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

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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 $\Pr \{T \leq t\} = G(t)$, 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

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

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

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

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) $$\int t dG(t) = m_1,$$

or

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

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 $p$) $\sup_{p \in \mathcal{F}} \Phi(F, p)$ and $\inf_{p \in \mathcal{F}} \Phi(F, p)$, where $\Phi(F, p) = \int e^{-pt} dF(t)$ and $\mathcal{F}$ represents one or other of the classes of probability distribution functions:

1 Work performed under the auspices of the United States Atomic Energy Commission.
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

\[
0 < n(F, p) < \infty, \quad \log n(F, p)
\]

is strictly decreasing and convex for \( p \geq 0 \).

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

**Lemma 1.**

\[
\inf_{F \in \mathcal{F}(m_1)} \Phi(F, p) = \inf_{F \in \mathcal{F}(m_1, m_2)} \Phi(F, p) = e^{-m_1 p}, \quad 0 \leq p < \infty.
\]

**Proof.** (i) We first show that \( e^{-m_1 p} \leq \Phi(F, p) \) for all \( F \in \mathcal{F}(m_1) \). 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 \( \log \Phi(F, p) \geq -m_1 p \) for all \( p \geq 0 \).

(ii) By choosing \( \alpha \) sufficiently small in the example

\[
F(t) = \begin{cases} 
0, & t < m_1 - \sigma[(1-\alpha)]^\frac{1}{2} \\
1 - \alpha, & m_1 - \sigma[(1-\alpha)]^\frac{1}{2} \leq t < m_1 + \sigma[(1-\alpha)]^\frac{1}{2} \\
1, & t \geq m_1 + \sigma[(1-\alpha)]^\frac{1}{2},
\end{cases}
\]

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

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

**Lemma 2.**

\[
\sup_{F \in \mathcal{F}(m_1)} \Phi(F, p) = 1, \quad 0 \leq p < \infty.
\]

**Proof.** We need only show that for any given non-negative \( p \) and positive \( \epsilon \) there exists \( F \in \mathcal{F}(m_1) \) such that \( 1 - \Phi(F, p) < \epsilon \). Such an \( F \) is obtained by choosing \( \alpha \) sufficiently small in the following example:
LEMMA 3.

\[
\sup_{F \in \mathcal{F}(m_1, m_2)} \Phi(F, \rho) = 1 - \frac{m_1^2}{m_2} + \frac{m_1^2}{m_2} \exp \left( - \frac{m_2 \rho}{m_1} \right), \quad 0 \leq \rho < \infty.
\]

PROOF. (i) We first establish the inequality,

\[
\chi(F, \rho) \equiv \Phi(F, \rho) - 1 + \frac{m_1^2}{m_2} - \frac{m_1^2}{m_2} \exp \left( - \frac{m_2 \rho}{m_1} \right) \leq 0.
\]

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

\[
\rho(F, \rho) \equiv \log \Phi(F, \rho) - \log m_1 + m_2 \rho/m_1 \geq 0.
\]

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

(ii) If \( m_2 = m_1^2 \) the assertion of the lemma is trivial since in this case

\[
\sup_{F \in \mathcal{F}(m_1, m_2)} \Phi(F, \rho) = \exp(-m_1 \rho).
\]

If \( m_2 > m_1^2 \) then by choosing \( \alpha \) sufficiently small (\( \alpha > 0 \)) in the example,

\[
F(t) = \begin{cases} 
0, & t < m_1 - \sigma[(m_1^2-m_2 \alpha)(\sigma^2+m_2 \alpha)^{-1}]^{1/2}, \\
1 - \frac{m_1^2}{m_2} + \alpha, & m_1 - \sigma[(m_1^2-m_2 \alpha)(\sigma^2+m_2 \alpha)^{-1}]^{1/2} \leq t < m_1 + \sigma[(\sigma^2+m_2 \alpha)(m_1^2-m_2 \alpha)^{-1}]^{1/2}, \\
1, & t \geq m_1 + \sigma[(\sigma^2+m_2 \alpha)(m_1^2-m_2 \alpha)^{-1}]^{1/2},
\end{cases}
\]

(where \( \sigma = (m_2-m_1^2)^{1/2} \)) we see that for any given non-negative \( \rho \) and positive \( \varepsilon \) there exists \( F \in \mathcal{F}(m_1, m_2) \) such that

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

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
\[ \inf_{G \in \mathcal{F}(m_1)} c(G) = \frac{\log A}{m_1}, \quad \sup_{G \in \mathcal{F}(m_1)} c(G) = \infty, \]

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

**Proof.** If \( G \in \mathcal{F}(m_1) \) satisfies the conditions of the lemma then we know from Lemma 1 that \( \Phi(G, \hat{\rho}) \geq \exp (-m_1 \hat{\rho}) \), and in particular \( \Phi(G, c(G)) = A^{-1} \geq \exp [-m_1 c(G)] \). Hence \( c(G) \geq m_1^{-1} \log A \). Furthermore given any \( \epsilon > 0 \) it follows from Lemma 1, since \( \exp (-m_1 \hat{\rho}) < A^{-1} \) if \( \hat{\rho} = m_1^{-1} \log A + \epsilon \), that there exists \( G \in \mathcal{F}(m_1, m_2) \) satisfying the conditions of Lemma 4 such that \( \Phi(G, m_1^{-1} \log A + \epsilon) < A^{-1} \). Since \( \Phi(G, \hat{\rho}) \) is a decreasing function of \( \hat{\rho} \) this inequality implies that \( c(G) < m_1^{-1} \log A + \epsilon \). 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 \( m_1^{-1}(m_2 - m_1) \leq (A - 1)^{-1} \)). 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 \( \nu \), Lemma 4 gives

\[ \log A \leq m_1 \nu \leq \frac{1}{1+\nu^2} \log \frac{A}{1-(A-1)^{-1}}. \] (4)

For reasonably small values of \( \nu \) (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 \( \nu \):

\[ \begin{array}{llll}
\nu = 0.2, & 0.693 \leq m_1 \nu \leq 0.706; \\
\nu = 0.4, & 0.693 \leq m_1 \nu \leq 0.748; \\
\nu = 0.6, & 0.693 \leq m_1 \nu \leq 0.838; \\
\nu = 0.8, & 0.693 \leq m_1 \nu \leq 1.046; \\
\nu = 1.0, & 0.693 \leq m_1 \nu \leq \infty. \\
\end{array} \]

We note finally that for given \( A \) and \( m_1 \) the least upper bound for \( c \) increases monotonically to \( \infty \) as \( \nu \) increases from zero to \( (A-1)^{-1} \). Consequently if we specify that the mean lifetime be \( m_1 \) and that the coefficient of variation satisfy the inequality \( \nu \leq \nu_0 < (A-1)^{-1} \), then the best bounds which can be given for \( c \) are obtained from (4) on setting \( \nu = \nu_0 \).
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References


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