ON POPULATION GROWTH IN A RANDOMLY VARYING ENVIRONMENT

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Abstract.—If a population is growing in a randomly varying environment, such that the finite rate of increase per generation is a random variable with no serial autocorrelation, the logarithm of population size at any time t is normally distributed. Even though the expectation of population size may grow infinitely large with time, the probability of extinction may approach unity, owing to the difference between the geometric and arithmetic mean growth rates.

A problem of recurrent interest to population ecology is the question of "density-dependent" control of population numbers. The literature on this subject is so vast and so well known to ecologists that it cannot and need not be referenced here. Briefly, the question is to what extent the actual growth rates of populations are affected by the population density, and so to what extent density and resource shortage must be taken into account in explaining the observed history of population numbers.

The solution to this difficult and not always well-defined problem involves, among other things, an adequate description of how a population would change its numbers if its growth rate were *not* related to number, but only to variations in the independent environment (including other species, of course). Thus, we ask whether the observed variation in numbers of a species could be satisfactorily explained by supposing that at all times numbers are growing by the simple exponential growth law, but that the exponential rate of increase r is varying according to some extrinsic law unrelated to N, the population number. As stated, this proposition about variation in r is so general that no theoretical or experimental distinction could possibly be made between this hypothesis and that of density dependence. More specification is required. We assume a stationary distribution for r. Specifically, then, we want to ask how population numbers will change if the population is undergoing simple geometric increase or decrease with a rate that varies at random independently of both N and t.

Although many sophisticated treatments of stochastic population growth exist for a variety of models,[1, 2] it is our purpose in this note to point out a peculiarity of multiplicative population growth which is apparently not widely appreciated and which gives rise to some confusion.

Consider a population of size N_t at time t, which in a single reproductive period has a multiplicative increase l_t so that

$$N_{t+1} = N_t l_t \tag{1}$$

and in general

$$N_t = N_0 \prod_{i=1}^{t} l_i. \tag{2}$$

We now suppose that the rate of multiplication l_t varies randomly from generation to generation with some stationary probability density function $f(l)$. We should like to know the probability that N_t lies within some specified limits. A case of interest is the probability that $N_t > 0$, that is, that the population is still in existence at time t; but we might equally well want to know the chance that population is greater than the initial size ($N_t > N_0$). The exact specification of these probabilities is more or less difficult, depending upon the nature of the probability density function $f(l)$.

A usual first approach to the problem would be to find the expectation of N_t. If the l_t are independent of each other, then from equation (2) above

$$E(N_t) = N_0 E(\prod_{i=1}^{t} l_i) = N_0 \lambda^t, \tag{3}$$

where λ is the true mean of the l_i. Then if the *average* ratio between successive generations is greater than unity, no matter how slightly ($\lambda > 1$), the expectation of population size becomes infinite as t grows larger without bound, whereas, if $\lambda < 1$, the population expectation eventually shrinks to zero. The trouble with this approach is that, although it is a correct description of the behavior of the expected population size, it may give a completely erroneous picture of nearly every population.

It is well known that there is a class of distributions whose expectation may grow without bound, while the probability that the variate takes a value different from zero becomes vanishingly small. This paradox can be illustrated by a trivial example. Let X be a variate that takes the value N^2 with probability $1/N$ and the value 0 with probability $(N - 1)/N$. Then

$$E(X) = N^2 \left(\frac{1}{N}\right) + 0\left(\frac{N-1}{N}\right) = N$$

so that the expectation grows without bound as N goes to infinity. Yet the probability that X takes the value 0 approaches unity as N grows large. It is the characteristic of multiplicative processes, like the growth equation given in equation (2), that they may behave in exactly the same anomalous fashion. *That is, whereas $E(N_t)$ may grow infinitely large as t grows large, each population may be virtually certain to go to extinction!*

