THE EFFECT OF RANDOM VARIATIONS OF DIFFERENT TYPES ON POPULATION GROWTH

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Abstract.—The probability distributions of population size are derived for populations living in randomly varying environments for both density-dependent and density-independent population growth. The effects of random variation in the rate of increase, the carrying capacity, and sampling variation in numbers are examined.

In a preceding paper, Lewontin and Cohen[1] discussed the effect of random variation in finite growth rate on the probability that a population will have a particular size at a given time. That paper considered only a population growing without any effect of population size N on growth rate r. Moreover, it considered only the effect on population growth of random variation in the growth rate itself. In the present paper I shall extend their results in two directions. I shall consider both unlimited population growth and density-dependent growth, and I shall examine the effects of sampling variation in adult numbers due to finite population size, variation in the growth rate r, and random variation in the upper limit to growth where there is density dependence.

Density-Independent Growth.—(a) *Sampling variation in adult numbers:* The deterministic equation for population growth without any density limitation is simply

$$\frac{dN}{dt} = r(t)N, \tag{1}$$

where $r(t)$ is the instantaneous growth rate at time t.

Let us assume that sampling variation occurs only in the death of adults (that is, that the number of zygotes produced is large compared to the adult population and is therefore relatively less subject to random fluctuations). Then if v is the mean viability, the variance of survivorship in a population of size N is $Nv(1-v)$. The growth equation can be rewritten

$$\frac{dN}{dt} = r(t)N + \sqrt{v(1-v)}\,\epsilon(t)\sqrt{N}, \tag{2}$$

where $\epsilon(t)$ is a random variable with mean 0 and variance 1. This case cannot be subsumed under random variation in r, because in the present case the variation is proportional to $\sqrt{N}$. If it were proportional to N, then of course equation (1) could be put in the form given by Lewontin and Cohen.[1] Dividing through by $\sqrt{N}$ and substituting $y = \sqrt{N}$, we obtain

$$\frac{dy}{dt} = {}^{1}/_{2}r(t)y + {}^{1}/_{2}\sqrt{v(1-v)}\,\epsilon(t). \tag{3}$$

Multiplying both sides by $e^{-1/2\int_0^t r(\tau)d\tau}$ and subtracting $1/2 r(t)e^{-1/2\int_0^t r(\tau)d\tau}y$, we obtain

$$e^{-1/2\int_0^t r(\tau)d\tau}\frac{dy}{dt} - 1/2 r(t)e^{-1/2\int r(\tau)d\tau}y = 1/2\sqrt{v(1-v)}e^{-1/2\int_0^t r(\tau)dt}\epsilon(t). \qquad (4)$$

The left-hand side is $\dfrac{d}{dt}\left\{e^{-1/2\int_0^t r(\tau)d\tau}\right\}$ so that, integrating both sides, we have

$$y = y_0 e^{1/2\int_0^t r(\tau)d\tau} + 1/2\sqrt{v(1-v)}\ e^{1/2\int_0^t r(\tau)d\tau}\int_0^t e^{-1/2\int_0^\tau r(s)ds}\epsilon(\tau)d\tau. \qquad (5)$$

Thus each $\epsilon(\tau)$ is weighted according to the total accumulated growth since time τ.

Now let $r(\tau)$ be a constant r. Then y becomes

$$y = y_0 e^{1/2 rt} + 1/2\int_0^t e^{1/2 r(t-\tau)}\epsilon(\tau)d\tau. \qquad (6)$$

The expected value of y is

$$E(y) = y_0 e^{1/2 rt}, \qquad (7)$$

and since the different $\epsilon(\tau)$ are independent, the variance of y is

$$\sigma_y{}^2 = 1/4 v(1-v)\int_0^t e^{r(t-\tau)}d\tau, \qquad (8)$$

or

$$\sigma_y{}^2 = \frac{1}{4r}v(1-v)(e^{rt}-1). \qquad (9)$$

Thus the random fluctuations do not affect the average y. But $N = y^2$, so that from equations (7) and (9)

$$E(N) = N_0 e^{rt} + \frac{1}{4r}v(1-v)[e^{rt}-1]. \qquad (10)$$

Hence $E(N)$ is increased because of random sampling fluctuation when r is positive. Since $\epsilon(s)$ is derived from a binomial process and is roughly normal, y can be approximated by a normal distribution with mean $y_0 e^{1/2 rt}$ and variance $\frac{1}{4r}v(1-v)(e^{rt}-1)$, while N will be distributed as noncentral χ^2 with 1 d.f. This N will be skewed to the left so that there will be a very high probability that $N < E(N)$.

