

Tuljapurkar and Orzack (1980) Notes

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Video Notes

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Introduction

This is a hard paper. The math is challenging. The style is very different from previous papers. Given how different and difficult it is, it can be hard to know what to do with it. However, this is a mistake. This work is of fundamental importance for population dynamics and life history theory. Since this paper Rather than trying to pull out the key mathematical concept that underlies the overall theoretical statement, as I have done with notes on most previous papers, I will here highlight the key implications of the paper (and subsequent work by these authors).

Population Size is Skewed

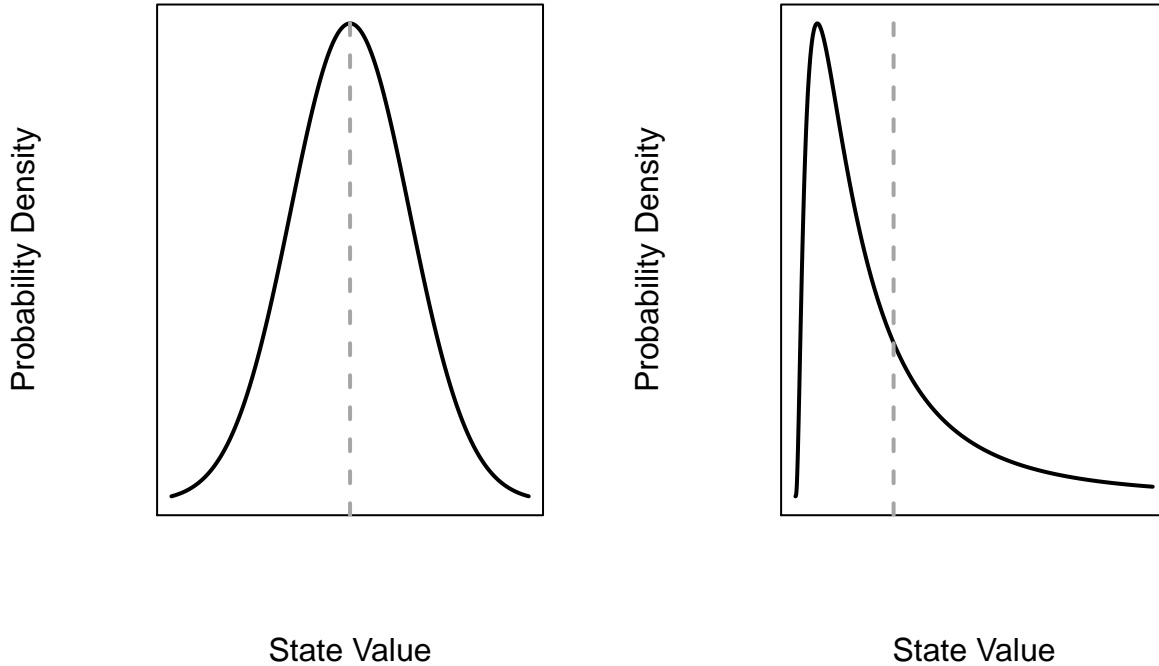
One of the main results is that the logarithm of the cumulative growth rate (which is essentially just population size) is normally distributed. If a random variable $Z = \log(X)$ is normally distributed, this means that X itself is *lognormally* distributed. The lognormal distribution is characterized by substantial skew.

A couple of points about the lognormal distribution: Unlike the normal distribution, its support is on the non-negative real numbers. In other words, it is not defined for negative values. This feature makes it useful for representing biological measurements that cannot be negative, like population size. It is defined by two parameters, μ and σ , which are typically known as the log-mean and log-standard deviation. Both of these parameters are involved in the moments of the distribution (e.g., the mean and variance). This turns out to be generally true; we just get conditioned into thinking about a one-to-one relationships between a probability distribution's parameters and its moments because this is the case with the normal distribution. For the lognormal distribution, the mean is given by $\exp(\mu + \frac{\sigma^2}{2})$ and the variance by $[\exp(\sigma^2) - 1] \exp(2\mu + \sigma^2)$. So a larger log-standard deviation means a greater mean and a larger log-mean means greater variance!

