Notes on Cole (1954)

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Videos

1. Derivation of Cole's r_{max}

2. Cole's Paradox

3. Calculating r_{max} in `R`

1 Introduction

Cole introduces two major concepts. First, we can deduce the demographic consequences of changes in life-history characteristics like average litter size or age at first reproduction. Second, we can gain insight into the adaptive nature of life histories by comparing them across taxa. It's hard to imagine, but prior to Cole (1954), the idea of comparing life histories to gain insight into adaptation was not seriously considered. In concluding his paper, Cole (1954, 135) noted that "the writer [i.e., Cole] believes that life-history characteristics may also be profitably examined in this way."

It is very important to bear in mind how laborious it was to solve complex equations in the middle part of the 20th century and before. It is therefore reasonable that there hadn't been much previous work exploring the demographic consequences of different life-history variables. It's harder to explain why comparative biologists would not look at life histories the way they looked at, say, morphology.

The major obstacle to linking life-history traits to demographic patterns is the lack of models of demographic schedules. This actually remains a challenge. For example, we frequently assume constant mortality rates (at least during adulthood), implying exponentially-distributed lifespans. As we saw in the discussion of Coale (1957), the assumption of strictly constant addition of mortality has no effect on age structure (and this translates into selection). This suggests

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that the assumption of constant mortality could be problematic. Parametric mortality models are hard to work with (they are notoriously difficult to estimate statistically) and often miss important features of specific mortality schedules. Sixty-six years later, demographic models remain a challenge.

While his derivation of a simple formula for calculating what has become known as r_{max} has certainly been useful, the real lasting value of Cole's paper, at least from the standpoint of life history theory, is drawing attention to the adaptive value of reproductive effort. The optimal allocation of reproductive effort is arguably the central question in life history theory (Schaffer (1983) refers to this as "the general life history problem"). In his landmark book, Fisher laid out the charge of life history theory "It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and the environment would render profitable the diversion of a greater or lesser share of the available resources toward reproduction."

While Fisher may be famous for his initial musing on the topic, Cole really framed at least the next 30 years of research into life histories. Ultimately, the question of semelparity vs. iteroparity is one of reproductive effort, as Gadgil and Bossert (1970) would later clarify. It is in this way the Cole (1954) really inaugurates the serious study of life history theory.

1.1   Cole's r_{max}

The video to accompany this derivation is here.

For Cole (1954), we will switch from the continuous-time framework for the characteristic equation that we discussed in reading Coale (1957) to a discrete form. Demographic data are typically measured for discrete chunks of time (e.g., years, quinquennia), so there is much to be said for a discrete-time formulation of the characteristic equation. We'll see later that there is actually a better way of specifying this using matrices, but we'll go with the more standard form of the discrete Euler-Lotka equation here:

$$1 = \sum_{x=\alpha}^{x=\omega} e^{-rx} l_x m_x, \tag{1}$$

where we change the notation for discrete variables: l_x is the survival to age x and m_x is the age specific fertility. That is, discrete variables get subscripted by their time index while continuous variables use function notation – l_x vs. $l(x)$.

As Cole goes from the characteristic equation (his eqn 19) to the key equation of the paper (i.e., r_{max}, his eqn 21), he writes: "In the present paper we are concerned primarily with the limiting case of *potential* meaning of life-history phenomena. Consequently the writer has chosen to deal with survivorship curves of the physiological type and thus to investigate the ultimate effects of life-history phenomena for a species which is able to reduce mortality during the reproductive part of the life span to a negligible value."

In other words, he assumes away mortality! This is one of two major times that he does this in the paper.

Cole's eqn. (19) is:

$$e^{r\alpha} = \psi_\alpha + \psi_{\alpha+1}e^{-r} + \psi_{\alpha+2}e^{-2r} + \ldots + \psi_\omega e^{-r(\omega-\alpha)}$$

where $\psi_x = l_x m_x$ (my notation).

Where does this come from? Start with the characteristic equation, eqn. 1. Multiply both sides of the equation by $e^{r\alpha}$.

What does that do? Suppose there are only two age classes, α and $\alpha + 1$. The characteristic equation is

$$1 = e^{-r\alpha}\psi_\alpha + e^{-r(\alpha+1)}\psi_{\alpha+1}$$

Now multiply both sides by $e^{r\alpha}$:

$$e^{r\alpha} = e^{-r\alpha}e^{r\alpha}\psi_\alpha + e^{-r(\alpha+1)}e^{r\alpha}\psi_{\alpha+1}$$

Using the rules for exponentials, we are left with

$$e^{r\alpha} = \psi_\alpha + e^{-r}\psi_{\alpha+1}.$$

Returning to the full equation and assuming a mean litter size for each adult age is b and no mortality, the characteristic equation becomes:

$$e^{r\alpha} = b(1 + e^{-r} + e^{-2r} + \ldots + e^{-r(\omega-\alpha)}).$$

The expression in parentheses is a finite geometric series, for which we know the closed-form solution:

$$\frac{1 - e^{-rn}}{1 - e^{-r}},$$

where $n = \omega - \alpha + 1$.

