

Notes on Charnov (1991)

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Videos

- [Derivation of Mortality Scaling Law](#)
- [Derivation of Optimal \$\alpha\$](#)

1 Charnov's Production Model

According to [Charnov \(1991\)](#), the causal chain for mammalian life histories can be summarized as follows (see figure 1):

- Adult mortality is determined by the environment – i.e., is “extrinsic”
- Maturity occurs at an age that maximizes lifetime reproductive success (e.g. R_0 , the net reproduction number)
- At maturity, all energy that would otherwise go to growth (personal production) is shunted to offspring production
- The amount of energy available for offspring production is determined by body size
- “In the long term, *the birth rate must equal the death rate* in natural populations” [Charnov \(1993, 89\)](#).
- Population stationarity maintained by density-dependent juvenile mortality

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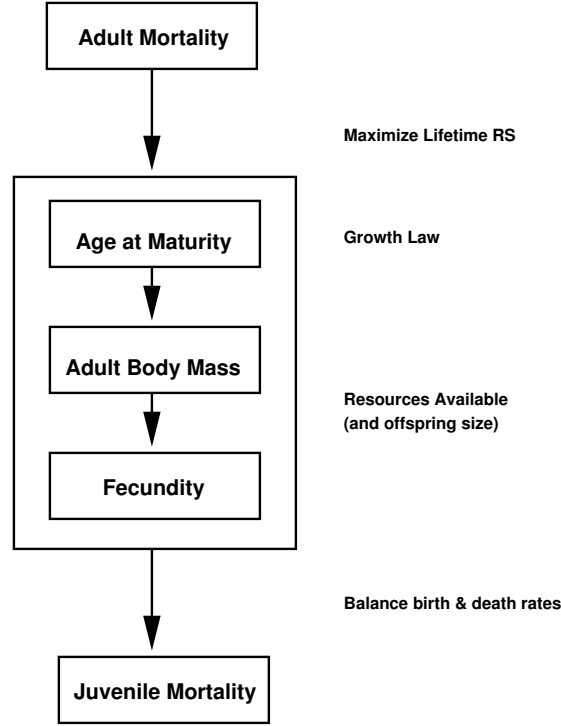


Figure 1: Graphical depiction of the flow of causality in Charnov's model for mammalian life histories.

1.1 Growth Allometry

The model begins with growth allometry. The instantaneous growth rate is a power function of current size:

$$\frac{dW}{dT} = AW^a \quad (1)$$

To solve equation 1, separate the variables and integrate between 0 (age of weaning when production shifts from the mother to the offspring) and T . The integration constant will be $W(0)$, size at weaning

$$\frac{1}{1-a} W^{1-a} - \frac{1}{1-a} W(0)^{1-a} = At$$

Charnov assumes that $a = 0.75$, so we will use that value from now on.

$$W(T)^{0.25} = 0.25AT + W(0)^{0.25} \quad (2)$$

Let α denote age at first reproduction (AFR), and define $\delta = W(0)/W(\alpha)$, the ratio of weight at α to weaning weight. Solve equation 2 for $W(\alpha)$:

$$W(\alpha)^{0.25} = \frac{0.25\alpha A}{(1-\delta)^{0.25}}.$$

AFR scales $\propto W^{0.25}$, which is empirically about right.

1.2 Allometry of Fertility

Let b denote the ratio of average clutch size (of females) to the expected inter-clutch interval – i.e., b is the fertility rate. Assume it takes $(C/2)W(0)$ units of energy to raise an offspring of size $W(0)$ at independence from its mother. C represents units of potential parental growth diverted to offspring production. Let τ be the time required to rear one offspring to independence: $1/2\tau = b$. In τ time units, the parent can deliver $A\tau W(\alpha)^{0.75}$ units of energy to the offspring. To get b , set

$$A\tau W(\alpha)^{0.75} = (C/2)W(0)$$

Again, write $\delta = W(0)/W(\alpha)$, and solve for $1/2\tau$. This involves dividing through by τ and C and then multiplying the left side of the equation by $W(\alpha)/W(\alpha)$.

$$b = \frac{A}{C\delta} W(\alpha)^{-0.25} \quad (3)$$

Annual fertility will scale with body mass to the -0.25 power – again, about right if $a = 0.75$. Of course, this only applies to taxa with similar A , δ , and C values.

1.3 Age at Maturity

Assume high, but declining juvenile mortality which reaches an asymptote just prior to AFR. Denote the instantaneous age-specific juvenile mortality rate $z(x)$. The fraction of a cohort still surviving at age α is thus

$$l(\alpha) = e^{-\int_0^\alpha z(x)dx} = e^{-z\alpha}.$$

where z is the mean of juvenile mortality.