To get a sense of this, we can plot the standard normal and lognormal distributions side-by-side. When we plot `dnorm(x)` for some range of x values without any other arguments, we are plotting the standard normal density of x , meaning that the mean is zero and the standard deviation is one. The equivalent standard lognormal distribution has a log-mean equal to zero and a log-sd equal to one.

```
x <- seq(-3,3,length=1000)
x1 <- seq(0,6,length=1000)
par(mfrow=c(1,2))
plot(x,dnorm(x), type="l", lwd=2,
      axes=FALSE, frame=TRUE,
      xlab="State Value", ylab="Probability Density")
abline(v=0, lty=2, lwd=2, col=grey(0.65))
```

```
plot(x1,dlnorm(x1), type="l", lwd=2,
     axes=FALSE, frame=TRUE,
     xlab="State Value", ylab="Probability Density")
abline(v=exp(0.5), lty=2, lwd=2, col=grey(0.65))
```



For the normal distribution, the highest point in the probability distribution (i.e., the mode) corresponds exactly to the expected value of the distribution. However, this is not the case for the lognormal distribution. The expected value (i.e., the mean) is out in the tail, because means are sensitive to extreme values. The mode is generally much lower than the mean in a skewed distribution like the lognormal. From the standpoint of population dynamics, **this is a very important point**. It means that the arithmetic average does not describe the typical behavior of the population. [Tuljapurkar and Orzack \(1980\)](#) write that “lognormality implies that the modal value of Λ_t is much less than the mean even for small σ^2 .” The mode of a lognormal distribution is given by $\exp(\mu - \sigma^2)$ (which is always less than $\exp(\mu + \frac{\sigma^2}{2})$, the mean).

Note that in [Tuljapurkar and Orzack \(1980\)](#), the log-mean of the lognormal distribution of Λ/t is a and the log-variance is σ^2 (that Λ is divided by t is why they call them “scaled”). This, of course, means that the mode of the distribution of Λ_t is

$$\frac{\Lambda^*}{t} = a - \sigma^2.$$

Be Skeptical of Simple Optima

Many of the papers we’ve read make predictions about optimal life histories. For example, in the simple model of [Schaffer \(1974\)](#), optimal reproductive effort is defined where

$$\frac{dB}{dE} = -\frac{dP}{dE}.$$

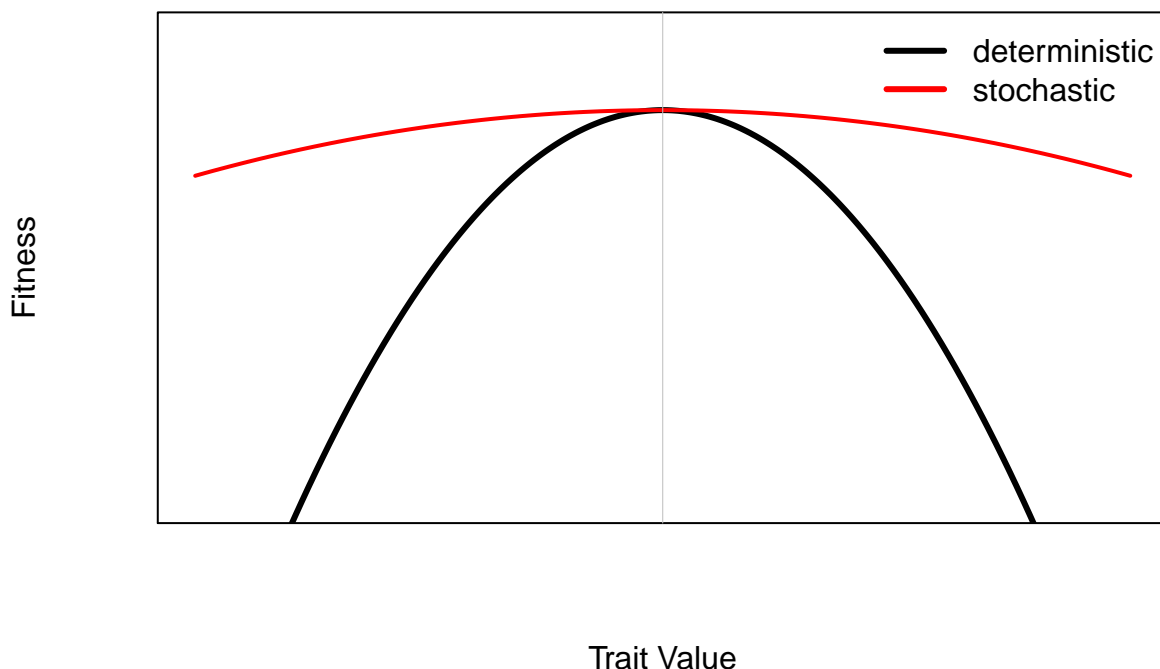
That is, optimal effort is that which perfectly balances the loss in adult survival with the increase in fertility that comes with increased effort.