(b) *Variance in r:* It was shown in the previous paper[1] that when the random variation occurs in r, $N(t) = N_0 e^{\int r(t)dt}$. Thus $N(t)$ depends on all past values of r with equal weight. The central limit theorem applies to $\int r(t)dt$, which approaches the normal distribution with mean $\bar{r}t$ and variance $t\sigma_r{}^2$. Thus N/N_0 has a logarithmico-normal distribution

$$f\left(\frac{N}{N_0}\right) = \frac{N_0}{\sigma N\sqrt{2\pi}}\ e^{-\frac{1}{2t\sigma_r{}^2}(\ln\frac{N}{N_0}-\bar{r}t)^2}. \qquad (11)$$

This function has a single peak at $N = N_0 e^{(\bar{r}-\sigma_r{}^2)t}$ so that the mode increases or decreases as $\bar{r}$ is greater or less than $\sigma_r{}^2$.

Density-Dependent Growth.—If there is an upper limit to population growth, equation (1) may be modified to the form $\dfrac{dN}{dt} = r(t)N\left(1 - \dfrac{N}{K}\right)$, where K is the carrying capacity.

Once again we can treat separately random variation in r, random sampling variation, and variation in k.

(a) *Random r:* Here we can separate variables and obtain

$$\frac{dN}{N\left(1 - \dfrac{N}{K}\right)} = r(t)dt, \tag{12}$$

so that

$$\ln \frac{N}{K - N} = \ln \frac{N_0}{K - N_0} + \int r(t)dt \tag{13}$$

$$N(t) = \frac{KN_0 e^{\int_0^t r(s)ds}}{K - N_0 + N_0 e^{\int_0^t r(s)ds}}. \tag{14}$$

Thus if $\bar{r} > 0$, $N(t) \to K$, while if $\bar{r} < 0$, $N(t) \to 0$. Since N is now bounded, we can use the diffusion equation methods described by Kimura[2] to find the limit distribution. In his notation, let $M(N)$ be the mean change in N given N, and $V(N)$ the variance of the change. Then the limit distribution is given by

$$\Phi(N) = \frac{C}{V(N)} e^{2\int \frac{M(N)}{V(N)}dN}, \tag{15}$$

where

$$C = 1 \bigg/ \int_0^\infty \left(\frac{1}{V(N)} \exp 2\int \frac{M(N)}{V(N)} dN\right) dN.$$

In our case, $M(N) = \bar{r}N\left(1 - \dfrac{N}{K}\right)$, and $V(N) = \sigma_r^2 N^2\left(1 - \dfrac{N}{K}\right)^2$. Then

$$\Phi(N) = \frac{C}{\sigma_r^2 N^2\left(1 - \dfrac{N}{K}\right)^2} \exp \frac{2\bar{r}}{\sigma_r^2} \int \frac{dN}{N\left(1 - \dfrac{N}{K}\right)}, \tag{16}$$

which is

$$\Phi(N) = \frac{CN^{2\left(\frac{\bar{r}}{\sigma^2}-1\right)}}{\sigma_r^2}\left(1 - \frac{N}{K}\right)^{-2\left(\frac{\bar{r}}{\sigma^2}+1\right)}. \tag{17}$$

Thus $\Phi(N)$ increases toward infinity as $N \to K$. It will be U-shaped if $\bar{r}/\sigma^2 < 1$. Then there are accumulations of populations near 0 and K. But if $\bar{r} > \sigma^2$, the populations will accumulate at K. This $\Phi(N)$ is, however, an artifact of the model, since as $N \to K$ variation in r has no effect, and a population at K remains

there. With even a small amount of random variation the ascending curve near K will be replaced by a peak.

