Math. Proc. Camb. Phil. Soc. (1978), **83**, 183
Printed in Great Britain

Derivatives of the spectral radius as a function of non-negative matrix elements

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(*Received* 13 *June* 1977)

1. *Introduction.* Let $A = (a_{ij})$ be a non-negative $n \times n$ matrix, that is, $a_{ij} \geqslant 0$, $i, j = 1, \ldots, n; n > 1$. We write $A \geqslant 0$. Let $r = r(A)$ be the spectral radius of A; assume $r > 0$ throughout to avoid trivial cases. Let $d^m r/da_{ij}^m$ be the mth derivative of r with respect to the element a_{ij}, all other elements of A being held constant.

We give an explicit formula for dr/da_{ii} in terms of principal minors of $rI - A$. We show that $0 \leqslant dr/da_{ii} \leqslant 1$, and $\lim_{a_{ii}\to\infty} dr/da_{ii} = 1$. We also obtain an explicit formula for d^2r/da_{ii}^2 in terms of minors of $rI - A$ and show that $d^2r/da_{ii}^2 \geqslant 0$; that is, the spectral radius of a non-negative matrix is a convex function of each element of the main diagonal. When A is non-negative and irreducible, all the preceding weak inequalities $\geqslant$ concerning the derivatives are replaced by strict inequalities $>$.

When A is a non-negative matrix in Frobenius normal form

$$A = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1,n-1} & a_{1n} \\ 1 & 0 & \cdots & 0 & 0 \\ 0 & 1 & \cdots & 0 & 0 \\ & & \cdots & & \\ 0 & 0 & & 1 & 0 \end{pmatrix}$$

with positive first row (and also under much weaker assumptions about the first row), then $d^2r/da_{1n}^2 < 0$. Since a non-negative matrix in Frobenius normal form is similar to a so-called Leslie matrix used in demography, these results have immediate interpretations.

Kingman (4) shows that if, for all i, j and some fixed interval of the real variable θ, $a_{ij}(\theta)$ are positive and $\log a_{ij}(\theta)$ are convex, then $\log r$ viewed as a function of θ is also convex. Seneta ((8), pp. 82–83) extends this result to non-negative matrices $A(\theta)$ in which certain elements are fixed at 0. Kingman ((4), p. 284) remarks that it is not necessarily true that, if the a_{ij} are convex functions of θ, then so is r. Thus r is not always a convex function of each a_{ij}, but we now see that it is a convex function when $i = j$.

Lax ((5), p. 182) shows that in a linear space $\{X\}$ of real $n \times n$ matrices X each having only real eigenvalues, the spectral radius $r = r(X)$ is a convex function of every element of X.

In spite of the apparent similarity among the results, the methods of proof used here and by Lax (5) and Kingman (4) appear distinct.

2. *Notation.* Let $Q_{k,n}$ be the collection of all strictly increasing sequences of k positive integers less than or equal to n, where $1 \leqslant k \leqslant n$. For example if $P \in Q_{3,5}$,

P might be (2, 3, 4) with elements $p_1 = 2$, $p_2 = 3$, and $p_3 = 4$. $Q_{k,n}$ is void if $k < 1$ or $k > n$.

The matrix formed from any real matrix $M_{n\times n}$ (where the subscript denotes the order) by deleting both the rows and columns indexed by the elements of $P \in Q_{k,n}$ and retaining the remaining rows and columns in their natural order is denoted $M(P)$. The matrix formed from M by including only those elements which fall in both the rows and columns indexed by P is denoted $M[P]$. Thus if M is 2×2, $M(2) = m_{11}$ and $M[2] = m_{22}$. A matrix formed by deleting, or retaining only the intersection of, the rows indexed by P_1 and the columns indexed by P_2 where $P_1 \neq P_2$, P_1, $P_2 \in Q_{k,n}$, is written $M(P_1|P_2)$, or $M[P_1|P_2]$. Thus if M is 2×2, $M(2|1) = m_{12}$ and $M[2|1] = m_{21}$.

