

Notes on Lewontin & Cohen (1969)

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Introduction

Lewontin and Cohen (1969) open their paper with the motivating problem of density-dependent population regulation. There is a broad assumption that population growth rates *must* be limited by resources somehow; otherwise, the size of every population would grow without bound. This is actually a strong assumption. Orzack (1993) has argued that, despite appeals to the logical necessity of density-dependent population regulation, such regulation is anything but necessary. He writes, “the necessary inclusion of density-dependent population regulation in models of life history evolution would be appropriate if there were evidence that this process is *always* involved in determining the direction and outcome of life history evolution.” (Orzack, 1993, 87). Orzack suggests that this evidence is lacking in biology. Lewontin and Cohen (1969) were among the first to suggest an alternative to the necessity that density-dependence keeps populations from growing without bound. This alternative is that stochastic factors, unrelated to density, keep populations from growing in perpetuity. Stated simply, Lewontin and Cohen (1969) “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.”

A key goal of this paper is to point out “a peculiarity of multiplicative population growth which is apparently not widely appreciated and which gives rise to some confusion.” More than 50 years later, it turns out, people remain very confused (Peters, 2019; Price and Jones, 2020).

Population Size Has a Lognormal Distribution

Assume that there is an annual organism subject to variable environments which affect its growth rate. Given N_t individuals at time t , the population size in the next interval will be:

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

In general, the population size at time t will be:

$$N_t = N_0 \prod_{i=1}^t \lambda_i$$

where N_0 is the initial population size.

The values of λ_i are random and we can assume they are drawn from some stationary distribution (meaning it doesn’t change with time; importantly, it also doesn’t change with N). We want to ask the question what is the probability that N_t will be greater than some specified value. For example, what is the probability that the population is not extinct, $N_t > 0$? Or what is the probability that the population has increased, $N_t > N_0$? We begin by calculating the expected population size:

$$E(N_t) = N_0 E \left(\prod_{i=1}^t \lambda_i \right) = N_0 \bar{\lambda}^t$$

If $\bar{\lambda} > 1$, then the population grows without bound and if $\bar{\lambda} < 1$, it decays toward extinction. [Lewontin and Cohen \(1969\)](#) note, however, that while the population will grow toward infinity when $\bar{\lambda} > 1$, this doesn't necessarily accurately characterize the typical behavior of the population. They present the simple example of a random variate X which takes on the value of N^2 with probability $1/N$ and the value zero with probability $(N-1)/N$. The expectation of X is therefore

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

Clearly, as N gets large, the expectation grows without bound. However, as N gets large the probability that X takes the value 0 approaches unity. This is very peculiar behavior, but it is characteristic of growth processes.

Consider a more concrete example of a population that has a 50% chance of quadrupling ($\lambda_1 = 4$) or of going extinct ($\lambda_2 = 0$) each generation. The expected growth rate is $\bar{\lambda} = 2$, so after 100 generations, the expected population size exceeds 1×10^{30} (i.e., 2^{100}). However, the probability that the population has gone extinct is $1 - 0.5^{100} = 1 - 7.9^{-31} = 1$! Bruh.

Returning to the problem of the probability that the population falls in a certain range, consider the question of whether the population at time t lies between the values K_1 and K_2 . It is convenient to work with natural logarithms. Note that because the logarithm is a monotone transform, the following statement is true:

$$Pr\{K_1 \leq N_t \leq K_2\} = Pr\{\log K_1 \leq \log N_t \leq \log K_2\}.$$

Substitute $\log N_t = \log N_0 + \sum_{i=1}^t \log \lambda_i$ into the right-hand side of the equation for $\log N_t$. Subtract $\log N_0$ from all the terms in the inequality and divide all the terms by t , yielding

$$Pr\{K_1 \leq N_t \leq K_2\} = Pr\left\{\frac{1}{t} \log \frac{K_1}{N_0} \leq \overline{\log \lambda} \leq \frac{1}{t} \log \frac{K_2}{N_0}\right\}.$$

We assumed that the λ_i values are independent and identically distributed. The Central Limit Theorem (CLT) therefore says that $\overline{\log \lambda}$ is a sample mean and will therefore be approximately normally distributed with mean μ and variance $(1/t)\sigma^2$.

Note that the CLT says that for a series of random samples of size n with sample mean \bar{X} taken from a distribution characterized by mean μ and (finite) variance σ^2 , then the variate

$$Z = \frac{\bar{X}_n - \mu}{\sigma/\sqrt{n}},$$

as $n \rightarrow \infty$ has a standard normal distribution.

