

Notes on Charnov & Schaffer (1973)

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Videos

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1 Introduction

At the time this paper was published, Charnov and Schaffer were recently-graduated students of two of the great evolutionary ecologists of the 20th century. Charnov worked with Gordan Orians at the University of Washington, while Schaffer did his graduate work with Robert MacArthur at the University of Pennsylvania. As indicated in the footnote to this brief note in *American Naturalist*, the two submitted very similar papers nearly simultaneously and the editors got them to combine their efforts in a single paper. Within a year, Schaffer would publish two more fundamental papers in life history theory ([Schaffer 1974a,b](#)), while Charnov would move on to write a remarkable series of germinal papers in the foraging theory (e.g., [Charnov 1976](#)) and the theory of sex allocation (e.g., [Charnov 1982](#)). He would later return to the study of life histories ([Charnov 1991](#)), producing the theoretical framework probably most favored by evolutionary anthropologists (which we will discuss in the last week of class).

The solution to the paradox turns out to be a simple matter of some algebra. Incorporating juvenile and adult mortality fundamentally changes Cole's result. This said, there is a somewhat more involved solution (that was actually anticipated by Cole if you read his long paper past the paradox). The mechanics of this will look familiar because they involve identifying a geometric series from a (simplified) characteristic equation.

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2 Resolution to Cole's Paradox

2.1 Fixed Age at First Reproduction

Charnov & Schaffer resolved Cole's Paradox by noting that it follows from the rather outrageous assumption of no mortality – either juvenile or adult. Define juvenile survival S_j and assume that S_a is no longer fixed at $S_a = 1$, but that it is free to vary.

The dynamics of the semelparous life history are given simply by

$$N_{t+1} = S_j b_s N_t.$$

Fitness for the semelparous life history is clearly given by:

$$\lambda_s = S_j b_s.$$

For the iteroparous life history, the size of the population at the next time step will be given, like the semelparous life history, by the product of fertility and juvenile recruitment, but also by the fraction of adults surviving to the next time step:

$$N_{t+1} = S_j b_i N_t + S_a N_t = \lambda_s N_t,$$

making fitness for the iteroparous life history

$$\lambda_i = S_j b_i + S_a$$

Set the two fitnesses equal to each other and solve for b_s , the semelparous clutch size that makes the semelparous and iteroparous fitnesses equal.

$$b_s = b_i + \frac{S_a}{S_j}. \tag{1}$$

We see that it is now the ratio of adult to juvenile mortality that will determine the relative benefit of iteroparity. If S_a is high relative to S_j , the semelparous clutch size will have to be much greater than the iteroparous clutch size and iteroparity will be more likely.

This result actually anticipates [Schaffer \(1974b\)](#). What does a large value of S_a/S_j mean? It means that the present value of adults is greater than that of juveniles. If you can't count on a juvenile surviving to adulthood, it's best to hold back on reproductive effort.

2.2 Variable Age at First Reproduction

This will look really familiar, because it involves the same techniques that [Cole \(1954\)](#) used. First, remember the identity for an infinite geometric series:

$$\sum_{k=0}^{\infty} ar^k = \frac{a}{1-r}$$

Note that $r = r^{k+1}/r^k$ is a constant ratio. Also note that for $k = 0$, the first term in this series is $r^0 = 1$ (if it isn't, the series has a more complicated closed form).

2.2.1 Iteroparous Life History

Without much ceremony, [Charnov and Schaffer \(1973\)](#) note the the characteristic equation for the iteroparous life history is

$$1 = b_i S_\alpha \left[\frac{1}{\lambda^\alpha} + \frac{P}{\lambda^{\alpha+1}} + \frac{P^2}{\lambda^{\alpha+2}} + \cdots \right], \quad (2)$$

where b_i is the (constant) annual fertility of the iteroparous life history, α is age at first reproduction, S_α is the fraction of offspring surviving to age α (i.e., the recruitment fraction), λ is the multiplicative rate of increase, and P is the annual survival probability of adults. Note that I have changed the notation somewhat from the usage in [Charnov and Schaffer \(1973\)](#) in an attempt at greater consistency.

Multiply both sides by $\lambda^\alpha/\lambda^\alpha$ (which, of course, is the same as multiplying by 1):

$$1 = \frac{b_i S_\alpha}{\lambda^\alpha} \left[1 + \frac{P}{\lambda} + \frac{P^2}{\lambda^2} + \frac{P^3}{\lambda^3} + \cdots \right].$$

That's very cool because now we have the constant ratio we need for the geometric series: $r = P/\lambda$. This allows us to write the characteristic equation as

$$1 = \frac{b_i S_\alpha}{\lambda^\alpha} \left[\frac{1}{1 - P/\lambda} \right]. \quad (3)$$

2.2.2 Semelparous Life History

The characteristic equation for the semelparous life history is simply equation 3 but without the geometric-series term in the square brackets (and with b_s rather than b_i for litter size):

$$1 = \frac{b_s S_\alpha}{\lambda^\alpha},$$

which clearly indicates that $\lambda^\alpha = b_s S_\alpha$.

Now substitute this into equation 3:

$$1 = \frac{b_i S_\alpha}{b_s S_\alpha} \left[\frac{1}{1 - P/\lambda} \right].$$

Rearranging, we arrive at the relationship:

$$\frac{b_i}{b_s} = 1 - P/\lambda. \quad (4)$$

So what does this mean? For a fixed value of λ (as with Cole, we are looking for the litter sizes that equalize fitness), what will the ratio of iteroparous-to-semelparous litter size be? Note that $1 \geq P/\lambda \geq 0$ since P is a probability and $\lambda \geq 1$ (since if the long-term growth rate of a life history is less than one, that life history goes extinct). The closer that P/λ is to unity, the more that iteroparity is favored since the ratio b_i/b_s is very low. This means that the litter size of the iteroparous life history can be a small fraction of that of the semelparous life history and still equal its fitness.

Consider quite reasonable values for a human population of $P = 0.98$ and $\lambda = 1.02$. This makes $b_i/b_s = 0.039$. The litter size of the semelparous life history has to be 25 times greater than that of the iteroparous life history to equal its fitness. Now, the greater an organism's growth potential is (i.e., Cole's r_{max} , remembering that $\lambda = e^r$) and the lower its annual survival probability, the easier it will be for the semelparous life history to match the fitness of the iteroparous life history.

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