The determinant of M is $|M|$, where M is $n \times n$. The determinant of a scalar is the scalar itself. Define $|M(1,\ldots,n)| = 1$ and $|M(P)| = 0$ if $P \in Q_{K,N}$ where $n < K \leqslant N$, in order to avoid discussing the cases $n = 2$ and $n = 3$ separately.

If P^* is any permutation of P containing k distinct positive integers $\leqslant n$ not in strictly increasing order, then $M[P^*]$ is formed by applying the same permutation to the rows and columns of $M[P]$. While $M[P^*] \neq M[P]$ in general, $|M[P^*]| = |M[P]|$. Similarly, if P_i^* is a permutation of P_i, $i = 1, 2$, $P_1^* \neq P_2^*$, then $M[P_1^*|P_2^*] \neq M[P_1|P_2]$ in general, and there may be a difference in sign between $|M[P_1^*|P_2^*]|$ and $|M[P_1|P_2]|$.

Throughout $A_{n\times n} \geqslant 0$, $D_{n\times n} = rI_{n\times n} - A$, and $f(x, M) = |xI - M|$. Thus

$$f(r, A) = |D| = 0.$$

Without loss of generality, we shall prove results about $d^m r/da_{ii}^m$ for $i = 1$ only.

3. *First derivative*

LEMMA 1 ((7), *p.* 72). *Let M be a fixed real $n \times n$ matrix, x a real scalar,*

$$f(x, M) = |xI - M|.$$

For $k = 1, 2, \ldots$, $\partial^k f(x, M)/\partial x^k = k!\,\Sigma_{P\in Q_{k,n}}|(xI - M)(P)|$. In particular

$$\partial f/\partial x = \textstyle\sum_{i=1}^n |(xI - M)(i)| \quad \textit{and} \quad \partial^2 f/\partial x^2 = 2\sum_{i<j}|(xI - M)(i,j)|.$$

LEMMA 2 ((3), *pp.* 69–70). *If $A \geqslant 0$, $r = r(A) > 0$, $P \in Q_{k,n}$ for some k, $1 \leqslant k < n$, then $|D(P)| = |rI - A(P)| \geqslant 0$. Here I is of order $(n-k)\times(n-k)$. If A is also irreducible, then $|D(P)| > 0$.*

THEOREM 1. *If $A_{n\times n} \geqslant 0$ is irreducible, $r = r(A) > 0$, $D = rI - A$, then*

$$0 < dr/da_{11} = |D(1)|/\textstyle\sum_{i=1}^n |D(i)| < 1. \qquad (1)$$

Proof. Since $f(r, A) = 0$, $dr/da_{11} = -(\partial f/\partial a_{11})/(\partial f/\partial x)|_{x=r}$ by implicit differentiation. Expanding $|D|$ by the first row and differentiating with respect to a_{11} gives

$$-\partial f/\partial a_{11} = |D(1)|.$$

Lemma 1 gives $\partial f/\partial x$. Since A is irreducible, $|D(i)| > 0$, $i = 1, \ldots, n$, by Lemma 2. The strict inequalities in equation (1) follow.

From Theorem 1, it follows immediately that $\sum_{i=1}^n dr/da_{ii} = 1$ when $A \geqslant 0$ is irreducible.

COROLLARY 1. *If* $A_{n \times n} \geqslant 0$, $r = r(A) > 0$, *then* $0 \leqslant dr/da_{11} \leqslant 1$.

Proof. In the canonical form for reducible non-negative matrices ((3), p. 75), a_{11} falls in an irreducible square submatrix A_1 of A lying along the main diagonal of A. If $r(A_1) < r(A)$ then $dr(A)/da_{11} = 0$. Otherwise $r(A_1) = r(A)$. If A_1 is 1×1 containing only the element $a_{11} = r(A_1) = r(A)$, then $dr/da_{11} = 1$.

COROLLARY 2. *If* $A \geqslant 0$, *then* $\lim_{a_{11} \to \infty} dr/da_{11} = 1$.