In a world characterized by variability (i.e., the real world), these very precise tolerances will not hold. Here it is worth a more extended quote from [Tuljapurkar and Orzack \(1980\)](#): “even if the expected total number grows geometrically at a rate $\lambda^* > 1$, so that $\log E[A_t]/t \approx \log \lambda^*$ for large t , it can easily happen that the most probable geometric rate of change, $\log \Lambda^*/t < (\log \lambda^* - \sigma^2)$, is zero or negative. In fact, if one argued that some populations should on the average be stationary in number and took this to mean that $\log \lambda^* = 0$, then $\log \Lambda^*/t < 0$ for *any* environmental variance, however small.” (emphasis in original)

We need to not forget that population growth in variable environments is, well, variable. We cannot say precisely what the population size, growth rate, variance in this growth rate, etc. will be at any given instant. All we can do (hopefully) is express these quantities probabilistically.

One consequence of this reality is that fitness tends to be a flatter function of variable phenotypes than it is in deterministic models. This flatness means that the fitness difference between the optimal phenotype and that of some sub-optimal phenotype might be quite small. We can visualize this as a comparison of two quadratic functions with the same optimum but where one falls away from this optimum much faster.

```
x <- seq(-5,5,length=500)
plot(x, -x^2 + 5, type="l", lwd=3,
      axes=FALSE, frame=TRUE,
      xlim=c(-5,5), ylim=c(-10,8),
      xlab="Trait Value", ylab="Fitness")
lines(x, -0.1*x^2 + 5, lwd=2, col="red")
abline(v=0, col="grey", lwd=0.5)
legend("topright", c("deterministic","stochastic"),
      col=c("black","red"), lwd=3, bty="n")
```



Note Quite the Geometric-Mean Criterion

Lewontin and Cohen (1969) emphasized the geometric mean as the appropriate measure of fitness in a variable environment. This idea was taken up in a big way by Gillespie (1974) (and subsequent publications) and the idea of trading off some mean growth to reduce variance in the growth rate became known as “bet-hedging” following Slatkin’s (1974) accompanying discussion of Gillespie’s paper.

It turns out that the geometric-mean principle does not strictly apply to structured populations. The problem is that there is an interaction between the structure and the environmental variability. Consider the situation where there is a large mortality shock in a human population at time $t = 0$. This means that starting at about $t = 20$, there will be an echo of this mortality crisis because the women who would begin childbearing are not there. There is a correlation between these time periods, even if the environmental variability is itself independent.

The fact that the geometric-mean criterion is not strictly applicable to structured populations does not mean that variance-reducing strategies don’t apply. Quite the contrary. As Tuljapurkar and Orzack (1980) note, “We would like to emphasize the importance of the difference between multivariate fitness measures and univariate ones. Consider two genotypically distinct populations in the same fluctuating environment. Our results suggest that the genotype with the smaller growth rate a can achieve higher fitness as measured by smaller $Q(t)$ by decreasing the variance σ^2 . The decrease in variance can be achieved by increased homeostasis, the development of buffers which reduce variation in response to environment.”