Define

$$\tau_1 = \frac{\frac{1}{t} \log \frac{K_1}{N_0} - \mu}{\sigma/\sqrt{t}}$$

and

$$\tau_2 = \frac{\frac{1}{t} \log \frac{K_2}{N_0} - \mu}{\sigma/\sqrt{t}}.$$

These quantities have the form of the standard normal variates, as noted above. The probability that N_t lies between K_1 and K_2 is therefore given by the standard normal probability integral:

$$Pr\{K_1 \leq N_t \leq K_2\} = Pr\{\tau_1 \leq \tau \leq \tau_2\}.$$

Consider the following example. A population lives in an environment characterized by two states that affect the rate of increase. The first has a growth rate of $\lambda_g = 1.55$. The second has a growth rate of $\lambda_b = 0.5$. Assume that both states are equally likely and that the state of the environment is independent of previous states (i.e., there is no correlation in environmental state). The average rate of increase is therefore $\bar{\lambda} = 1.025$, fairly robust positive growth (doubling approximately every 27 years). After 100 years, the population will be 11.8 times as large as the initial size. The average of the logarithms, however, is $\mu = -0.127$ and the variance is $\sigma^2 = 0.32$. We can calculate the probability that the population is larger than its initial size, N_0 by calculating the normal probability integral where we substitute values of N_0 as the lower bound (i.e., K_1 in the equation for τ_1) and ∞ for the upper (i.e., K_2 in the equation for τ_2). The probability that $N_{100} > N_0$ is 0.012.

We can do a quick calculation using the R capabilities to integrate functions with `integrate()` to see what the probability that this population will increase beyond $N = 1$ in 100 years is.

```
mu <- -0.127
sigma2 <- 0.32
t <- 100
tau1 <- ((1/t)*log(1) - mu)/(sqrt(sigma2/t))
integrate(dnorm,tau1,Inf)
```

```
## 0.01238201 with absolute error < 2.7e-06
```

So what does this tell us? The average rate of increase is 1.025, which means that the population should – or seems like it should – grow without bound. In fact, it turns out to be very unlikely that the population will grow at all! Now, instead of considering the average growth rate, let us consider the average of the logarithm of the growth rate – the geometric mean. [Lewontin and Cohen \(1969\)](#) note that for the present case, when $\mu > 0$, the quantity $\log(K_1/N_0) - \mu$ will be less than zero and (remember that $K_1 = N_0$ in this case therefore, $\log(K_1/N_0) = 0$). The value of τ_1 will therefore get increasingly negative at a rate proportional to \sqrt{t} . This means that we are integrating a normal density from some increasingly large negative number to infinity. This integral will be large and will approach unity as τ_1 gets very small. On the other hand, if μ is negative $\log(K_1/N_0) - \mu$ will be positive and τ_1 will increase at a rate proportional to \sqrt{t} . As τ_1 gets larger, the limits to integration get closer and the total probability represented by that integral becomes smaller. In the limit as t gets very large, the probability that the population has increased will approach zero.

