambda a / b)] . \tag{23}
\end{equation*}
$$

So we have to evaluate $L \psi(\lambda a / b)$, the value of which is given in the following proposition.

Proposition 10. The explicit value of the Laplace transform of $\psi$ at $\lambda a / b$ is given by

$$
\begin{equation*}
L \psi(\lambda a / b)=\frac{1}{r \alpha}\left[1-\prod_{n=1}^{\infty}\left(1+\frac{r \alpha}{\lambda} b^{n}\right)^{-1}\right] \tag{24}
\end{equation*}
$$

Proof. Let us rewrite relation (22) as

$$
\begin{equation*}
L \psi=\sigma-\tau \cdot(L \psi \circ A) \tag{25}
\end{equation*}
$$

where

$$
\sigma(p)=\frac{p+\lambda}{p(p+\lambda+r \alpha)}, \quad \tau(p)=\frac{\lambda r \alpha}{p(p+\lambda+r \alpha)}, \quad A(p)=\frac{p+\lambda a}{b}
$$

Iterating (25) and noticing that the $n$th iterate of $A$ is $A^{n}(p)=(p+\lambda) / b^{n}-\lambda$, we easily obtain

$$
L \psi=\sum_{n=0}^{N}(-1)^{n}\left(\sigma \circ A^{n}\right) \prod_{k=0}^{n-1}\left(\tau \circ A^{k}\right)+(-1)^{N+1}\left(L \psi \circ A^{N+1}\right) \prod_{n=0}^{N}\left(\tau \circ A^{n}\right) .
$$

Observe that the Laplace transform $L \psi\left(A^{N+1}(p)\right)$ converges to 0 as $N$ goes to $\infty$ since $\psi$ is decreasing. The same fact holds for the product $\prod_{n=0}^{N} \tau\left(A^{n}(p)\right)$ by virtue of the estimate

$$
\begin{aligned}
& \prod_{n=0}^{N} \tau\left(A^{n}(p)\right) \\
& \quad=b^{N(N+1)}\left[\frac{\lambda r \alpha}{(p+\lambda)^{2}}\right]^{N+1} \prod_{n=0}^{N}\left(1-\frac{\lambda}{p+\lambda} b^{n}\right)^{-1} \prod_{n=0}^{N}\left(1+\frac{r \alpha}{p+\lambda} b^{n}\right)^{-1} \\
& \quad \leq\left(1+\frac{\lambda}{p}\right)\left[\frac{r \alpha b^{N}}{(p+\lambda)^{2}}\right]^{N+1} \prod_{n=1}^{\infty}\left(1-b^{n}\right)^{-1}
\end{aligned}
$$

Hence the following expression for $L \psi$ is valid:

$$
\begin{aligned}
L \psi(p)= & \sum_{n=0}^{\infty}(-1)^{n} \sigma\left(A^{n}(p)\right) \prod_{k=0}^{n-1} \tau\left(A^{k}(p)\right) \\
= & \frac{1}{p+\lambda} \sum_{n=0}^{\infty}(-1)^{n} b^{n^{2}}\left[\frac{\lambda r \alpha}{(p+\lambda)^{2}}\right]^{n} \\
& \times \prod_{k=0}^{n}\left(1-\frac{\lambda}{p+\lambda} b^{k}\right)^{-1} \prod_{k=0}^{n}\left(1+\frac{r \alpha}{p+\lambda} b^{k}\right)^{-1}
\end{aligned}
$$

This yields, for $p=\lambda a / b$,

$$
L \psi(\lambda a / b)=-\frac{1}{r \alpha} \sum_{n=1}^{\infty} \frac{b^{n^{2}}}{Q_{n}(b)}\left(-\frac{r \alpha}{\lambda}\right)^{n} \prod_{k=1}^{n}\left(1+\frac{r \alpha}{\lambda} b^{k}\right)^{-1}
$$

Now this quantity can be simplified by using (A.4) with $z=-r \alpha / \lambda$ to get

$$
L \psi(\lambda a / b)=\frac{1}{r \alpha}\left[1-\left(1+\frac{r \alpha}{\lambda}\right) \sum_{m, n \geq 0} \frac{Q_{m+n}(b) b^{n^{2}}}{Q_{m}(b) Q_{n}(b)}\left(-\frac{r \alpha}{\lambda}\right)^{m+n}\right]
$$

