BOUNDS FOR THE ASYMPTOTIC GROWTH RATE OF AN AGE-DEPENDENT BRANCHING PROCESS

P. J. BROCKWELL [1]

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Let $M(t)$ denote the mean population size at time t (conditional on a single ancestor of age zero at time zero) of a branching process in which the distribution of the lifetime T of an individual is given by $\Pr\{T \leqq t\} = G(t)$, and in which each individual gives rise (at death) to an expected number A of offspring $(1 < A < \infty)$. Then it is well-known (Harris [1], p. 143) that, provided $G(0+)-G(0-) = 0$ and G is not a lattice distribution, $M(t)$ is given asymptotically by

$$M(t) \sim \frac{A-1}{cA^2 \int te^{-ct}dG(t)} e^{ct}, \qquad t \to \infty, \tag{1}$$

where c is the unique positive value of p satisfying the equation

$$\int e^{-pt}dG(t) = A^{-1}. \tag{2}$$

In many biological problems the distribution function G is not known precisely and it is of interest to find bounds for the asymptotic growth rate c (sometimes known as the Malthusian parameter for the population), given only that

(a) $$\int tdG(t) = m_1,$$

or

(b) $$\int tdG(t) = m_1 \quad \text{and} \quad \int t^2dG(t) = m_2,$$

where $m_1, m_2 < \infty$.

In this note we shall find the best possible bounds for c under these conditions and, in the course of the derivation, determine the functions (defined for all real non-negative values of p) $\sup_{F\in\mathscr{F}} \Phi(F, p)$ and $\inf_{F\in\mathscr{F}} \Phi(F, p)$, where $\Phi(F, p) = \int e^{-pt}dF(t)$ and $\mathscr{F}$ represents one or other of the classes of probability distribution functions:

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$$\mathscr{F}(m_1) = \left\{F : F(0-) = 0, \int t dF(t) = m_1\right\},$$

$$\mathscr{F}(m_1, m_2) = \left\{F : F(0-) = 0, \int t dF(t) = m_1, \int t^2 dF(t) = m_2\right\}.$$

Bounding techniques for branching processes have been used previously by Heathcote and Seneta [2], Senate [3] and Brook [4]. Lemmas 2 and 3 below were used by Brook to obtain an upper bound for the extinction probability.

Before deriving the results, which are given as a series of lemmas, we note that if F is the distribution function of a proper non-zero non-negative random variable and

$$\Phi_n(F, p) = \int t^n e^{-pt} dF(t), \qquad n = 0, 1, 2, \cdots,$$

then it is well-known that if $\Phi_n(F, 0) < \infty$, $\log \Phi_n(F, p)$ is strictly decreasing and convex for $p \geqq 0$.

It will be assumed throughout that $m_1 > 0$ since Lemmas 1—3 are trivial if $m_1 = 0$.

LEMMA 1.

$$\inf_{F \in \mathscr{F}(m_1)} \Phi(F, p) = \inf_{F \in \mathscr{F}(m_1, m_2)} \Phi(F, p) = e^{-m_1 p}, \qquad 0 \leqq p < \infty.$$

PROOF. (i) We first show that $e^{-m_1 p} \leqq \Phi(F, p)$ for all $F \in \mathscr{F}(m_1)$. Denote by D_p the operator d/dp. Then since $\log \Phi(F, p) = 0$ at $p = 0$ and $D_p \log \Phi(F, p) = -m_1$ at $p = 0$ it follows from the convexity of $\log \Phi(F, p)$ that $\log \Phi(F, p) \geqq -m_1 p$ for all $p \geqq 0$.