(b) *Sampling variation:* Here there is no explicit solution to the equation $\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) + \epsilon(t)\sqrt{N}$. However, we can use the diffusion equation method. Now $M(N) = rN\left(1 - \frac{N}{K}\right)$, and $V(N) = \sigma_\epsilon^2 N$. Thus

$$\Phi(N) = \frac{C}{\sigma_\epsilon^2 N} e^{\frac{2rN}{\sigma_\epsilon^2}\left(1 - \frac{N}{2K}\right)}. \tag{18}$$

The slope of $\Phi(N)$ is $\left(-\frac{V'}{V} + \frac{2M}{V}\right)$ so that near $N = 0$ the slope is negative. The maxima and minima are found at the roots of $rN\left(1 - \frac{N}{K}\right) = \frac{1}{2}\sigma_\epsilon^2$. Thus $\Phi(N)$ falls to a minimum at $\frac{K}{2} - \sqrt{\left(\frac{K}{2}\right)^2 - \frac{\sigma_\epsilon^2 K}{2r}}$ and rises to a maximum at $\frac{K}{2} + \sqrt{\left(\frac{K}{2}\right)^2 - \frac{\sigma_\epsilon^2 K}{2r}}$. As the variance increases, the modes approach each other, and when $\sigma_\epsilon^2 = rK$, $\Phi(N)$ is a monotonic descending curve. Here large r ameliorates the effect of σ_ϵ^2 in reducing the modal (and presumably also the mean) population size.

(c) *Random K:* In order to solve equation (12) for random K we make the substitutions $\frac{1}{K(t)} = Q(t)$ and $\frac{1}{y} = N$. Then $-\frac{dy}{y^2} = \frac{r}{y}\left(1 - \frac{Q(t)}{y}\right)dt$ or

$$\frac{dy}{dt} = -ry + rQ(t). \tag{19}$$

This can be solved by multiplying both sides by e^{rt}, adding rye^{rt} to both sides, and integrating directly. This gives

$$y = y_0 e^{-rt} + \int_0^t e^{-r(t-s)} Q(s) ds, \tag{20}$$

so that

$$N = N_0 \Big/ \left\{ e^{-rt} + N_0 \int_0^t \frac{e^{-r(t-s)}}{K(s)} ds \right\}. \tag{21}$$

Thus $N(t)$ depends on a weighted harmonic mean of the K's, with r determining how quickly past values of K are damped out.

The diffusion equation approach is applicable when there is no correlation among the K's. However, it is more convenient to look at the equation for $y = \frac{1}{N}, \frac{dy}{dt} = -ry + rQ(t)$. Now for $r > 0$, y is bounded, and we may use the diffusion approach. Thus $M(y) = -ry + r\bar{Q}$, $V(y) = r^2\sigma_Q^2$, and

$$\Phi(y) = Ce^{-\frac{1}{r\sigma_Q^2}(y^2 - 2\bar{Q}y)}. \tag{22}$$

Thus $1/N$ is distributed normally with mean $\overline{Q}$ and variance $^1/_2\overline{r}\sigma_Q{}^2$, and the harmonic mean of K is the median N.   Clearly, N is reduced by the variance of K, and this effect is increased with increasing r.

In summary, sampling variance increases the expected size of density-independent populations, but with an upper limit K it results in bimodality.   Most populations are either near zero or near a peak between $K/2$ and K.   Variation in r without density dependence does not alter the expected value of $\ln N$, and therefore it increases the expected N.   Variable r, when there is a ceiling to population growth, results in the concentration of population near K if the variance of r is less than the mean, and otherwise gives a bimodal distribution with populations near K and zero.   In either case, N is some function of the integral of $r(t)$ over all past values with equal weight.

When the carrying capacity K itself varies, N is equal to a weighted harmonic mean of the K's, with greater weight given to recent values.   The rate at which the effects of past K's are damped out depends on r, larger r giving rapid damping.

[1] Lewontin, R. C., and D. Cohen, these PROCEEDINGS, **62**, 1056 (1969).

[2] Kimura, M., in *Cold Spring Harbor Symposia on Quantitative Biology*, vol. 20 (1955), pp. 33–53.