Performing the summation on the diagonals $m+n=s$, we find

$$
L \psi(\lambda a / b)=\frac{1}{r \alpha}\left[1-\left(1+\frac{r \alpha}{\lambda}\right) \sum_{s=0}^{\infty} Q_{s}(b)\left(-\frac{r \alpha}{\lambda}\right)^{s} \sum_{n=0}^{s} \frac{b^{n^{2}}}{Q_{n}(b)^{2} Q_{s-n}(b)}\right]
$$

The intermediate sum turns out to be equal to $1 / Q_{s}(b)^{2}$; this fact is proved in the Appendix (Lemma A.1.). Consequently,

$$
L \psi(\lambda a / b)=\frac{1}{r \alpha}\left[1-\left(1+\frac{r \alpha}{\lambda}\right) \sum_{s=0}^{\infty} \frac{1}{Q_{s}(b)}\left(-\frac{r \alpha}{\lambda}\right)^{s}\right]
$$

Finally, invoking (A.1) immediately leads to (24).
As a result, inserting (24) in (23) yields (5).
REMARK 1. The iterative method used in this proof was employed by Piau [15] for evaluating the limiting solution of the general quasi-renewal equation and then the asymptotic expected distance $\lim _{t \rightarrow+\infty} \mathbb{E}\left(D_{t}\right)$.

REMARK 2. The limiting result concerning $\varphi$, (4), may be derived in the same way without solving (13). Indeed, it can be shown that the functional $L_{\delta} \varphi$ defined as

$$
L_{\delta} \varphi(p)=\int_{\delta}^{\infty} e^{-p t} \varphi(t) d t
$$

satisfies the following relation:

$$
L_{\delta} \varphi(p)=\frac{1}{p} e^{-\delta\left[p+\lambda\left(1-e^{-\alpha}\right)\right]}-\frac{\lambda}{p}\left(1-e^{-\alpha}\right) e^{a \delta(p+\lambda) / b} L_{\delta} \varphi((p+\lambda a) / b)
$$

Iterating this identity, we obtain after some algebra

$$
L_{\delta} \varphi(\lambda a / b)=\frac{1}{\lambda} e^{-\lambda \delta\left(1 / b-e^{-\alpha}\right)} \sum_{n=1}^{\infty}(-1)^{n-1} \frac{b^{n(n+1) / 2}}{Q_{n}(b)}\left(1-e^{-\alpha}\right)^{n-1}
$$

which in turn may be simplified into

$$
\frac{e^{-\lambda \delta\left(1 / b-e^{-\alpha}\right)}}{\lambda\left(1-e^{-\alpha}\right)}\left[1-\prod_{n=1}^{\infty}\left[1-\left(1-e^{-\alpha}\right) b^{n}\right]\right]
$$

by using (A.2) with $z=-b\left(1-e^{-\alpha}\right)$. Finally,

$$
\lim _{t \rightarrow+\infty} \varphi(t)=\lim _{p \rightarrow 0^{+}} p L_{\delta} \varphi(p)=e^{-\lambda \delta\left(1-e^{-\alpha}\right)}-\lambda\left(1-e^{-\alpha}\right) e^{\lambda \delta a / b} L_{\delta} \varphi(\lambda a / b)
$$

and we retrieve (4).
4.3. The random variable $D_{t}$. The proof of (3) is similar to that of (2). First, notice that (10) gives

$$
\chi(t)=e^{-r \alpha t} \quad \text { for } t \in[0, \delta] .
$$

Second, we solve (10) on the interval $[\delta,+\infty$ ) by introducing $\tilde{\chi}$ defined as $\tilde{\chi}(t)=e^{\lambda t} \chi(t+\delta)$ for any $t \geq 0$.

