MAXIMIZING FITNESS IN POPULATIONS: A MATHEMATICAL REPRESENTATION

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BACKGROUND

Biologists have long been interested in evolving populations and how their growth is affected by the environment. Population growth, or death, is seemingly based on the idea of natural selection. A mathematical representation of population growth can help explain and predict growth patterns among organisms in a variety of environmental circumstances.

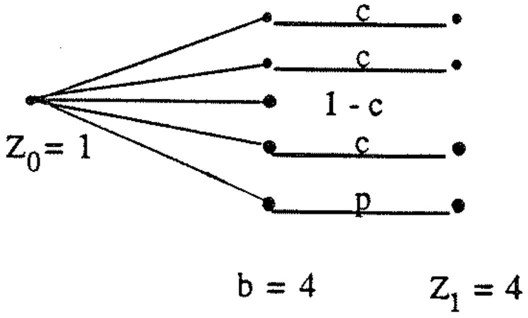
The model that will be described is based on the idea of fitness. Biologists see fitness as one of the most important ideas of evolution, if not *the* most important. The basic concept of fitness is success in reproduction. In general, however, there is no one formal definition for fitness and as one biologist puts it, fitness is "something everyone understands, but nobody can define precisely" (Stearns 1976). The following model analyzes fitness in three different ways. Since the model is based on maximizing fitness, it concentrates on:

1. Maximizing the mean rate of growth
2. Minimizing the probability of extinction
3. Maximizing the mean time to extinction.

Biologically, the model is very uncomplicated. It carries the assumptions that reproduction is asexual and cyclical (e.g. every year or every six months). It also is based on the idea that initially there exists only one organism ($Z_0 = 1$, as will be described later). Overall, the organism being dealt with is a very simplified one. The model appears as very basic and unrealistic, however, in reality it can be described as the "possible first step toward an eventual representation of a higher animal or man" (Cooper 1987, 8).

BRANCHING PROCESS

Population growth is depicted here in the form of a branching process in a fixed environment in which Z_n represents the population size at the end of the nth generation. The following simple example illustrates how the branching process proceeds and introduces the parameters associated with the population branching process.



Starting with one organism (as previously mentioned), $Z_0 = 1$. A fixed number b of offspring is produced in the first generation. In this case, b = 4. Each of these offspring has the probability c of surviving (independently of the others) to reproduce, while the parent has the probability p of surviving (independently of the others) to reproduce in the next generation. Thus, the probability of not surviving to reproduce is equal to 1- c for offspring and 1- p for parents. In the illustration, one offspring did not survive and the parent did survive to reproduce in the next generation. In terms of these parameters, the mean growth rate is: $\lambda = bc + p$.

We have the following theorem for a fixed environment (i.e., for fixed values of b,c and p).

Theorem1. Assume $P(Z_1 = 0) + P(Z_1 = 1) < 1$ and let $q = P(Z_n = 0$ for some $n) =$ probability of extinction of the branching process. Then, $q = 1$ iff $\lambda < 1$.

Logically, if the mean growth rate is less than 1, extinction will certainly occur. When $\lambda = 1$, one might think that the population will never go extinct. However, this is incorrect. Since 1 is a mean, the number of offspring will not be constantly equal to one and will eventually fluctuate below one, leading to extinction.

While the average $\lambda = bc + p$ refers to only one environment, our model incorporates the possibility of having two different environments where:

i = 1 represents a "good year"

i = 2 represents a "bad year".

Each of these two environments will in turn have its own growth rate associated with its own parameters:

$$\lambda_i = b_i c_i + p_i \ , \ i = 1,2.$$

The probability of each environment occurring has to be taken into account. Obviously, since there are only two possible environments, the sum of their probabilities will equal to zero:

Π_1 = probability of a good year

Π_2 = probability of a bad year.

The environment of each generation is selected by a "coin toss" each time and thus is independent of environments selected in previous years.