Proof. First suppose A is irreducible. Then $a_{11} = r(A[1]) < r = r(A) \leqslant$ maximal row sum of A ((3), p. 63). When a_{11} is large enough, the maximal row sum of A is $\sum_{j=1}^{n} a_{1j}$. Hence as a_{11} increases without limit, so does $r = r(A)$, but $r - a_{11}$ does not exceed a constant $\sum_{j=2}^{n} a_{1j}$. Thus for $i = 2, \ldots, n$, and for large a_{11}, $|D(i)|$ is dominated by $\prod_{j \neq i}(r - a_{jj})$ which increases as a_{11}^{n-2}, whereas for large a_{11}, $|D(1)|$ increases as a_{11}^{n-1}. Thus $\lim dr/da_{11} = \lim 1/(1 + \sum_{i=2}^{n} (|D(i)|/|D(1)|)) = 1$.

Now suppose A is reducible. Then $a_{11} \leqslant r \leqslant$ maximal row sum $=$ sum of the first row when a_{11} is large enough. Also for a_{11} large enough, the expression for dr/da_{11} in equation (1) has a non-zero denominator. Then the argument in the preceding paragraph applies to the irreducible square submatrix A_1 which contains a_{11} in the canonical form of A, proving the corollary.

It follows incidentally from $a_{11} \leqslant r \leqslant$ maximal row sum of A that $\lim_{a_{11} \to \infty} r/a_{11} = 1$ for any $A \geqslant 0$. From Corollaries 1 and 2 it follows that $d(r/a_{11})/da_{11} \leqslant 0$, for any $A \geqslant 0$, with strict inequality when A is irreducible, and $\lim_{a_{11} \to \infty} d^m r/da_{11}^m = 0$ for $m > 1$.

4. *Second derivative*

THEOREM 2. *If* $A_{2 \times 2} \geqslant 0$, *then*

$$d^2r/da_{ii}^2 \geqslant 0 \quad \textit{and for} \quad i \neq j, \quad d^2r/da_{ii}^2 = d^2r/da_{jj}^2, \quad d^2r/da_{ij}^2 \leqslant 0.$$

If $A_{2 \times 2} > 0$, *the inequalities are strict.*

Proof. Apply the standard formula for the second derivative obtained by implicit differentiation to the characteristic equation. (The formula for d^2r/da_{11}^2 appears in equation (2) below.)

The proof of Theorem 2 is both trivial and uninformative about the general case. The lowest order in which the problems of full generality arise is 5×5. Moreover, the concavity of r as a function of all off-diagonal elements does not generalize to matrices A of higher order than 2×2, even when $A > 0$.

A crucial tool in the general case is the Law of Extensible Minors, due to Muir in 1881, as restated by Stouffer ((10), p. 165):

LEMMA 3. *If any identical relationship be established among a number of minors of a general determinant (the determinant itself may be included as a minor), the minors being denoted by means of their principal diagonals, then a new relationship involving the minors of a determinant with k additional rows and columns is always obtainable by annexing the k new elements in the principal diagonal to the end of the diagonal of every minor occurring in the identity, and then multiplying each term by such a power of the principal minor of order k, consisting of new elements only, as will make the relationship homogeneous in the elements.*

LEMMA 4. *If $A \geqslant 0$, $i \neq j$, and P is any strictly increasing sequence of length k $(0 \leqslant k \leqslant n-2)$ of positive integers $\leqslant n$ and different from both i and j, then*

$$|D[i,P|j,P]| \leqslant 0.$$

If $A > 0$, or if $A \geqslant 0$ is irreducible and $k = n-2$, then $|D[i,P|j,P]| < 0$.

Proof. If $k=0$, $|D[i,P|j,P]| = |D[i|j]| = d_{ij} = -a_{ij} \leqslant 0$. If $k=1$, $P=(p)$, then $|D[i,p|j,p]| = d_{ij}d_{pp} - d_{pj}d_{ip} = -a_{ij}(r-a_{pp}) - a_{pj}a_{ip} \leqslant 0$, since $r - a_{pp} \geqslant 0$ by Lemma 2, and $A \geqslant 0$. If $k > 1$, let p be the first element of P and P' be the remaining $k-1$ elements, so that $P = (p, P')$. By a general relation of Muir and Metzler ((7), p. 372, section 387), rediscovered by Stouffer ((10), p. 166) we have