Proposition 11. The function $\tilde{\chi}$ satisfies the following functional differential equation:

$$
\begin{equation*}
\frac{d \tilde{\chi}}{d t}(t)-\lambda \tilde{\chi}(t)+\lambda b \tilde{\chi}(b t)=\lambda \rho e^{\lambda \rho t-r \delta \alpha} \tag{26}
\end{equation*}
$$

where $\rho=b-r \alpha / \lambda$, together with the initial condition $\tilde{\chi}(0)=e^{-r \delta \alpha}$.
Proof. We rewrite (10) in terms of $\tilde{\chi}$ as

$$
\begin{equation*}
\tilde{\chi}(t)=\lambda \int_{b t}^{t} \tilde{\chi}(s) d s+e^{(\lambda b-r \alpha) t-r \delta \alpha} . \tag{27}
\end{equation*}
$$

Differentiating (27) immediately yields (26).
Proposition 12. The function $\tilde{\chi}$ admits a Taylor expansion $\tilde{\chi}(t)=$ $\sum_{n=0}^{\infty} \chi_{n} t^{n} /(n!)$ with

$$
\begin{equation*}
\chi_{n}=\lambda^{n} e^{-r \delta \alpha} Q_{n}(b) \sum_{k=0}^{n} \frac{\rho^{k}}{Q_{k}(b)} \tag{28}
\end{equation*}
$$

Proof. Differentiating $n$ times (26) gives

$$
\frac{d^{n+1} \tilde{\chi}}{d t^{n+1}}(t)=\lambda \frac{d^{n} \tilde{\chi}}{d t^{n}}(t)-\lambda b^{n+1} \frac{d^{n} \tilde{\chi}}{d t^{n}}(b t)+(\lambda \rho)^{n+1} e^{\lambda \rho t-r \delta \alpha} .
$$

For $t=0$, we get the following relation for the Taylor coefficients $\chi_{n}$ :

$$
\chi_{0}=e^{-r \delta \alpha} \quad \text { and } \quad \chi_{n+1}=\lambda\left(1-b^{n+1}\right) \chi_{n}+(\lambda \rho)^{n+1} e^{-r \delta \alpha}, \quad n \geq 0
$$

Dividing this equality by $\lambda^{n+1} Q_{n+1}(b)$ yields

$$
\frac{\chi_{n+1}}{\lambda^{n+1} Q_{n+1}(b)}=\frac{\chi_{n}}{\lambda^{n} Q_{n}(b)}+e^{-r \delta \alpha} \frac{\rho^{n+1}}{Q_{n+1}(b)}
$$

from which (28) ensues.
Now, let us check the convergence of the associated Taylor series. Since $Q_{k}(b) \geq Q_{\infty}(b)=\prod_{n=1}^{\infty}\left(1-b^{n}\right)$ for all $k$, the following inequality holds:

$$
\left|\sum_{k=0}^{n} \frac{\rho^{k}}{Q_{k}(b)}\right| \leq \begin{cases}2|\rho|^{n+1} /\left[|\rho-1| Q_{\infty}(b)\right], & \text { if }|\rho|>1, \\ (n+1) / Q_{\infty}(b), & \text { if }|\rho|=1, \\ 1 /\left[(1-\rho) Q_{\infty}(b)\right], & \text { if }|\rho|<1,\end{cases}
$$

and then, since $0<Q_{n}(b)<1$, there exists a constant $C>0$ such that for all $n$,

$$
\left|\chi_{n}\right| \leq \begin{cases}C|\lambda \rho|^{n}, & \text { if }|\rho|>1 \\ C n \lambda^{n}, & \text { if }|\rho| \leq 1\end{cases}
$$

Consequently, the Taylor series $\sum_{n=0}^{\infty} \chi_{n} t^{n} /(n!)$ is convergent.

As a result, expression (3) follows and the limiting result (6) may be deduced from (3) by using (16) together with (A.1). Indeed, we notice that

$$
\begin{equation*}
Q_{n}(b) \sum_{k=0}^{n} \frac{\rho^{k}}{Q_{k}(b)} \underset{n \rightarrow \infty}{\longrightarrow} \prod_{n=1}^{\infty}\left(1-b^{n}\right) \sum_{n=0}^{\infty} \frac{\rho^{n}}{Q_{n}(b)} \tag{29}
\end{equation*}
$$

and due to (A.1) the right-hand side of (29) coincides with

$$
\left[\prod_{n=1}^{\infty}\left(1-b^{n}\right)\right]\left[\prod_{n=0}^{\infty}\left(1-b^{n} \rho\right)\right]^{-1}=\prod_{n=1}^{\infty}\left[1+\frac{r \alpha}{\lambda} \frac{b^{n-1}}{1-b^{n}}\right]^{-1}
$$

at least for $|\rho|<1$. This establishes formula (6) for sufficiently small $\alpha$. Actually, (6) holds for any $\alpha>0$ by analycity.