The branching process that is obtained by alternating among environments is denoted again by $\{ Z_n, n \geq 0 \}$ and is called a branching process in a random environment. Denote the environmental process by $\{ \varsigma_n, n \geq 0 \}$, so that $P(\varsigma_n = i) = \Pi_i$, for i = 1,2. Associated with a value ζ (= 1 or 2) of ς_n is a probability generating function (p.g.f.)

$$\phi_{\zeta}(t) = \sum_j p_j(\zeta)t^j , \text{ for } 0 \leq t \leq 1,$$

where $p_j(\zeta)$ is the probability that an organism in the nth generation and in environment ζ will produce j offspring in the next generation (Wilkinson 1969, p. 478). Thus, the branching process proceeds by producing particles according to the p.g.f. $\phi_{\zeta_1}(t)$ (ζ_1 is the value of the first environmental variable) and we then obtain Z_1 particles in the first generation; then the environmental process chooses a new value ζ_2 and each of the Z_1 particles then independently produces new particles according to the p.g.f. $\phi_{\zeta_2}(t)$, and so on.

In order to avoid trivialities, it is assumed that

1) $p_0(\zeta) < 1$ for all ζ

2) $p_0(\zeta) + p_1(\zeta) < 1$ for some ζ.

For k = 1,2, ..., and $0 \leq t \leq 1$, let

$$\Lambda_n^{(k)}(t) = E[\, t^{Z_n} \mid Z_0 = k]$$

$$= \sum_{i=1}^{2} \Pi_i \Lambda_{n-1}^{(k)}(\phi_i(t)) \, .$$

This is the probability generating function for Z_n assuming $Z_0 = k$ (Wilkinson 1969, p. 479).

If we let $q_k = P(Z_n = 0 \text{ , for some } n \mid Z_0 = k)$ = probability of extinction of the branching process $\{Z_n\}$ given that there are initially k particles, then it is easy to see that q_k satisfies the following infinite system of equations:

$$q_k = \sum_{i=1}^{\infty} p_i^{(k)}$$

for $k = 1,2, \ldots$ and where $p_i^{(k)} = P(Z_1 = i \mid Z_0 = k)$ for $i = 0,1,2,\ldots$,

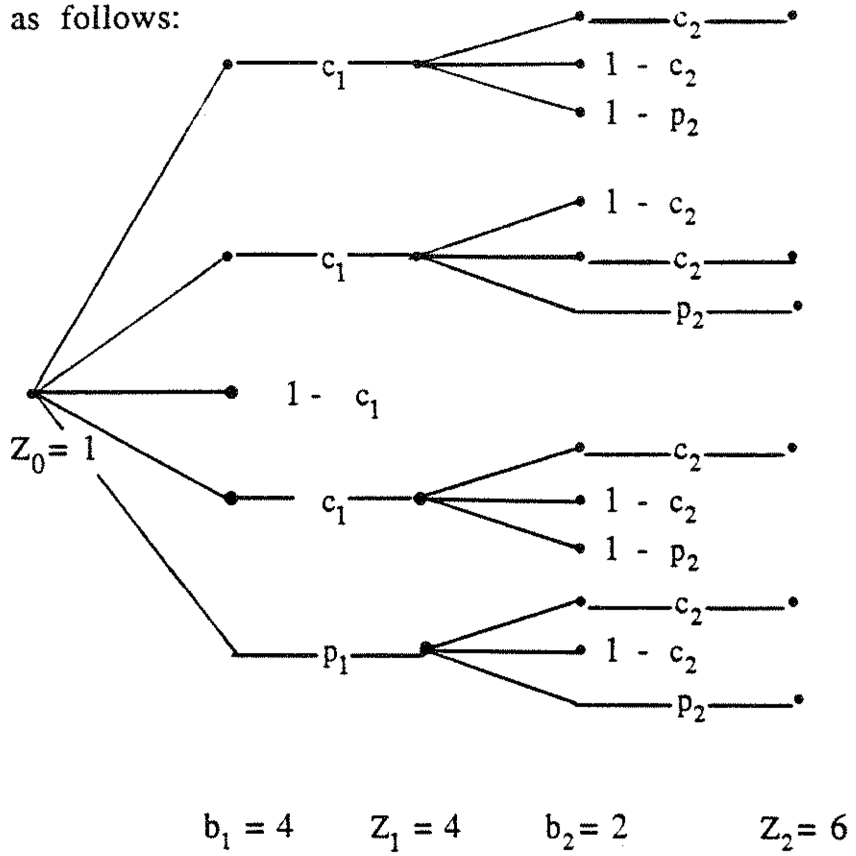
The following basic result (Wilkinson 1969, Theorem A, p. 479 and Corollary 2.1, p. 484) allows us to approximate the extinction probabilities by solving a truncation of this infinite system of equations.