Assume population stationarity, that is, $r = b - d = 0$. An appropriate fitness measure in a stationary population is the net reproductive number R_0 . Our usual definition of R_0 is the sum of the net maternity function. However, we can also write R_0 as the product of some averages. Specifically,

$$R_0 = l(\alpha)bE(\alpha), \quad (4)$$

where $E(\alpha)$ is the expectation of further life at AFR. Assume constant instantaneous adult mortality rate, M – this implies

$$E(\alpha) = \frac{1}{M}.$$

A useful way to parse this is to think of R_0 as the product of survival to age at maturity $l(\alpha)$ and the expected number of offspring produced in a female's lifetime $bE(\alpha)$. This latter quantity is essentially the gross reproduction rate.

The optimal value of α can be found by differentiating $\log R_0$ in equation 4 with respect to α and setting equal to zero. Note that Charnov employs a key assumption here that juvenile

mortality bottoms out *just before* α . Because of this, only b and $l(\alpha)$ are functions of α in the equation for R_0 and the derivative $\partial E(\alpha)/\partial\alpha = 0$. A little algebra shows that

$$\frac{\partial \log b}{\partial \alpha} = z(\alpha) = M, \quad (5)$$

where $z(\alpha)$ is the mortality rate at AFR. When an individual reaches age α , their mortality is no longer governed by the conditions of juvenility (i.e., determined on average by the mother). It follows that $z(\alpha) = M$, that is, the mortality of juveniles around age α is simply equal to the average adult mortality rate M .

Offspring production is assumed to simply be diversion of energy into the growth of another so

$$\frac{\partial \log b}{\partial \alpha} = \frac{\partial \log dW/dT}{\partial \alpha}. \quad (6)$$

From equation 3, we set

$$b = \frac{AW^{0.75}}{CW(0)}.$$

From the relationship in equation 6, we can differentiate either this or equation 1 (they have the same derivative). Using the production equation, setting $a = 0.75$, as Charnov does, we get

$$\frac{d}{d\alpha} \log \left[\frac{dW}{dt} \right] = \frac{0.75W'(\alpha)}{W(\alpha)}.$$

Note that $W'(\alpha) = AW(\alpha)^{0.75}$ by definition. Remember also that the ESS condition states that age of first reproduction is set where the marginal decrease in the log of annual fertility is exactly balanced by adult mortality (equation 5). This leads directly to the allometric equation for M , the adult instantaneous mortality rate.

$$M = 0.75AW(\alpha)^{-0.25}. \quad (7)$$

Charnov can be a bit fast-and-loose with notation. In this case, he's a little loose with the time-dependence of $W(t)$. Just remember, what we care about is adult body mass, so the relevant $W(t)$ to include in equation 1 when we do the substitution to get to this important result is $W(\alpha)$.

Note that there is another big (and somewhat cryptic) assumption leading to equation 7. The substitution for b is not, in fact, the same as the relationship for b in equation 3. The goal was to derive $\partial \log b/\partial\alpha$ in the absence of a change on $W(0)$ with α . Evidence that Charnov cites to support this is that the allometry of total offspring biomass with respect to adult mass scales to a power very similar to a (0.69 vs. the predicted 0.75). The causal connection of M on $W(\alpha)$ is via natural selection on age at maturity. Adult body mass is *caused* by adult mortality rates and not the other way around.

1.4 Juvenile Mortality

As above, let z be the average instantaneous juvenile mortality rate so that

$$e^{-\int_0^\alpha z(x)dx} = e^{-z\alpha}.$$

By the population stationarity assumption $R_0 = 1$. Re-write the relationship for R_0 as

$$R_0 = \frac{be^{-\bar{z}\alpha}}{M}.$$

Now plug in the values for M , b , and α already derived, yielding

$$\bar{z} = \left[\log \left(\frac{1}{C\delta A} \right) \right] \left(\frac{0.25A}{1 - \delta^{0.25}} \right) W(\alpha)^{-0.25} \quad (8)$$

Average immature mortality will scale to a -0.25 power of adult body mass. That is, in species with similar C , δ and A values.

1.5 Dimensionless Numbers

We can combine the values of α , M , b , and \bar{z} to form dimensionless combinations of parameters. In Charnov's formalism, these values take on fixed values for taxa with the same values of C and δ . A does not enter the equations. The intuition behind this loss of A in the dimensionless numbers is that all of the life history traits derive from physiological production. A will thus appear in everything and ends up canceling out.