There is some slightly hairy algebra to get to Cole's classic formula:

$$e^{r\alpha} = b\left(\frac{1 - e^{-rn}}{1 - e^{-r}}\right)$$

Divide both sides by b and then multiply both sides by $1 - e^{-r}$:

$$\frac{e^{r\alpha}}{b} - \frac{e^{r\alpha}e^{-r}}{b} = 1 - e^{-rn}.$$

Multiply by b and divide by $e^{r\alpha}$ and simplify the resulting exponentials:

$$1 = be^{-r\alpha} - be^{-r(\alpha+n)} + e^{-r}.$$

Then we just re-order the terms to get Cole's famous equation:

$$1 = e^{-r} + be^{-r\alpha} - be^{-r(n+\alpha)}. \tag{2}$$

This is the equation the defines what became known as Cole's r_{max}. It represents the best-case scenario for the growth of a population (since it assumes no mortality).

1.1.1 Extending Cole

As Slade et al. (1998) note, we can just as easily assume that mortality is non-trivial. Continue to assume that mortality is constant within adults. Changes in age-specific mortality for pre-reproductives do not matter – all we need is the fraction of newborn individuals who survive to breeding age, f. Assume that all adults have a constant survival probability p. The fraction alive at age $x > \alpha$ is thus $fp^{x-\alpha}$.

The generalization of Cole's r_{max} equation that Slade et al. derive is:

$$1 = p\,e^{-r} + f\,b\,e^{-r\alpha} - f\,b\,p^{n+1}e^{-r(n+\alpha)}.$$

This is actually pretty handy because we often know the ballpark values for these different life history traits, even if we don't have detailed age-specific schedules.

1.2 Cole's Paradox

An accompanying video is here.

The real contribution of Cole's paper to life history *theory* is a result that became known as *Cole's Paradox*. The paradoxical nature of his result arises from the observation that nature is replete with iteroparous organisms despite the fact that Cole's analysis suggests that semelparous organisms should be able to out-compete iteroparous ones pretty easily.

Note that the rate of increase, r, is given by the difference of the natural logarithms of population size in two consecutive time periods. Furthermore, by the renewal reasoning of populations $N_{t+1} = bN_t$. Let the fitness of the semelparous life history be r_S and the average litter size be b_S. We thus have:

$$r_S = \log\left[\frac{N_{t+1}}{N_t}\right] = \log\left[\frac{b_S N_t}{N_t}\right] = \log(b_S).$$

Now let fitness for the iteroparous case be r_I. We use equation 2 with $\alpha = 1$ and $\omega = \infty$. This latter assumption means that the last term in equation 2 is zero, leaving:

$$
\begin{aligned}
1 &= e^{-r} + be^{-r} &&(3)\\
1 &= e^{-r}(1+b)\\
0 &= -r + \log(b+1)\\
r_I &= \log(b+1)
\end{aligned}
$$

What does this tell us? In order for life history that reproduces once to equal the fitness of an infinitely-long-lived life history with average litter size b, the semelparous life history only needs to add a single offspring to the average litter: $b_S = b + 1$. Energetically, it seems like a fairly small ask to add a single offspring to a litter when compared to the investment it would take to live forever. Thus, the paradox. If it's that easy for a semelparous life history to match the fitness of an immortal iteroparous one, why do we see so many iteroparous organisms? Cole writes succinctly, "For an annual species, the absolute gain in intrinsic population growth which

could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size."

Let us not forget that Cole assumed away all mortality. This turns out to be problematic and makes this statement simply not true. As Stephen Stearns wryly noted, it's usually a good idea to consider mortality when trying to understand the evolution of life histories.

Cole's Paradox is clearly of relevance for thinking about humans since we are highly iteroparous (at least as far as animals go).

References

Coale, A. J. (1957). How the Age Distribution of a Human Population is Determined. In D. Smith and N. Keyfitz (Eds.), *Mathematical Demography: Selected Papers*, pp. 167–172. Berlin, Heidelberg: Springer Berlin Heidelberg.

Cole, L. C. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology 29*(2), 103–137.

Gadgil, M. and W. H. Bossert (1970). Life historical consequences of natural selection. *American Naturalist 104*, 1–24.

Schaffer, W. (1983). The application of optimal control theory to the general life history problem. *American Naturalist 121*, 418–431.

Slade, N., R. Gomulkiewicz, and H. Alexander (1998). Alternatives to Robinson and Redford's method of assessing overharvest from incomplete demographic data. *Conservation Biology 12*(1), 148–155.