The proofs of Theorems 2 and 3 are now complete.

REMARK 3. Since (10) satisfied by $\chi$ is a genuine quasi-renewal equation, formula (3) of [15] may apply; then, it is possible to derive directly the asymptotical value of $\chi$. Indeed,

$$
\lim _{t \rightarrow+\infty} \chi(t)=\lim _{t \rightarrow+\infty} \chi(t+\delta)=\lambda \sum_{n=0}^{\infty}(-1)^{n} \operatorname{Lh}\left(\lambda\left(\frac{1}{b^{n}}-1\right)\right) \frac{b^{n(n-1) / 2}}{Q_{n}(b)}
$$

where $h(t)=e^{-(\lambda a+r \alpha) t-r \delta \alpha}$. Plainly,

$$
\operatorname{Lh}\left(\lambda\left(\frac{1}{b^{n}}-1\right)\right)=\frac{e^{-r \delta \alpha}}{\lambda} \frac{b^{n}}{1-\rho b^{n}}
$$

On expanding $1 /\left(1-\rho b^{n}\right)$ into a series we get

$$
\begin{aligned}
\lim _{t \rightarrow+\infty} \chi(t) & =e^{-r \delta \alpha} \sum_{m=0}^{\infty}(-1)^{m} \frac{b^{m(m+1) / 2}}{Q_{m}(b)} \sum_{n=0}^{\infty}\left(\rho b^{m}\right)^{n} \\
& =e^{-r \delta \alpha} \sum_{n=0}^{\infty}\left[\sum_{m=0}^{\infty} \frac{b^{m(m-1) / 2}}{Q_{m}(b)}\left(-b^{n+1}\right)^{m}\right] \rho^{n}
\end{aligned}
$$

The term within brackets in the last equality turns out to simplify into $\prod_{k=n+1}^{\infty}(1-$ $\left.b^{k}\right)=\left[\prod_{k=1}^{\infty}\left(1-b^{k}\right)\right] / Q_{n}(b)$ in view of (A.2) with $z=-b^{n+1}$. Then

$$
\lim _{t \rightarrow+\infty} \chi(t)=e^{-r \delta \alpha} \prod_{n=1}^{\infty}\left(1-b^{n}\right) \sum_{n=0}^{\infty} \frac{\rho^{n}}{Q_{n}(b)}
$$

and we retrieve (6) thanks to (A.1).
4.4. The random variable $L_{t}$. Since we did not get any explicit expression for the Laplace transform of $L_{t}$, we exhibit an algorithm for computing $\lim _{t \rightarrow+\infty} \omega(t)$. Set $\omega(\alpha, t)=\mathbb{E}\left(e^{-\alpha L_{t}}\right)$ [we shall write $\omega(t)$ for simplicity].

As in the foregoing sections, we begin by writing out an integral equation for $\omega$ by conditioning on the event $T_{1}=s$. We observe that

$$
\left(L_{t} \mid T_{1}=s\right) \stackrel{\text { law }}{=} \begin{cases}L_{t-s}, & \text { if } 0 \leq s \leq a(t-\delta)^{+} \\ r t-\tilde{P}_{t-s}, & \text { if } a(t-\delta)^{+}<s \leq a t \\ (r+c)(t-s)-\tilde{P}_{t-s}, & \text { if } a t<s \leq t \\ 0, & \text { if } s>t\end{cases}
$$

from which it follows

$$
\omega(t)=\lambda \int_{0}^{a(t-\delta)^{+}} \omega(t-s) e^{-\lambda s} d s+\gamma(t)
$$

or, equivalently for $t \geq \delta$,

$$
\omega(t)=\lambda e^{-\lambda t} \int_{b t+a \delta}^{b t} \omega(s) e^{\lambda s} d s+\gamma(t)
$$

where

$$
\begin{aligned}
\gamma(t)= & \lambda e^{-r \alpha t} \int_{a(t-\delta)^{+}}^{a t} \psi^{-}(t-s) e^{-\lambda s} d s \\
& +\lambda \int_{a t}^{t} \psi^{-}(t-s) e^{-(r \alpha / b)(t-s)-\lambda s} d s+e^{-\lambda t}
\end{aligned}
$$

and

$$
\psi^{-}(t)=\mathbb{E}\left(e^{\alpha \tilde{P}_{t}}\right)=\psi(-\alpha, t)
$$