Theorem 2. $q_1 < 1$ if and only if $\lambda_1^{\Pi_1} \lambda_2^{\Pi_2} > 1$ and given $\gamma < 1$ so that $\phi_i(t) \leq 1$ for $\gamma \leq t$, then

$$(I - A_n)^{-1} \vec{p_n} \leq \vec{q_n} \leq (I - A_n)^{-1} \vec{p_n} + \gamma^{n+1} \vec{1}$$

where $\vec{p_n} = (p_0^{(1)}, \ldots, p_0^{(n)})'$, $\vec{q_n} = (q_1, \ldots, q_n)'$, $\vec{1} = (1,\ldots,1)'$ (here ' denotes the transpose of a vector) , $A_n = \begin{pmatrix} p_1^{(1)} & p_2^{(1)} & \dots & p_n^{(1)} \\ p_1^{(2)} & p_2^{(2)} & \dots & p_n^{(2)} \\ \dots & \dots & \dots & \dots \\ p_1^{(n)} & p_2^{(n)} & \dots & p_n^{(n)} \end{pmatrix}$ and where the inequalities are componentwise.

An illustration of the branching process in the random environment is given as follows:



As shown above, $b_1 = 4$, whereas, $b_2 = 2$. The probabilities of survival can also be distinguished from one another by examining the branching diagram.

The expected growth rate for the process is given by the <u>arithmetic</u> mean:

$$E[\,Z_1\,] = \lambda_1\Pi_1 + \lambda_2\Pi_2$$

whereas, the probability of extinction is determined by the <u>geometric</u> mean:

$$\lambda = \lambda_1^{\Pi_1}\lambda_2^{\Pi_2}.$$

We are interested in computing q_1 = probability of extinction given $Z_0 = 1$; note that q_1 is a component of the vector $\vec{q_n} = (q_1, \dots, q_n)'$.

A BIOLOGICAL PARAMETER

We introduce a new biological parameter E, reproductive effort. This parameter represents the fraction of resources that an organism devotes to reproduction, and can vary between the use of no resources ($E = 0$) or the use of all of the organism's resources ($E = 1$). Accordingly, the mean growth rates are dependent upon the reproductive effort:

$$\lambda_i(E) = b_i(E)c_i(E) + p_i(E) \quad \text{for } i = 1 \text{ or } 2, \text{ and } 0 \le E \le 1,$$

and

$$\lambda(E) = \lambda_1(E)^{\Pi_1} \lambda_2(E)^{\Pi_2}.$$

The probability of extinction $q_1(E)$ also depends on E.

It is helpful to restate the three strategies for our model based upon reproductive effort.

1. Find the reproductive effort $\hat{E}_\lambda$ that maximizes the mean rate of growth $\lambda(E)$.
2. Find the reproductive effort $\hat{E}_q$ that minimizes the probability of extinction $q_1(E)$ (given $Z_0 = 1$ for a fixed value of E).
3. Find the reproductive effort $\hat{E}_\tau$ that maximizes the expected time to extinction $\tau(E)$ for the branching process.