Four Measures of Growth

Tuljapurkar and Orzack (1980) note that there are four quantities that characterize the growth of populations in variable environments:

1. growth of the mean population number, $\log \lambda^*$, $\log \lambda^* = \lim_t (\log E[\Lambda_t]/t)$
2. growth of the logarithm, $\exp(a)$, $a = \lim_t (E[\log \Lambda_t]/t)$
3. the scaled variance of a , $\sigma^2 = \lim_t (\text{Var}[\log \Lambda_t]/t)$
4. growth of modal population, $\log \lambda_m = \lim_t (\log \Lambda^*/t)$

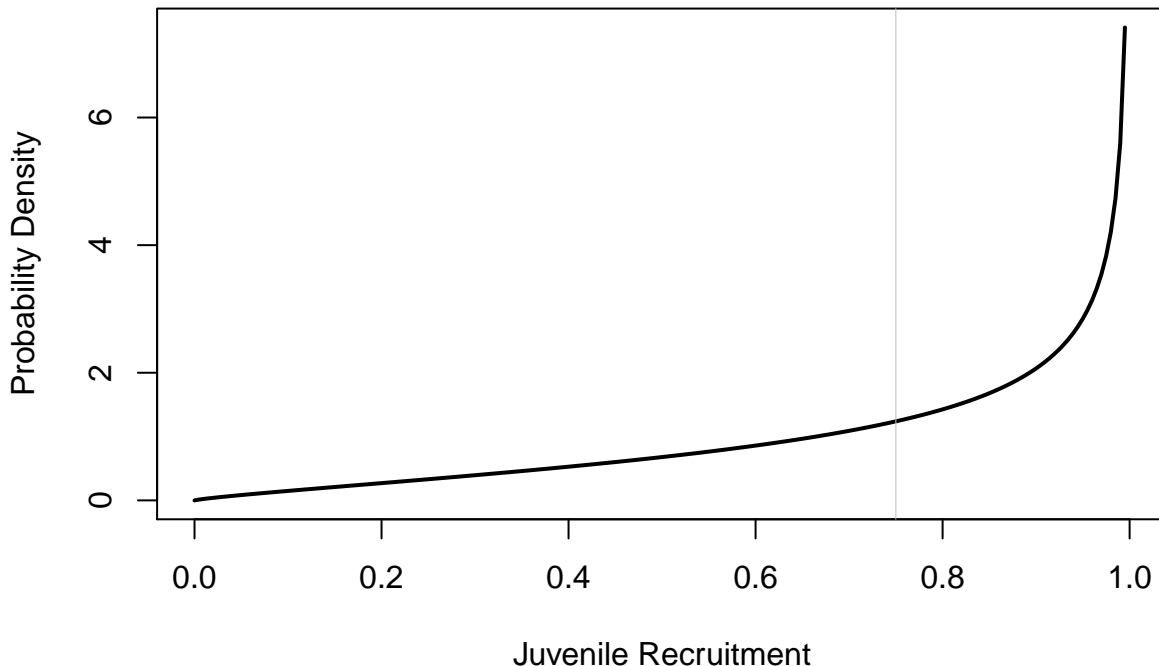
Simulation

Simulation is a powerful tool for understanding the effects of variability on population dynamics. Here, we can do a simple population projection of a Leslie matrix \mathbf{A} where we substitute a random value for juvenile recruitment, a_{21} for the mean value at each time interval. We will draw this random value from a beta distribution, which has support on the interval $[0, 1]$, making it convenient for simulating probabilities like survival.

```
p <- seq(0,1,length=200)
## parameters for beta distribution
a <- 1.8
b <- 0.6
a/(a+b)
```

```
## [1] 0.75
```

```
plot(p, dbeta(p,shape1=a,shape2=b), type="l", lwd=2,
     xlab="Juvenile Recruitment", ylab="Probability Density")
abline(v=a/(a+b), col="grey", lwd=0.5)
```