Set $\tilde{\omega}(t)=e^{\lambda t} \omega(t+\delta), \tilde{\gamma}(t)=e^{\lambda t} \gamma(t+\delta)$. The function $\tilde{\omega}$ solves the functional differential equation

$$
\frac{d \tilde{\omega}}{d t}(t)-\lambda \tilde{\omega}(t)-\lambda b \tilde{\omega}(b t)=\frac{d \tilde{\gamma}}{d t}(t), \quad \tilde{\omega}(0)=\gamma(\delta) .
$$

Let us introduce the Taylor expansions of $\tilde{\omega}$ and $\tilde{\gamma}, \tilde{\omega}(t)=\sum_{n=0}^{\infty} \omega_{n} t^{n} /(n!)$ and $\tilde{\gamma}(t)=\sum_{n=0}^{\infty} \gamma_{n} t^{n} /(n!)$. The coefficients $\omega_{n}$ are given by induction:

$$
\omega_{0}=\gamma_{0}=\gamma(\delta) \quad \text { and } \quad \omega_{n+1}=\lambda\left(1-b^{n+1}\right) \omega_{n}+\gamma_{n+1}, \quad n \geq 0
$$

Iterating this relation easily yields

$$
\omega_{n}=Q_{n}(b) \lambda^{n} \sum_{k=0}^{n} \frac{\gamma_{k}}{Q_{k}(b) \lambda^{k}} .
$$

Then

$$
\omega(t+\delta)=\sum_{n=0}^{\infty}\left[Q_{n}(b) \sum_{k=0}^{n} \frac{\gamma_{k}}{Q_{k}(b) \lambda^{k}}\right] e^{-\lambda t} \frac{(\lambda t)^{n}}{n!},
$$

and by (16) and introducing back the hidden variable $\alpha$, we obtain

$$
\lim _{t \rightarrow+\infty} \omega(\alpha, t)=\prod_{n=0}^{\infty}\left(1-b^{n}\right) \sum_{n=0}^{\infty} \frac{\gamma_{n}(\alpha)}{Q_{n}(b) \lambda^{n}}
$$

In the above formula, the coefficients $\gamma_{n}$ are not explicitly known. So we sketch an algorithm for computing them numerically.

Since $\gamma$ is expressed by means of $\psi^{-}$, we first write a functional differential equation for $\psi^{-}$. Differentiating (20) and putting $\tilde{\psi}(t)=\psi^{-}(t) e^{\lambda t}$, it is easily seen that the function $\tilde{\psi}$ satisfies

$$
\begin{aligned}
& \frac{d^{2} \tilde{\psi}}{d t^{2}}(t)-(\lambda+r \alpha) \frac{d \tilde{\psi}}{d t}(t)+\lambda r \alpha \tilde{\psi}(t)-\lambda b r \alpha \tilde{\psi}(b t)=0, \\
& \tilde{\psi}(0)=1, \quad \frac{d \tilde{\psi}}{d t}(0)=\lambda+r \alpha
\end{aligned}
$$

The coefficients of the expansion $\tilde{\psi}(t)=\sum_{n=0}^{\infty} \psi_{n} t^{n} /(n!)$ follow the recursion below:

$$
\psi_{0}=1, \quad \psi_{1}=\lambda+r \alpha
$$

and

$$
\psi_{n+2}-(\lambda+r \alpha) \psi_{n+1}+\lambda r \alpha\left(1-b^{n+1}\right) \psi_{n}=0, \quad n \geq 0
$$

We did not find any closed form for $\psi_{n}$. However, the sequence $\left(\gamma_{n}\right)_{n \geq 0}$ is numerically tractable according to the scheme

$$
\left(\psi_{n}\right)_{n \geq 0} \rightarrow \tilde{\psi} \rightarrow \tilde{\gamma} \rightarrow\left(\gamma_{n}\right)_{n \geq 0}
$$

