Count based PVA

1. *Estimating the per-capita growth rate (r, m) and its standard deviation s from empirical data.*

a. Pairwise approach:

See SFC Mathcad lab on PVA. Take successive pairs of Ns and estimate the ratio:

$\lambda_t = N_{t+1}/N_t$

$$\hat{r} = \hat{\mu} = mean(\ln \lambda_t)$$

$$\hat{\sigma} = \sqrt{\sum \frac{(\ln \lambda_t - \hat{r})^2}{length - 1}}$$

Where length = length of time series, # of estimates of N.

Definitional formula for standard deviation. Square root of sum of squared residuals divided by degrees of freedom.

b. Regression approach:

$$N_{t+1} = N_t \lambda$$
$$N_t = N_0 \lambda^t$$
$$N_t = N_0 e^{rt}$$

$$\lambda = e^r$$
$$\ln(\lambda) = r$$

$$r = \frac{\ln(\frac{N_t}{N_0})}{t} = \frac{\ln(N_t) - \ln(N_0)}{t}$$

It would be inefficient to estimate r using just the first (N0) and last (Nt) estimates of N. use log-linear regression of population size on time instead:

$$\ln(N) = a + bt$$

$$\ln(N) = N_0 + rt$$

intercept = initial population size, N_0
slope = estimated per-capita population growth rate, $\hat{r}$ (sometimes called $\hat{\mu}$). Also get estimated standard deviation of slope ($\hat{\sigma}$).

2. *Projecting N into the future with a stochastic growth rate estimate.*

$$N_{t+1} = N_t * e^{\mu \pm error}$$

$$N_{t+1} = N_t e^{\varepsilon_t}$$
where
$$\varepsilon = rnorm(\mu, \sigma)$$

Project a given number of years into future.
Repeat for many iterations (say 1000).
Can now determine stochastic growth rate (< deterministic growth rate) and its variance.
Can now determine quasi-extinction risk for given time interval.
Can put confidence limits on quasi-extinction risk estimates. (Morris & Doak Ch. 3).

3. Process error and sampling error – One serious issue in count based PVA involves eliminating observation error (sampling error) from the empirically measured variance in population growth rate. The observed variance in λ (or r or μ) is a combination of:

Process error – true variation in the population growth rate from one year to the next
Sampling error – random errors in estimation of population size that create apparent changes in growth rate that are spurious.

If one uses the Nt to calculate a single variance in the growth rate, it is an amalgamation of process error and sampling error. To project population dynamics into the future, we'd like to eliminate the sampling error from this variance – it is only the process error that will actually affect future dynamics.

There are two consequences of ignoring sampling error:

1. The ***projected dynamics will be too variable***, in comparison to reality. This will produce over-estimates of quasi-extinction probability. Overestimating the true variance of the growth process increases the odds of a simulated population trajectory reaching zero or some quasi-extinction threshold. The estimates of risk will therefore be conservative or pessimistic.