Naturally, we can also simulate this scenario quite easily.

```
# play lots of rounds
tmax <- 1000
# initial population size
x0 <- 1
# number of replicates
nmax <- 100
# variable to hold results
```

```

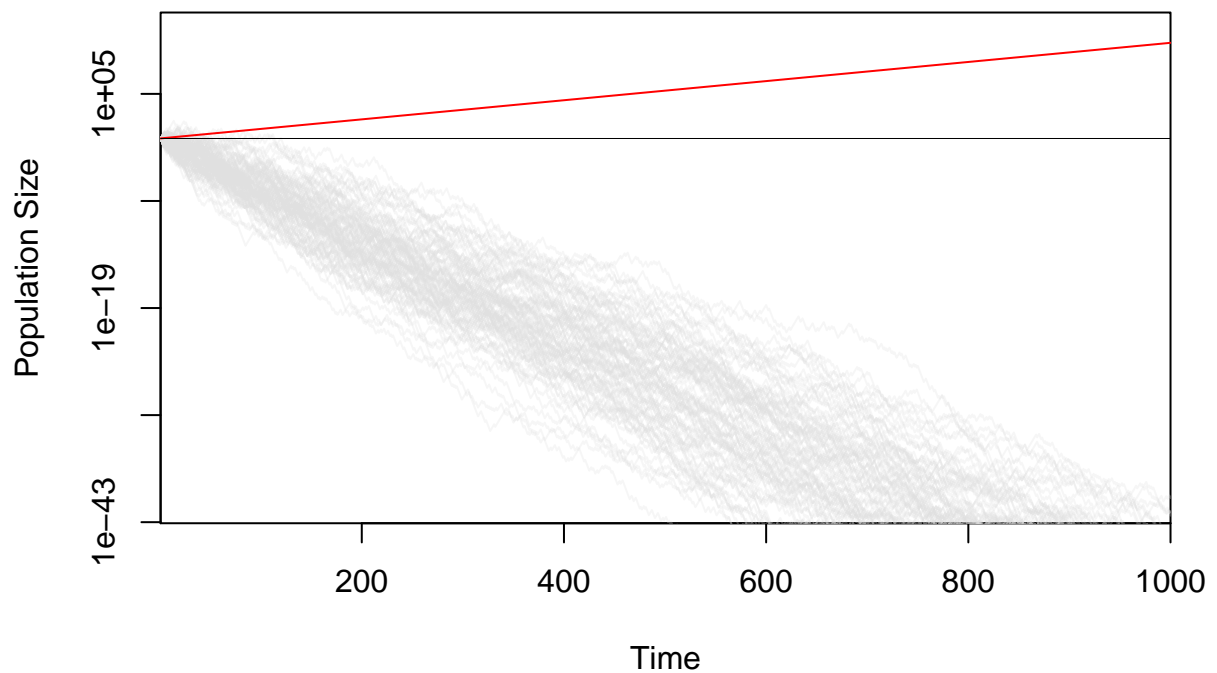
N <- NULL
# vector to hold results of each iteration
tmp <- rep(0,tmax)

for(i in 1:nmax){
  rr <- runif(tmax)
  tmp[1] <- x0
  for(j in 2:tmax){
    tmp[j] <- ifelse(rr[j]<0.5,
                     tmp[j-1]*1.55,
                     tmp[j-1]*0.5)
  }
  N <- cbind(N,tmp)
}

t <- 1:1000

# plot replicates with transparency
plot(1:1000,N[,1], log="y", type="l", xaxs="i",
     col=rgb(224,224,224,alpha=70,maxColorValue = 255),
     xlab="Time", ylab="Population Size",
     ylim=c(1e-41,1e12))
for(i in 2:100) lines(1:1000,N[,i],col=rgb(224,224,224,alpha=70,maxColorValue = 255))
lines(t,1.025^t, col="red")
abline(h=1,lwd=0.5)

```



Every sample run eventually goes to zero in finite time.

The Relationship Between the Arithmetic and Geometric Mean

How is it that the arithmetic mean can be so misleading? We see that it is the geometric mean that really matters in this case. What is the relationship between the arithmetic and geometric mean? Expand λ around its mean value, $\bar{\lambda}$, noting that if $f(\lambda) = \log(\lambda)$, then $f'(\lambda) = 1/\lambda$ and $f''(\lambda) = -1/\lambda^2$:

$$\log(\lambda) = \log(\bar{\lambda}) + \frac{\lambda - \bar{\lambda}}{\bar{\lambda}} - \frac{(\lambda - \bar{\lambda})^2}{2\bar{\lambda}^2} + \dots$$

Now, take expectations of both sides:

$$E(\log(\lambda)) = \log(\bar{\lambda}) - \frac{\sigma^2}{2\bar{\lambda}}$$

The left-hand side of this equation is the geometric mean. This expression makes it clear that the geometric mean will be less than the arithmetic mean (the first term on the right-hand side). The greater the variance in the values of λ_t , the greater the difference between the arithmetic and geometric means will be.

In a commentary on Gillespie (1974), entitled “Hedging One’s Evolutionary Bets,” Slatkin (1974) introduced the term “bet-hedging” to evolutionary biology, referring to adaptive strategies specifically aimed at reducing variance in fitness. There must be a trade-off between the mean and variance for bet-hedging to make sense. Boyce and Perrins (1987) produced what is probably the canonical result in the application of bet-hedging theory, finding that in an environment characterized by high variability in quality from year to year, great tits (*Parus major*) with large clutches suffer disproportionately during bad years. The geometric mean fitness best predicts observed clutch size.

Kelly Probabilities and Life Histories

In the last sentence of their paper, Lewontin and Cohen (1969) write “The reader may note a similarity between the problem treated here and the problem of the growth of a repeatedly gambled capital.” They cite a cryptic paper in the *Bell Systems Technical Journal* (Kelly, 1956). In this paper, Kelly defined what became his eponymous betting strategy, which is “almost surely” guaranteed to outperform any other strategy in the long term.

A Kelly bet is when one doubles the probability of success and then subtracts one. So if the probability of success on a repeated gamble is $p = 0.7$, then the Kelly bet is $(2 \cdot 0.7) - 1 = 0.4$. The best strategy is to bet 40% of your bankroll. It turns out that Kelly bets maximize the geometric mean. Kelly betting has not been used extensively in life history theory, with the exception of Donaldson-Matasci et al. (2008) (who also employ the fitness-set approach of Levins (1968)).

More on this later...

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