Indeed the following relation:

$$
\tilde{\gamma}(t)=e^{-\lambda \delta}\left[\lambda \int_{0}^{b(t+\delta)} \tilde{\psi}(s) e^{-(r \alpha / b) s} d s+\lambda e^{-r \alpha(t+\delta)} \int_{b(t+\delta)}^{b t+\delta} \tilde{\psi}(s) d s+1\right]
$$

enables to deduce $\tilde{\gamma}$ directly from $\tilde{\psi}$.

## APPENDIX

Here are collected some formulae (the so-called " $q$-series"; here $q$ is $b$ ) we used throughout this work. We refer to the book of Andrews on the theory of partitions [1]. These formulae are valid for any $|b|<1$ and $|z|<1$.

- Formula 2.2.5, page 19 (Euler):

$$
\begin{equation*}
\prod_{n=0}^{\infty}\left(1-b^{n} z\right)^{-1}=\sum_{n=0}^{\infty} \frac{1}{Q_{n}(b)} z^{n} \tag{A.1}
\end{equation*}
$$

- Formula 2.2.6, page 19 (Euler):

$$
\begin{equation*}
\prod_{n=0}^{\infty}\left(1+b^{n} z\right)=\sum_{n=0}^{\infty} \frac{b^{n(n-1) / 2}}{Q_{n}(b)} z^{n} \tag{A.2}
\end{equation*}
$$

- Formula 3.3.6, page 36 (Rothe):

$$
\begin{equation*}
\prod_{k=0}^{n-1}\left(1+b^{k} z\right)=\sum_{k=0}^{n} \frac{Q_{n}(b) b^{k(k-1) / 2}}{Q_{k}(b) Q_{n-k}(b)} z^{k} . \tag{A.3}
\end{equation*}
$$

- Formula 3.3.7, page 36 (Rothe):

$$
\begin{equation*}
\prod_{k=0}^{n}\left(1-b^{k} z\right)^{-1}=\sum_{k=0}^{\infty} \frac{Q_{n+k}(b)}{Q_{n}(b) Q_{k}(b)} z^{k} . \tag{A.4}
\end{equation*}
$$

Lemma A.1. The following relation is satisfied:

$$
\begin{equation*}
\sum_{n=0}^{s} \frac{b^{n^{2}}}{Q_{n}(b)^{2} Q_{s-n}(b)}=\frac{1}{Q_{s}(b)^{2}} \tag{A.5}
\end{equation*}
$$

Since we did not find any reference to the foregoing formula in the literature, we provide here a proof of it.

Proof of Lemma A.1. Let us multiply the left-hand side of (A.5) by $Q_{s}(b)$. This yields

$$
Q_{s}(b) \sum_{n=0}^{s} \frac{b^{n^{2}}}{Q_{n}(b)^{2} Q_{s-n}(b)}=\sum_{n=0}^{s} \frac{Q_{s}(b)}{Q_{n}(b)} \frac{b^{n^{2}}}{Q_{n}(b) Q_{s-n}(b)} .
$$

We invoke (A.3) with the choice $z=-b^{n+1}$ for computing $Q_{s}(b) / Q_{n}(b)$ :

$$
\frac{Q_{s}(b)}{Q_{n}(b)}=\prod_{k=n+1}^{s}\left(1-b^{k}\right)=\sum_{k=0}^{s-n}(-1)^{k} \frac{Q_{s-n}(b)}{Q_{k}(b) Q_{s-n-k}(b)} b^{k(k-1) / 2+(n+1) k}
$$

Therefore,

$$
Q_{s}(b) \sum_{n=0}^{s} \frac{b^{n^{2}}}{Q_{n}(b)^{2} Q_{s-n}(b)}=\sum_{n=0}^{s} \frac{1}{Q_{n}(b)} \sum_{k=0}^{s-n}(-1)^{k} \frac{b^{k(k+1) / 2+n(n+k)}}{Q_{k}(b) Q_{s-n-k}(b)}
$$