AN ENVIRONMENTAL PARAMETER

Environmental variation, denoted by s, adds a new complication to our model. It distinguishes between good and bad years and varies between the values of 0 and 1. There are two extreme cases in terms of interest to us:

Case I: Environmental variation affects offspring only.

$$b_1(E) = b_2(E) = b(E)$$
$$p_1(E) = p_2(E) = p(E)$$
$$c_1(E) = c(E)(1 + s) : \text{good year}$$
$$c_2(E) = c(E)(1 - s) : \text{bad year}$$

Case 2: Environmental variation affects parents only.

$$b_1(E) = b_2(E) = b(E)$$
$$c_1(E) = c_2(E) = c(E)$$
$$p_1(E) = p(E)(1 + s) : \text{good year}$$
$$p_2(E) = p(E)(1 - s) : \text{bad year.}$$

We see that as s increases, the difference between good and bad years also increases.

Theorem 2 gives us a basis for numerically calculating the extinction probability $q = q(s,E)$ for a fixed value of s and E in each of Case I and Case II.

Similarly, given $Z_0 = k$, let $\tau_k = \tau_k(s,E)$ be the expected time to extinction for the process $\{Z_n, n \geq 1\}$ (for fixed s and E), then we have that

$$\vec{\tau} = (I - A)^{-1}\vec{1}$$

where $\vec{\tau} = (\tau_1, \tau_2, \ldots)'$ and $\vec{1} = (1,1, \ldots)'$ and A is the infinite matrix

$$A = \begin{pmatrix} p_1^{(1)} & p_2^{(1)} & \cdots & p_n^{(1)} & \cdots \\ p_1^{(2)} & p_2^{(2)} & \cdots & p_n^{(2)} & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ p_1^{(n)} & p_2^{(n)} & \cdots & p_n^{(n)} & \cdots \\ \cdots & \cdots & \cdots & \cdots & \cdots \end{pmatrix}$$

(see (Parzen 1962, p. 241). We again are interested in finding τ_1. A similar truncation to that in Theorem 2 can be applied to calculate τ_1 numerically.

THE COMPUTER PROGRAM

The computer program corresponding to our model is designed to test the three reproductive studies described above. As such, specific forms are assumed for the functions b(E), c(E) and p(E). We then consider the two separate cases: Case I (environmental variation affects offspring only) and Case II (environmental variation affects parents only). For a fixed value of E and of s, we find the optimal reproductive efforts $\hat{E}_\lambda$, $\hat{E}_q$, $\hat{E}_\tau$ that optimize $\lambda(s,E)$, $q(s,E)$ and $\tau(s,E)$, respectively. $\lambda(s,E)$ is found by direct calculation, while $q(s,E)$ and $\tau(s,E)$ are found by solving the respective truncated system of equations as described above.

We first fix a value of s between 0 and 1 and then increment E by steps of 0.01 from 0 to 1; the parameter s is then incremented in steps of 0.05.

The program prints out the appropriate values of $\hat{E}_\lambda$, $\hat{E}_q$, $\hat{E}_\tau$ and these are then compared to see which strategy requires the least optimal reproductive effort. We are interested finally in how these three optimal reproductive efforts vary as functions of the parameter s in each of the two case I and II.

To test the model the following forms for b(E), c(E) and p(E) were chosen:

$b(E) = [\ \beta \ \frac{E^{1/4}}{2 - E^2}]$ for a fixed value of β ; (note: [x] denotes the greatest integer in x)

$c(E) = [\ k \ \frac{2-E^2}{2}\ ]$ for a fixed value of k; and

$p(E) = p^* \ (1 - E^2)$ for a fixed value of p^*.

RESULTS

The results were inconclusive for finding $\hat{E}_\tau$ due to problems in the program with the matrix manipulation. However, conclusive results were founc for $\hat{E}_\lambda$ and $\hat{E}_q$. In both case I and II, $\hat{E}_q$ was always less than or equal to $\hat{E}_\lambda$. Thus, less effort is needed to minimize the probability of extinction than is needed to maximize the mean growth rate. The effects of changing the probability Π_1 of a good year were also investigated. See Appendix A.