(ii) By choosing α sufficiently small in the example

$$F(t) = \begin{cases} 0, \; t < m_1 - \sigma[\alpha/(1-\alpha)]^{\frac{1}{2}}, \\ 1-\alpha, \; m_1 - \sigma[\alpha/(1-\alpha)]^{\frac{1}{2}} \leqq t < m_1 + \sigma[(1-\alpha)/\alpha]^{\frac{1}{2}}, \\ 1, \; t \geqq m_1 + \sigma[(1-\alpha)/\alpha]^{\frac{1}{2}}, \end{cases}$$

(where $\sigma = (m_2 - m_1^2)^{\frac{1}{2}}$) we see that for any given non-negative p and positive ε there exists $F \in \mathscr{F}(m_1, m_2)$ such that $\Phi(F, p) - e^{-m_1 p} < \varepsilon$.

REMARK. The example given in (ii) also shows that the infima are unchanged when taken over the subclass of $\mathscr{F}(m_1, m_2)$ in which $F(0+) - F(0-) = 0$ and F is a non-lattice distribution.

LEMMA 2.

$$\sup_{F \in \mathscr{F}(m_1)} \Phi(F, p) = 1, \qquad 0 \leqq p < \infty.$$

PROOF. We need only show that for any given non-negative p and positive ε there exists $F \in \mathscr{F}(m_1)$ such that $1 - \Phi(F, p) < \varepsilon$. Such an F is obtained by choosing α sufficiently small in the following example:

$$F(t) = \begin{cases} 0, & t < \alpha m_1, \\ 1-\alpha, & \alpha m_1 \leqq t < \alpha^{-1} m_1(1-\alpha+\alpha^2), \\ 1, & t \geqq \alpha^{-1} m_1 (1-\alpha+\alpha^2). \end{cases}$$

LEMMA 3.

$$\sup_{F \in \mathscr{F}(m_1, m_2)} \Phi(F, p) = 1 - \frac{m_1^2}{m_2} + \frac{m_1^2}{m_2} \exp\left(-\frac{m_2 p}{m_1}\right), \qquad 0 \leqq p < \infty.$$

PROOF. (i) We first establish the inequality,

$$\chi(F, p) \equiv \Phi(F, p) - 1 + \frac{m_1^2}{m_2} - \frac{m_1^2}{m_2} \exp\left(-\frac{m_2 p}{m_1}\right) \leqq 0. \tag{3}$$

Since at $p = 0$ there is equality in (3) it will be sufficient to show that $D_p \chi(F, p) \leqq 0$ for all non-negative p, or equivalently that

$$\rho(F, p) \equiv \log \Phi_1(F, p) - \log m_1 + m_2 p / m_1 \geqq 0.$$

Since $\rho(F, p) = 0$ at $p = 0$ and $D_p \rho(F, p) = 0$ at $p = 0$ it follows from the convexity of $\rho(F, p)$ that $\rho(F, p) \geqq 0$ for all $p \geqq 0$. This establishes the inequality (3).

(ii) If $m_2 = m_1^2$ the assertion of the lemma is trivial since in this case $\sup_{F \in \mathscr{F}(m_1, m_2)} \Phi(F, p) = \exp(-m_1 p)$. If $m_2 > m_1^2$ then by choosing α sufficiently small ($\alpha > 0$) in the example,

$$F(t) = \begin{cases} 0, & t < m_1 - \sigma[(m_1^2 - m_2\alpha)(\sigma^2 + m_2\alpha)^{-1}]^{\frac{1}{2}}, \\ 1 - \dfrac{m_1^2}{m_2} + \alpha, & m_1 - \sigma[(m_1^2 - m_2\alpha)(\sigma^2 + m_2\alpha)^{-1}]^{\frac{1}{2}} \\ & \qquad \leqq t < m_1 + \sigma[(\sigma^2 + m_2\alpha)(m_1^2 - m_2\alpha)^{-1}]^{\frac{1}{2}}, \\ 1, & t \geqq m_1 + \sigma[(\sigma^2 + m_2\alpha)(m_1^2 - m_2\alpha)^{-1}]^{\frac{1}{2}}, \end{cases}$$

(where $\sigma = (m_2 - m_1^2)^{\frac{1}{2}}$) we see that for any given non-negative p and positive ε there exists $F \in \mathscr{F}(m_1, m_2)$ such that

$$1 - \frac{m_1^2}{m_2} + \frac{m_1^2}{m_2} \exp\left(-\frac{m_2 p}{m_1}\right) - \Phi(F, p) < \varepsilon.$$

REMARK. The examples given in the proofs of Lemmas 2 and 3 show that the suprema are unchanged when the further restrictions are imposed that $F(0+) - F(0-) = 0$ and that F be a non-lattice distribution.