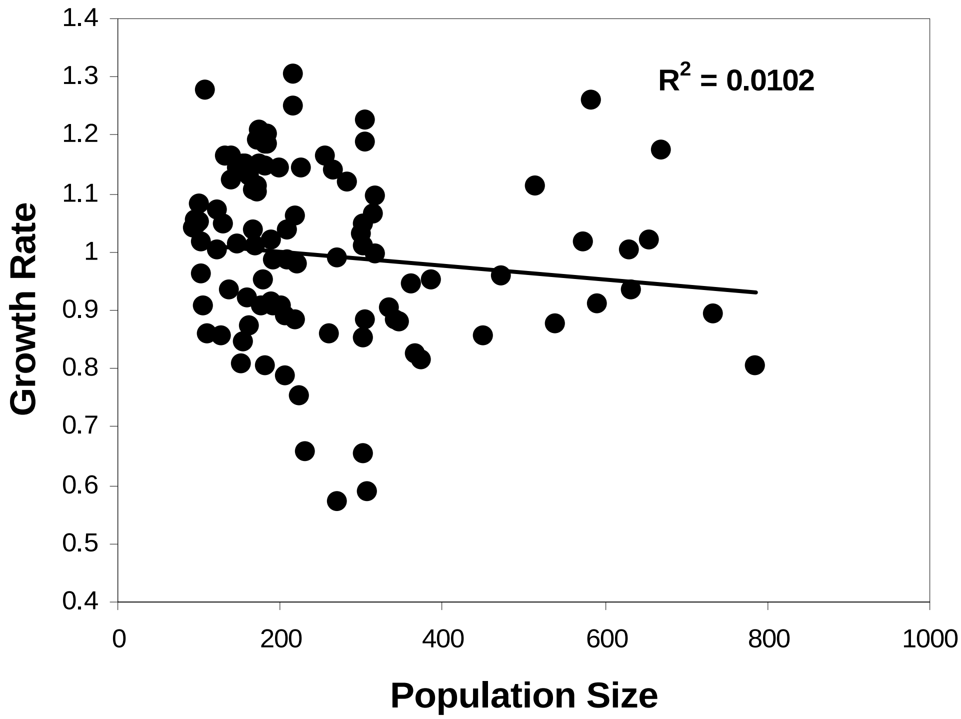
2. The ***effect of density dependence will be over-estimated***, in comparison to reality.

At equilibrium, a population with density-dependent regulation will tend to grow when it is below average size, and will tend to shrink when it is above average size. Obviously, this will make the distribution of population sizes cluster around a mean value with a tail on each side… something like a normal distribution.

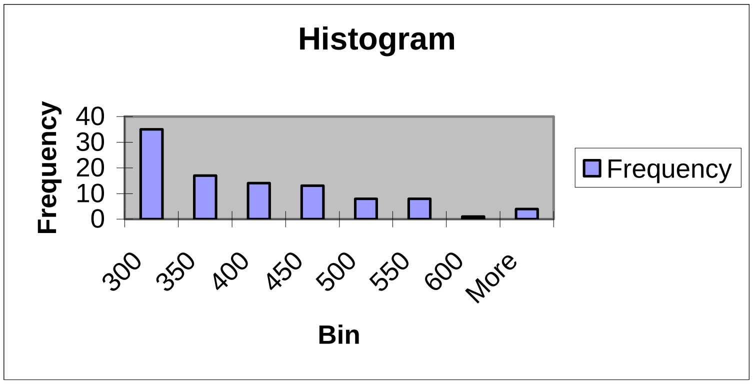
- A regression of λ on N will yield a negative slope, for such a population.

A population that is limited by density independent processes will not show this tendency. It is just as likely to experience good conditions when it is large or when it is small. This produces a uniform distribution of population sizes.

- A regression of λ on N will yield no slope, with density independence (and no sampling error).



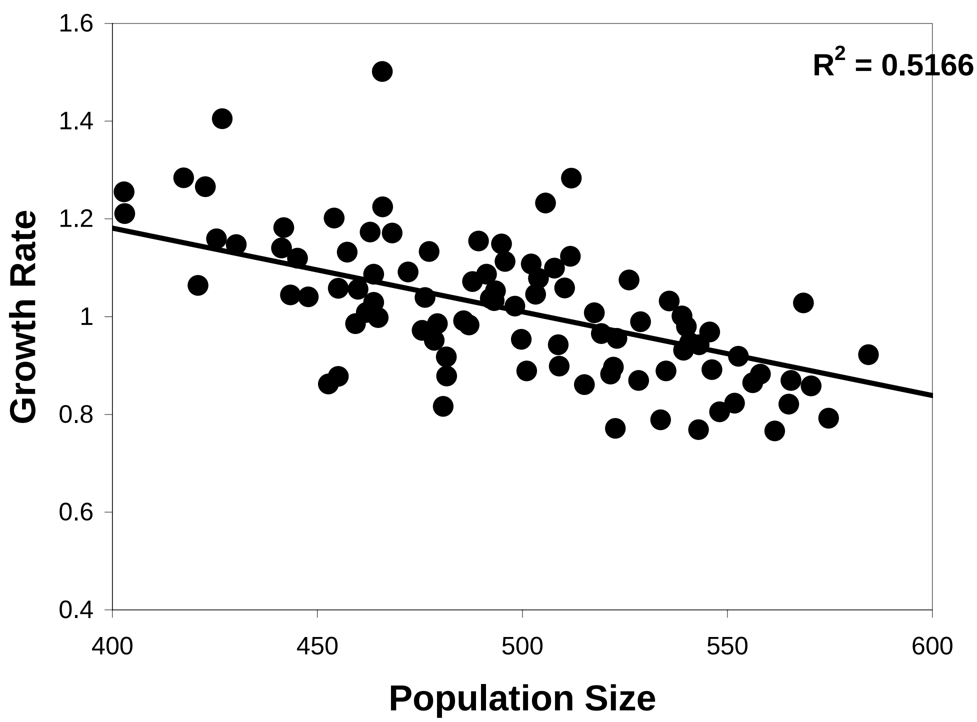
The plot above shows the regression of growth rate λ (= N_{t+1}/N_t) on N_t for a simulation with random draws from a distribution with $\hat{\lambda} = 1$ and $\hat{\sigma}_\lambda = 0.15$. Drawing growth rates from a normal distribution is a model of density independent growth — a random walk in N, which yields a uniform distribution of population sizes.