To show that this may be the case and to get a more satisfactory solution to our problem, let us return to the original statement and ask for the probability that N_t lies between two values, say K_1 and K_2. Since the logarithm of a variate is a monotone function

$$Pr\{K_1 \leq N_t \leq K_2\} = Pr\{\ln K_1 \leq \ln N_t \leq \ln K_2\}, \tag{4}$$

but from equation (2)

$$\ln N_t = \ln N_0 + \sum_{t=1}^{t} \ln l_i \tag{5}$$

so that from equations (4) and (5)

$$Pr\{K_1 \leq N_t \leq K_2\} = Pr\left\{\ln \frac{K_1}{N_0} \leq \sum_{t=1}^{t} \ln l_i \leq \ln \frac{K_2}{N_0}\right\}, \tag{6}$$

and dividing all parts of the inequality on the right by t we get

$$Pr\{K_1 \leq N_t \leq K_2\} = Pr\left\{\frac{1}{t} \ln \frac{K_1}{N_0} \leq (\overline{\ln l})_t \leq \frac{1}{t} \ln \frac{K_2}{N_0}\right\}, \tag{7}$$

where $(\overline{\ln l})_t$ is the arithmetic mean of the logarithms of the l_i over the previous t generations.

But if the l_i are independently and identically distributed with a finite mean and variance, $\ln l_i$ is also so distributed with a mean, say, $\mu_{\ln l}$, and a variance $\sigma^2_{\ln l}$.

Moreover, according to the Central Limit Theorem, $(\overline{\ln l})_t$, being a sample mean from such a distribution, is approximately normally distributed with mean $\mu_{\ln l}$ and variance equal to $\frac{1}{t}\sigma^2_{\ln l}$. Our problem is then solved.

Define $$\tau_1 = \frac{\frac{1}{t}\ln \frac{K_1}{N_0} - \mu_{\ln l}}{\sigma_{\ln l}/\sqrt{t}} \text{ and } \tau_2 = \frac{\frac{1}{t}\ln \frac{K_2}{N_0} - \mu_{\ln l}}{\sigma_{\ln l}/\sqrt{t}};$$

then

$$\text{Prob}\ \{K_1 \leq N_t \leq K_2\} \cong \text{Prob}\ \{\tau_1 \leq \tau \leq \tau_2\}$$

which is the standardized normal integral between τ_1 and τ_2 and can be looked up directly in the table of the normal distribution.

Let us take an example that illustrates the point made earlier about the danger of using the expected value of N_t to describe population behavior. Suppose that there are two environments such that in the first $l = 0.5$, whereas in the second environment $l = 1.7$. If these two environments have equal probability, $\mu_l = 1.1$, so that the expected value of N_t is growing larger by 10 per cent per generation. After, say, 100 generations, $E(N_{100}) = 1.1^{100}N_0 = 13781\ N_0$.

On the other hand, the actual behavior of the population is quite different: $\mu_{\ln l} = -0.08126$ and $\sigma^2_{\ln l} = 0.3744$. If we wish to know the probability that the population size is actually larger than the original value N_0, we set $K_1 = N_0$ and $K_2 = \infty$. Substituting into the expression for τ_1 and τ_2 and using the normal tables, we get that Prob $\{N_t > N_0\} = 0.092$.