LEMMA 4. *If* $A > 1$, $G(0-) = G(0+) = 0$, *G is a non-lattice distribution, and $c(G)$ is the unique positive root of equation* (2), *then*

$$\inf_{G\in\mathscr{F}(m_1)} c(G) = \frac{\log A}{m_1}, \quad \sup_{G\in\mathscr{F}(m_1)} c(G) = \infty,$$

$$\inf_{G\in\mathscr{F}(m_1,m_2)} c(G) = \frac{\log A}{m_1}, \quad \sup_{G\in\mathscr{F}(m_1,m_2)} c(G) = \begin{cases} \dfrac{m_1}{m_2}\log\dfrac{m_1^2A}{m_1^2A-m_2(A-1)} & \text{if } m_1^2A > m_2(A-1), \\ \infty & \text{if } m_1^2A \leqq m_2(A-1). \end{cases}$$

PROOF. If $G\in\mathscr{F}(m_1)$ satisfies the conditions of the lemma then we know from Lemma 1 that $\Phi(G, p) \geqq \exp(-m_1 p)$, and in particular $\Phi(G, c(G)) = A^{-1} \geqq \exp[-m_1 c(G)]$. Hence $c(G) \geqq m_1^{-1}\log A$. Furthermore given any $\varepsilon > 0$ it follows from Lemma 1, since $\exp(-m_1 p) < A^{-1}$ if $p = m_1^{-1}\log A+\varepsilon$, that there exists $G\in\mathscr{F}(m_1, m_2)$ satisfying the conditions of Lemma 4 such that $\Phi(G, m_1^{-1}\log A+\varepsilon) < A^{-1}$. Since $\Phi(G, p)$ is a decreasing function of p this inequality implies that $c(G) < m^{-1}\log A+\varepsilon$. This establishes the infima as given in the statement of the lemma. The suprema are established in an analogous way from Lemmas 2 and 3.

It is interesting to observe that specification of only the mean of F gives no finite upper bound for c. Specification of the second moment as well as the mean gives an upper bound for c only if the coefficient of variation is sufficiently small (i.e., only if $m_1^{-1}(m_2-m_1^2)^{\frac{1}{2}} < (A-1)^{-\frac{1}{2}}$). A large coefficient of variation allows the probability of a lifetime near zero to become too great for c to be bounded above.

In terms of a specified mean, m_1, and coefficient of variation v, Lemma 4 gives

$$\log A \leqq m_1 c \leqq \frac{1}{(1+v^2)}\log\frac{A}{1-(A-1)v^2}. \tag{4}$$

For reasonably small values of v (as frequently occur in biological problems) these bounds are rather close. For example in the particular case $A = 2$, we obtain the following bounds for various values of v:

$$\begin{aligned} v &= 0.2, & 0.693 &\leqq m_1c \leqq 0.706; \\ v &= 0.4, & 0.693 &\leqq m_1c \leqq 0.748; \\ v &= 0.6, & 0.693 &\leqq m_1c \leqq 0.838; \\ v &= 0.8, & 0.693 &\leqq m_1c \leqq 1.046; \\ v &= 1.0, & 0.693 &\leqq m_1c \leqq \infty. \end{aligned}$$

We note finally that for given A and m_1 the least upper bound for c increases monotonically to ∞ as v increases from zero to $(A-1)^{-\frac{1}{2}}$. Consequently if we specify that the mean lifetime be m_1 and that the coefficient of variation satisfy the inequality $v \leqq v_0 < (A-1)^{-\frac{1}{2}}$, then the best bounds which can be given for c are obtained from (4) on setting $v = v_0$.

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Argonne National Laboratory
Argonne, Illinois