The beta distribution is very flexible. As we can see from this figure, the parameterization we use produces a highly left-skewed distribution with a mode at one. This suggests that maybe the stochastic growth rate will be greater than the deterministic one since a run of good years could yield quite rapid growth. Maybe.

```
# 2x2 Leslie matrix
A <- matrix( c(0,0.125,0.75,0.95), nr=2, nc=2, byrow=TRUE)
# fitness of deterministic (mean) model
lambda <- eigen(A)$values[1]
imax <- 100 # number of time-steps per sim
jmax <- 100 # number of sims
no <- matrix( c(10,10), nr=2, nc=1)
N <- no
NN <- 20*lambda^(1:101)

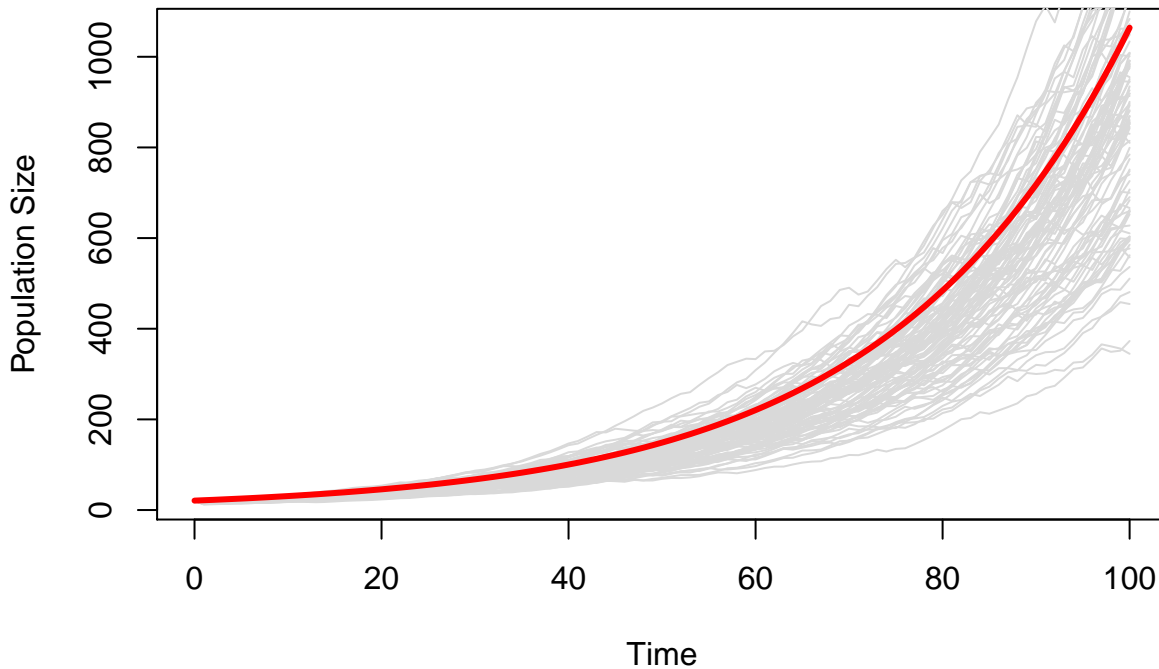
for(j in 1:jmax){
  N <- no
  sss <- rbeta(imax,shape1=a, shape2=b)
  pop <- no
  for(i in 1:imax){
    A[2,1] <- sss[i]
    pop <- A %*% pop
    N <- cbind(N,pop)
  }
}
```

```

NN <- cbind(NN, apply(N, 2, sum))
}

plot(0:100, NN[,1], type="n", xlab="Time", ylab="Population Size")
for(j in 2:(jmax+1)) lines(0:100, NN[,j], col=grey(0.85))
lines(0:100, NN[,1], col="red", lwd=3)

```



When infant survival is variable – even when its mean is identical to the deterministic case, and even when the mode is unity – the growth rate of the population is mostly less than that expected by the mean values.