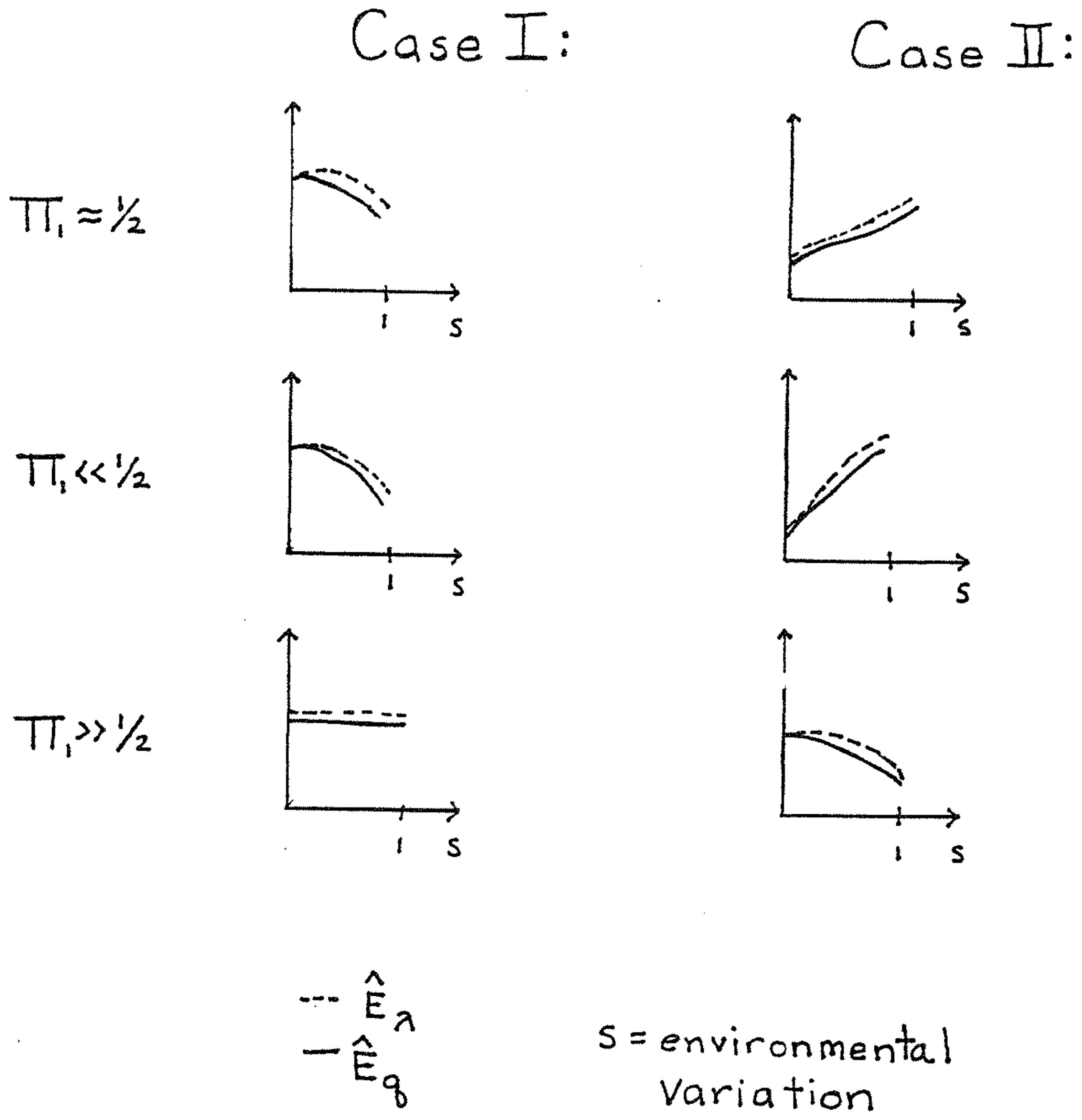
Appendix B presents the forms of the functions b(E), c(E) and p(E). For the first two functions, smooth curves are drawn for the graphs although in reality the graphs are step functions due to the function $[\ x\ ]$ involved in their definitions.