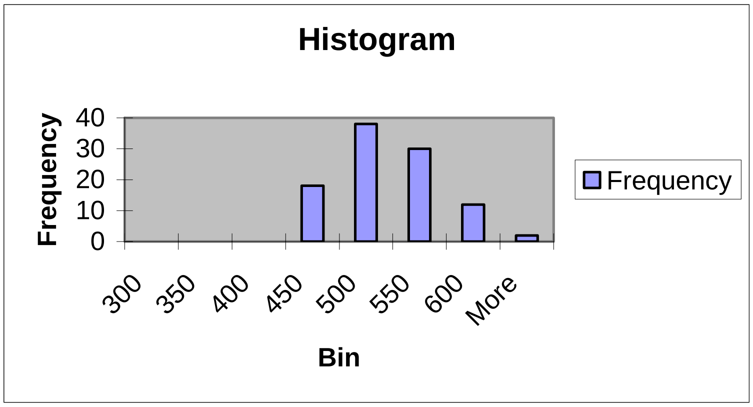
This is the frequency distribution of N for one sample of 100 years. (I should have had a few more bins below 300.)

Now consider a population that never actually changes size, but is counted each year with some random counting error. This will also produce a normal (or similar) distribution of population sizes. Sampling error mimics density-dependence!

- A regression λ on N will yield a negative slope, with density independence, but with sampling errors in the estimates of N.



The plot above shows the regression of growth rate λ (= N_{t+1}/N_t) on N_t for a simulation with random draws from a distribution of Ns with $\hat{N} = 500$ and $\hat{\sigma}_N = 50$, which yields $\hat{\lambda} = 1$ and $\hat{\sigma}_\lambda = 0.15$. These are the same mean and variance in growth rate as before, but now we implicitly have a model of density dependent growth, because N is likely to decrease when it is high and increase when it is low. If you happen to draw a low value of N from the normal distribution, the next N is likely to be bigger. If you happen to draw a very high value of N, the next N is likely to be smaller. ***So random sampling error mimics density dependence.***



This is the frequency distribution of N's drawn in a sample of 100 years.

See the Excel spreadsheet 'Eberhardt's density-dependence, revisited' for a simple demonstration of these relationships.

The implications of sampling error effects for count-based PVA are that one should either:

1. Restrict count based PVA analyses to counts that include little sampling error, reative to true variation in the growth rate.

or

2. Partition the sampling error out. This is tricky. Obviously, we would just remove the sampling error from each count, if we knew what it was. But we don't, so we can't. We can, however, obtain information on how repeatable counts are, to estimate the *overall* sampling error, assuming that it is constant across counts. In addition, maximum likelihood methods have recently been published (Staples et al. 2006) that simultaneously estimate the parameters of a growth model, the process variance, and the sampling error. It remains to be seen whether or not real time series data have enough information to do this job well. (This is asking a lot of relatively data – just N vs t!)