At the Workshop in Molecular Evolution I was asked so many questions about the interpretation of "g", the exponential growth parameter estimated by FLUCTUATE and LAMARC, that I've tried to write down the answer. (This also saves me from getting it wrong myself.)

The basic equation of population growth used in Lamarc is

$$\Theta_t = \Theta_{now} exp(-gt)$$

In this equation, Θ_t is $4N\mu$ at a given time t, where time is measured *backwards* (the tips are time 0, and times in the past have positive signs). Θ_{now} is $4N\mu$ at the tips of the tree (the time at which organisms were sampled) and is the Θ estimated by FLUCTUATE or LAMARC.

In this formulation, t is in mutational units; that is, one unit of t is the expected time for a mutation to occur at a single site. If your DNA mutates at a per-site rate of 10^{-8} then one unit of time is 10^8 generations.

Positive values of g indicate growth (population was smaller in the past and is getting bigger) and negative values indicate shrinkage (population was bigger in the past and is getting smaller).

To convert to more intuitive units will require an external estimate of μ, the neutral mutation rate, so that we can convert mutational time to generation or calendar time. Given such an estimate of μ, we can convert mutational times to generational times.

$$\Theta_{t\mu} = \Theta_{now} exp(-gt\mu)$$

The factor $t\mu$ is time measured in generations.

For a worked-out example:

FLUCTUATE has estimated $\Theta_{now} = 0.5$ and $g = 100$. We want to know how large our population was 1000 generations ago. We are willing to assume that our mutation rate is 10^{-6}. (If this assumption is shaky, we may want to consider upper and lower bounds for the mutation rate, and see what values of Θ they correspond to.)

$$\Theta_{1000} = \Theta_{now} exp(-g * 1000 * 10^{-6}) = 0.5 exp(-100 * 10^{-3}) = 0.5 exp(-0.1) = 0.4524$$

What does this mean? First off, an intuition check. I've said that positive g means growth into the future, and negative means shrinkage. We have positive g here and the Θ 1000 generations ago is smaller than the modern one, so that works out.

Secondly, it is easier to interpret N than $4N\mu$ so let's use our assumed value of μ to find the population size:

$$N = 4N\mu/\mu = 0.4524/10^{-6} = 4.524x10^5$$

This can be compared to our modern-day population of $2.0x10^6$.

It's important to note that if we had assumed a different value of μ our final interpretation would be very different. If μ were much lower, there would be almost no visible growth for these values of g and Θ. If μ were much greater, there would be

enormous growth.

It is frustrating to find g (and N) confounded with μ in this way, but there is no way around it if we are only observing mutational differences and have no direct observations of time.

One other fact, helpful in running the programs, is that the scale of g is not at all symmetrical. A value $g = +100$ is not very much growth for most values of μ and Θ. A value $g = -100$ is enormous shrinkage, and may produce pathological results if used as a starting point–the expected time to the common ancestor may be infinite with such extreme shrinkage! We recommend avoiding values of g such that $-g * \Theta > 1$ for your expected value of Θ.