While a large reproductive effort may be beneficial in certain circumstances (e.g., parents are continually being wiped out, therefore, it is best to reproduce with a high effort), it is usually undesirable. There must be a happy medium between $\hat{E}_q$ and $\hat{E}_\lambda$. Appendix C gives an example of this idea by depicting the probability of extinction for some fixed value of the environmental variation s. As s nears one, the optimal effort point will also be close to one.

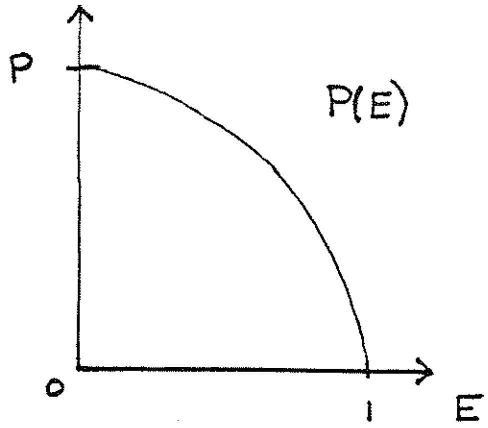
Appendix

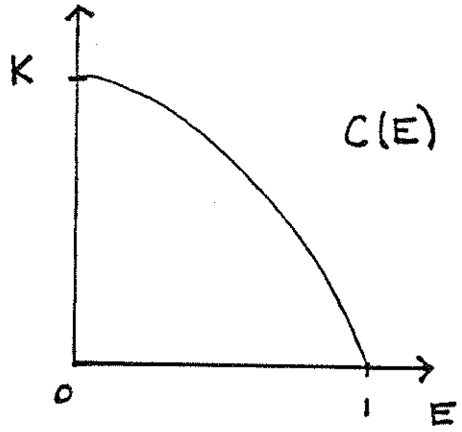
Appendix A

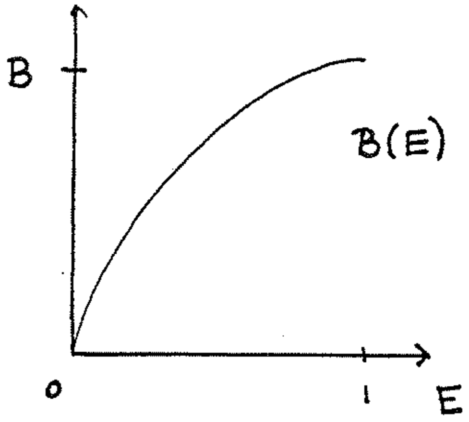
Effects of Changing π_1



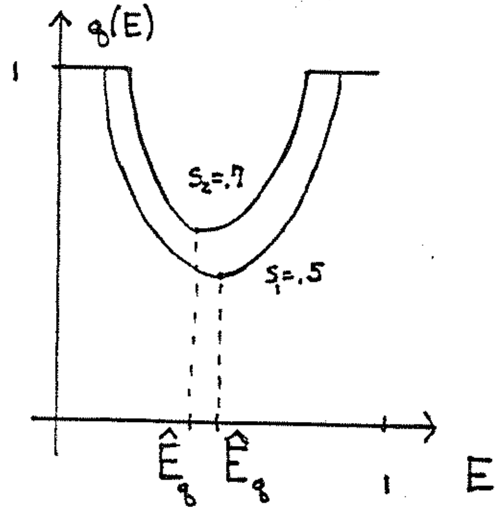
Appendix B







Appendix C



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