The number of mutations carried by a single cell is given by the sum over all mutations occurring during each of its past divisions:

$$m = \sum_{i}^{l} u_i \tag{1}$$

Without making any assumptions about the distributions of the number of past divisions l and the number of mutations per division u, The expected value of m can easily be found from the law of total expectation

$$\mathrm{E}(m) = \mathrm{E}(l)\,\mathrm{E}(u) \tag{2}$$

and the variance of m can be written through the law of total variance

$$\mathrm{Var}(m) = \mathrm{E}(l)\,\mathrm{Var}(u) + \mathrm{E}(u)^2\,\mathrm{Var}(l) \tag{3}$$

Now we introduce the fact that the number of mutations per division are Poisson distributed with parameter μ (i.e. $\mathrm{E}(u) = \mathrm{Var}(u) = \mu$) and subtract the mean from the variance:

$$\begin{aligned} \mathrm{Var}(m) - \mathrm{E}(m) &= \mu^2\,\mathrm{Var}(l) \\ \Rightarrow \frac{\mathrm{Var}(m) - \mathrm{E}(m)}{\mathrm{E}(m)} &= \mu\frac{\mathrm{Var}(l)}{\mathrm{E}(l)} \end{aligned}$$

so finally we can find the mutation rate from

$$\mu = \left(\frac{\mathrm{Var}(m)}{\mathrm{E}(m)} - 1\right)\frac{\mathrm{E}(l)}{\mathrm{Var}(l)} \tag{4}$$

If the number of divisions is Poisson distributed, then $\mathrm{E}(l) = \mathrm{Var}(l)$ so that $\mu = \mathrm{Var}(m)/\,\mathrm{E}(m) - 1$. This is the compound Poisson estimate which we will denote as $\tilde{\mu}$. If we take the $\mu = 1.2$ as true, then the CPD estimate $\tilde{\mu}$ gives an indication of how the system dynamics differ from the Poisson model. In particular, if $\tilde{\mu} < \mu$ then we must have $\mathrm{Var}(l) < \mathrm{E}(l)$, which could be an indication of the existence memory in the system, for example in the form of divisions occurring according to a timed cell cycle. Conversely, if $\tilde{\mu} > \mu$, we have $\mathrm{Var}(l) > \mathrm{E}(l)$, which implies that various lineages actually divided far more or far less than what would be appropriate for a memoryless system. Interestingly, the latter observation need not be at odds with current knowledge of stem cell dynamics, as the possibility of a quiescence state – which cells enter and exist according to some complex dynamics – could potentially lead to overdispersion compared to the Poisson model.

$$m_i = l_i + \sum_{j}^{y_i} u_{ji} \tag{5}$$

$$\begin{aligned} \mathrm{E}(m) &= \mathrm{E}(l) + \mathrm{E}(y)\,\mathrm{E}(u) \\ \mathrm{Var}(m) &= \mathrm{Var}(l) + \mathrm{E}(y)\,\mathrm{Var}(u) + \mathrm{E}(u)^2\,\mathrm{Var}(y) \end{aligned} \tag{6}$$

Take all distributions as Poisson ($\mathrm{E}(x) = \mathrm{Var}(x)$):

$$\begin{aligned} \mathrm{E}(l) &= \mathrm{Var}(l) = \lambda t \\ \mathrm{E}(y) &= \mathrm{Var}(y) = \gamma t \\ \mathrm{E}(u) &= \mathrm{Var}(u) = \mu \end{aligned}$$

Plug in:

$$\begin{aligned} &\mathrm{E}(m) = \lambda t + \gamma t \mu \\ &\mathrm{Var}(m) = \lambda t + \gamma t \mu + \mu^2 \gamma t \\ &\Rightarrow \gamma t = \frac{\mathrm{Var}(m) - \mathrm{E}(m)}{\mu^2} \\ &\Rightarrow \lambda t = \mathrm{E}(m) - \frac{\mathrm{Var}(m) - \mathrm{E}(m)}{\mu} \end{aligned}$$