Sensitivities Matter a Lot

Tuljapurkar went on to develop a great many more results about the dynamics of structured populations in variable environments. A general approximation, known as “Tuljapurkar’s small-noise approximation,” allows us to analytically approximate the logarithmic growth rate a , if the noise is sufficiently small. If we assume that environments are independent (which is a big assumption but it makes the formulae *much* simpler and allows us to make a point here), the small-noise approximation is:

$$a \approx \log \lambda - \frac{(\mathbf{v} \otimes \mathbf{v})^T \mathbf{c}_0 (\mathbf{u} \otimes \mathbf{u})}{2\lambda^2},$$

where, as usual, λ is the multiplicative growth rate (i.e., eigenvalue) of the mean matrix, \mathbf{A} (which has dimensions $k \times k$), \mathbf{v} is the reproductive values and \mathbf{u} the stable age-distribution of \mathbf{A} (i.e., left- and right-eigenvectors). The $k^2 \times k^2$ matrix \mathbf{c}_0 contains the covariances between fluctuations in the different elements of \mathbf{A} .

This big matrix product is essentially a measure of variance of $\log \lambda$. High variance means that the value of a will be smaller relative to the growth rate of the average $\bar{r} = \log \lambda$.

Remember that $\partial\lambda/\partial a_{ij} = v_i u_j$. The small noise approximation has a vector of all the products of \mathbf{v} (i.e., $(v_1 v_1, v_1 v_2, \dots, v_1 v_k, \dots, v_k v_k)$) on the left of this big matrix product and the products of \mathbf{u} (i.e., $(u_1 u_1, u_1 u_2, \dots, u_1 u_k, \dots, u_k u_k)$) on the right (this is what the Kronecker product, \otimes , means for two vectors). What this amounts to is a big multiplication of pairwise sensitivities for each of the $(i, j), (m, n)$ pairs of elements of the Leslie matrix \mathbf{A} .

Indeed, [Tuljapurkar \(1990\)](#) shows that we can re-write the small-noise approximation (again, for independent environments) as

$$a \approx \log \lambda - \frac{1}{2\lambda^2} \sum_{(ij)(mn)} \frac{\partial\lambda}{\partial a_{ij}} \frac{\partial\lambda}{\partial a_{mn}} \text{Cov}(ij, mn),$$

where

$$\text{Cov}(ij, mn) = E(H_t)_{ij}(H_t)_{mn},$$

the expectation of the product of the deviations from the mean values at time t for elements a_{ij} and a_{mn} .

Yikes, that's a lot of math. But we can take a lot away from this. a will always be less than $\bar{r} = \log \lambda$ if there is any variability at all¹. Remember, that big matrix multiplication is basically a variance term. How much smaller it is depends on how variability affects the different elements of \mathbf{A} . Variability that affects elements that have high fitness sensitivities associated with them will increase this variance and reduce a relative to \bar{r} more than traits with low fitness sensitivity. Furthermore, elements that have strong positive covariances with high-sensitivity elements will also increase the variance and make a relatively smaller. Note that if there are matrix elements with *negative* covariances, these can actually reduce the variance.

In terms of life history theory, a really exciting idea that comes out of this approach is that there are going to be life-cycle stages that act as “safe havens” for the organism. We expect selection to push life cycles toward occupying more time in these safe havens, all things being equal. Probably the canonical example of this is a phenomenon known as *diapause* ([Tuljapurkar and Istock, 1993](#)). When a plant sets its seeds, a certain fraction of these will remain ungerminated. These diapausing seeds may germinate the following season or several seasons hence. Hard seeds, particularly if they become buried, are relatively safe. Spending time in this ungerminated state is a way to spread out risk of catastrophic failure.

As a number of authors have noted (summarized in [Bogin, 1997](#)), humans possess a unique life-cycle stage, commonly called *childhood*. This is the period following when an infant is weaned but while it is still nearly completely dependent upon adults for feeding and protection. This period also happens to overlap with the lowest point in the curve of age-specific force of mortality. Is childhood a “safe harbor” in the human life cycle? Maybe.

¹This is technically only true for the case where environments are independent. It is possible that a can be larger than \bar{r} under certain forms of autocorrelation, but these cases are *very* unlikely to apply to environments relevant for human life histories. Among other things, it requires there be pretty strong negative covariances between traits. In part because of human requirements for parental care, our life-cycle transitions are probably all pretty strongly positively correlated with each other. A bad year for juvenile survival is probably a bad year for adult survival is probably a bad year for fertility.

References

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