There are three important dimensionless numbers in the Charnov formalism. All of these relate age at maturity α to the other demographic quantities in the life history, namely, juvenile mortality z , adult mortality M , and fertility b .

$$\alpha z = -\log(0.75C\delta) \quad (9)$$

$$\alpha M = 3(1 - \delta^{0.25}) \quad (10)$$

$$\alpha b = 4 \left(\frac{1 - \delta^{0.25}}{C\delta} \right) \quad (11)$$

What do dimensionless numbers tell us? It turns out that dimensionless numbers are exceptionally important in engineering and related disciplines.

Let's look at equation 10 first. This equation says that for species with similar δ values, the quantity αM will be constant. Remember that we assumed that lifespan was exponentially distributed so that $E(\alpha) = M^{-1}$. Thus αM is really the ratio of age at maturity to adult expected lifespan. Organisms with late ages at first birth are expected to have long lifespans. [Hawkes et al. \(1998\)](#) suggest that all the great apes share similar values of αM , with an approximate value of $\alpha M = 0.45$. Although the human value of α is nearly twice that of the other apes at 14.5¹,

¹Remember that α is only counted from age at weaning, so we need to subtract the weaning age of around 3 from the age at maturity of around 18 to get the human value for α . Clearly, there is much variation in these values.

Parameter	Description
$W(T)$	Body mass at age T
α	Age at first reproduction (=maturity)
b	Annual fertility rate in daughters
M	Annual adult instantaneous mortality rate ($1/M = E(\alpha)$)
δ	Ratio of weaning weight to adult weight $W(0)/W(\alpha)$
A	Production constant
C	Offspring metabolic cost
τ	Time to grow an offspring to independence (i.e., weaning age)
z	Average instantaneous juvenile mortality rate
R_0	Net reproduction number – fitness measure on a stationary population
a	Scaling exponent on growth allometry – nearly always $a = 0.75$

Table 1: Parameters of the Charnov model.

the average adult (i.e., post- α) lifespan is also nearly twice as large. This invariance of αM is a strong prediction.

The product αb is also predicted to be invariant for species with similar δ and C values. Thus species with late ages at first reproduction will have low fertility and vice-versa. Interestingly, [Hawkes et al. \(1998\)](#) suggest that the human value of αb is more than twice that of the other great apes. These authors attribute this discrepancy to the excess production which is shunted to offspring production which is allowed by intergenerational transfers. In essence, older women, by investing in their grandchildren’s growth and development, increase their daughters’ fertility. This follows from the logic of the Charnov model that growth and fertility are both processes that divert excess production into the production of new tissue.

1.6 Problems with the Charnov Model

There are two crucial assumptions in the Charnov model. The first is that the whole life history is shaped by external mortality of adults. The second is that the population is stationary, making R_0 the appropriate fitness measure.

On R_0 When we seek the optimal age of first reproduction, we take the partial derivative of R_0 with respect to α , giving us the relationship:

$$\partial b / \partial \alpha = Z(\alpha) = M.$$

But what if the population is not stationary? When the population is not stationary $r \neq 0$ and R_0 is no longer an appropriate fitness measure. This arises because timing of reproduction matters in the non-stationary population.

On Adult Mortality Analysis of the fitness sensitivities of the age-structured projection matrix shows that the life cycle transitions to which fitness is most sensitive are pre-reproductive mortality. [Hamilton \(1966\)](#) classically showed that the force of selection on survival declines

monotonically with age. The structure of the projection matrix also means that fertility transitions will have lower sensitivities than survival transitions.

Given the strength of selection acting on pre-reproductive survival, it is difficult to imagine how adult external mortality is the only force shaping the evolution of mammalian life histories. In fact, in the paper in which he resolved Cole’s paradox ([Charnov and Schaffer 1973](#)), Charnov explicitly envisions juvenile and adult mortality varying independently. Indeed, it is their ratio that determines optimal reproductive effort.

In the [Charnov \(1991\)](#) model for mammalian life histories, juvenile mortality is relegated to demographic book-keeping. Density-dependent mortality is assumed to act on juveniles in such a manner as to maintain a stationary population.

And remember from our discussion of [Tuljapurkar and Orzack \(1980\)](#) and [Lewontin and Cohen \(1969\)](#) that populations in a variable environment with long-run average growth rates of $r > 0$ can nonetheless have quite high probabilities of extinction. Populations in variable environments can thus be regulated even in the absence of density-related feedback. The fate of a novel mutation in such a population still depends on the average growth rate r , so analyzing the population without taking account of the expected population growth (i.e., by assuming stationarity) can yield misleading results.

Despite these shortcomings, the Charnov model for mammalian life histories has a number of desirable features. In particular, it is nice that the model binds together growth, metabolic productivity, and demography in a single package. Is it possible to extend the Charnov model to the case of non-stationary populations? It is. This is something that Mike Price did in his dissertation, but that’s for another time.

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