This special case illustrates a general point. If $\mu_{\ln l}$ is less than zero, then τ_1 will be positive and will grow increasingly so at a rate proportional to $\sqrt{t}$. As times goes on, τ_1 approaches infinity, and the normal integral between τ_1 and τ_2 approaches zero. Thus, if $\mu_{\ln l}$ is less than zero, the population goes to extinction with a probability that approaches unity in the limit. On the other hand, if $\mu_{\ln l}$ is greater than zero, τ_1 is less than zero when $K_1 = N_0$ and grows smaller at a rate proportional to $\sqrt{t}$. Then the probability of extinction goes to zero, and the probability that the population is larger than some arbitrary value goes to unity. The probability that the population becomes extinct or grows without bound depends upon the expectation of the logarithm of the growth rate. On the other hand, the expected value of population size depends directly on the expectation of the growth rate. Since the expectation of the logarithm of a variate is the logarithm of the *geometric mean*, if the geometric mean of the finite growth rate is less than unity, the population is sure to go to extinction, even if the arithmetic mean of the finite growth rate is greater than unity. Since the geometric mean is always less than the arithmetic mean, this may happen quite easily. The most obvious and usual case would be that in which the environment is usually favorable for growth, but there is an occasional very bad season. For example, suppose that the finite growth rate is 1.1 for 9 years out of 10 but only 0.3 every 10 years. Then $\mu_l = 1.02$, so that the expectation of population size grows at 2 per cent per year, but the geometric mean of the rates is only 0.841, and the population is sure to go to extinction fairly rapidly.

The difference in prediction of population behavior from the arithmetic mean of l and the geometric mean of l arises because of the difference between $E(\ln l)$ and $\ln E(l)$. Expanding $\ln l$ around λ, the mean of l, we get

$$\ln l \cong \ln \lambda + \frac{l - \lambda}{\lambda} - \frac{(l - \lambda)^2}{2\lambda^2}$$

so that

$$E(\ln l) \cong \ln \lambda - \frac{\sigma_l^2}{2\lambda^2}. \tag{8}$$

We see, then, that the expectation of $\ln l$ is smaller than the logarithm of the expectation of l by an amount equal to one half the squared coefficient of variation of l, so that as the l's grow more variable the effect grows greater.

Although the method we have derived for determining the probability that a population lies between two limits is not exact, it will be quite close for any distribution of l that is likely to be encountered, if the l_i are independent. If the l_i have a very strong serial autocorrelation, however, especially as they approach a cyclic process with *very long* cycle time, the convergence of $(\ln l)_t$ to a normal distribution will be very slow, and in the case of a perfectly cyclic environment of any fixed cycle length there is no convergence at all. However, for such environments the rule about the geometric mean governing the eventual population size is even better applicable and is, in fact, exact, rather than a probability statement. After one cycle of length k divided between j years in one environment and $k - j$ years in the other

$$N_k = l_1{}^j l_2{}^{k-j} N_0 \tag{9}$$

or $N_k = (G_l)^k N_0$ where G_l is the geometric mean of the l's.

Finally, we wish to observe that, if we consider a continuous time model, the discrepancy between geometric and arithmetic mean disappears. In a continuous time model we have

$$\frac{dN}{dt} = r(t)N, \tag{10}$$

where $r(t)$ is the value of the intrinsic rate of increase at time t, r being a random variable with mean μ_r and variance σ_r^2.

The solution to equation (10) is simply

$$N(t) = N_0 \exp \int_0^t r(t)dt = N_0 e^{\bar{r}_t t} \qquad (11)$$

so that

$$Pr\{K_1 \leq N_t \leq K_2\} = Pr\left\{\frac{K_1}{N_0} \leq e^{\bar{r}_t t} \leq \frac{K_2}{N_0}\right\} = Pr\left\{\frac{1}{t}\ln\frac{K_1}{N_0} \leq \bar{r} \leq \frac{1}{t}\ln\frac{K_2}{N_0}\right\}$$

which is identical with our previous result, with $\bar{r}_t$ playing the role of $(\overline{\ln l})_t$.

The reader may note a similarity between the problem treated here and the problem of the growth of a repeatedly gambled capital.[3]

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[1] Kendall, D. G., "Stochastic processes and population growth," *J. Roy. Stat. Soc., Ser. B*, **11**, 230–264 (1949).

[2] Bartlett, M. S., *An Introduction to Stochastic Processes* (Cambridge: Cambridge University Press, 1955).

[3] Kelley, J. L., *Bell System Tech. J.*, **35**, 917–926 (1956).