By summing over the diagonals $n+k=\sigma$, the foregoing double sum can be written as

$$
\begin{aligned}
\sum_{\sigma=0}^{s} & \frac{1}{Q_{s-\sigma}(b)} \sum_{k=0}^{\sigma}(-1)^{k} \frac{b^{k(k+1) / 2+\sigma(\sigma-k)}}{Q_{k}(b) Q_{\sigma-k}(b)} \\
& =\sum_{\sigma=0}^{s} \frac{b^{\sigma^{2}}}{Q_{\sigma}(b) Q_{s-\sigma}(b)} \sum_{k=0}^{\sigma} \frac{Q_{\sigma}(b) b^{k(k-1) / 2}}{Q_{k}(b) Q_{\sigma-k}(b)}\left(-b^{1-\sigma}\right)^{k} .
\end{aligned}
$$

Finally, the second sum in the last displayed equality can be evaluated by using once again (A.3) with the choice $z=-b^{1-\sigma}$. That sum equals 1 if $\sigma=0$ and otherwise equals $\prod_{k=0}^{\sigma-1}\left(1-b^{k-\sigma+1}\right)$ whose value vanishes for any $\sigma \geq 1$. Thereby,

$$
Q_{s}(b) \sum_{n=0}^{s} \frac{b^{n^{2}}}{Q_{n}(b)^{2} Q_{s-n}(b)}=\frac{1}{Q_{s}(b)}
$$

which completes the proof of Lemma A.1.

## REFERENCES

[1] Andrews, G. (1976). The theory of partitions. In Encyclopedia of Mathematics and Its Applications 2. Addison-Wesley, Reading, MA.
[2] Bertoin, J., Biane, P. and Yor, M. (2002). Poissonian exponential functionals, $q$-series, $q$-integrals, and the moment problem for log-normal distributions. Proceedings of Ascona. To appear.
[3] Callan, H. G. (1973). DNA replication in the chromosomes of eukaryotes. In Cold Spring Harbor Symposium on Quantitative Biology 38 195-203. CSHL Press, Woodbury, NY.
[4] Cordoliani, H. (1994). Les acides nucléiques. Nathan, Paris.
[5] Cowan, R. (2001). Stochastic models for DNA replication. In Handbook of Statistics (C. R. Rao and D. N. Shanbhag, eds.) 20 137-166. North-Holland, Amsterdam.
[6] CowAn, R. (2001). A new discrete distribution arising in a model of DNA replication. J. Appl. Probab. 38 754-760.
[7] Cowan, R. and ChiU, S. N. (1992). The mathematics of DNA replicating forks. Research Report 28, Univ. Hong Kong.
[8] Cowan, R. and Chiu, S. N. (1994). Stochastic model of fragment formation when DNA replicates. J. Appl. Probab. 31 301-308.
[9] Cowan, R., Chiu, S. N. and Holst, L. (1995). A limit theorem for the replication of a DNA molecule. J. Appl. Probab. 32 296-303.
[10] Dumas, V., Guillemin, F. and Robert, P. (2002). A Markovian analysis of additiveincrease multiplicative-decrease (AIMD) algorithms. Adv. in Appl. Probab. 34 85-111.
[11] Huberman, J. A. and Horwitz, H. (1973). Discontinuous DNA synthesis in mammalian cells. In Cold Spring Harbor Symposium on Quantitative Biology 38 233-238. CSHL Press, Woodbury, NY.
[12] Kornberg, A. (1980). DNA Replication. Freeman, San Francisco.
[13] Kowalski, J. and Denhardt, D. T. (1982). Adenovirus DNA replication in vivo. Properties of short DNA molecules exctracted infected from cells. Biochem. Biophys. Acta 698 260-270.
[14] Okazaki, R., Okazaki, T., Sakabe, K., Sugimoto, K., Kainuma, R., Sugimo, A. and IWATSUKI, N. (1968). In vivo mechanism of DNA chain growth. In Cold Spring Harbor Symposium on Quantitative Biology 33 129-143. CSHL Press, Woodbury, NY.
[15] Piau, D. (2000). Quasi-renewal estimates. J. Appl. Probab. 37 269-275.
[16] Piau, D. (2000). Addendum to "Quasi-renewal estimates." J. Appl. Probab. 37 1171-1172.

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