$$|D[i,P|j,P]||D[P']| = |D[i,P'|j,P']||D[P]| - |D[P|j,P']||D[i,P'|P]|.$$

For example, if $i=2$, $j=3$, $k=2$, $n=5$, $P=(4,5)$, then $p=4$, $P'=(5)$ and this identity becomes $|D[245|345]|\cdot|D[5]| = |D[25|35]|\cdot|D[45]| - |D[45|35]|\cdot|D[25|45]|$, which may readily be verified directly. By Lemma 2, $|D[P']| \geqslant 0$ and $|D[P]| \geqslant 0$. By the hypothesis of induction $|D[i,P'|j,P']| \leqslant 0$, $|D[P|j,P']| \leqslant 0$, and $|D[i,P'|P]| \leqslant 0$. Hence $|D[i,P|j,P]| \leqslant 0$. If $A > 0$, all the inequalities in the proof become strict. If $k = n-2$, then, again from (7), p. 372,

$$|D[i,j,P]||D[P]| = |D[i,P]||D[j,P]| - |D[i,P|j,P]||D[j,P|i,P]|.$$

Applying, if necessary, the same permutation to both rows and columns of $D[i,j,P]$, $|D[i,j,P]| = |D| = 0$. Therefore, assuming $A \geqslant 0$ irreducible and using Lemma 2, $|D[i,P|j,P]||D[j,P|i,P]| = |D[i,P]||D[j,P]| > 0$, so $|D[i,P|j,P]| < 0$.

Lemma 4 and Lemma 1 readily provide the explicit formula, for $1 \leqslant i < j \leqslant n$ and an irreducible $A \geqslant 0$, $dr/da_{ij} = -|D[j,P|i,P]|/\sum_{k=1}^{n}|D(k)| > 0$, where P is the strictly increasing sequence of $n-2$ positive integers from 1 to n left after deleting both i and j.

THEOREM 3. *If $A \geqslant 0$, $r = r(A) > 0$, then for $i = 1,\ldots,n$, $d^2r/da_{ii}^2 \geqslant 0$. If A is also irreducible, $d^2r/da_{ii}^2 > 0$.*

Proof. Since all elements of A except a_{11} are fixed, we write the characteristic equation of A as a function of r and a_{11} only: $f(r,a_{11}) = |D| = 0$. Assume A is irreducible. Then

$$d^2r/da_{11}^2 = -(\partial f/\partial r)^{-3}[(\partial^2 f/\partial a_{11}^2)(\partial f/\partial r)^2 - 2(\partial f/\partial r)(\partial f/\partial a_{11})(\partial^2 f/\partial r\,\partial a_{11}) + (\partial^2 f/\partial r^2)(\partial f/\partial a_{11})^2], \quad (2)$$

a standard formula. Lemma 1 gives $\partial f/\partial r = \partial f/\partial x|_{x=r}$ explicitly. Lemma 2 guarantees that $\partial f/\partial r > 0$ since $A \geqslant 0$ is irreducible, so the quotient on the right of equation (2) is defined. Since $|D|$ is linear in each element of A, $\partial^2 f/\partial a_{11}^2 = 0$, so the first term in the square brackets on the right of equation (2) vanishes. As in Theorem 1,

$$\partial f/\partial a_{11} = -|D(1)| < 0.$$

Thus $d^2r/da_{11}^2 > 0$ if and only if

$$\tfrac{1}{2}(\partial^2 f/\partial r^2)(\partial f/\partial a_{11}) - (\partial^2 f/\partial r\,\partial a_{11})(\partial f/\partial r) \equiv b > 0. \quad (3)$$

Lemma 1 implies $\partial^2 f/\partial a_{11}\,\partial r = -\sum_{1<i\leqslant n}|D(1,i)|$ and by substitution

$$\begin{aligned} b &= -\left(\textstyle\sum_{1\leqslant i<j\leqslant n}|D(i,j)|\right)\cdot|D(1)| + \left(\textstyle\sum_{1<i\leqslant n}|D(1,i)|\right)\left(\textstyle\sum_{1\leqslant i\leqslant n}|D(i)|\right) \\ &= \textstyle\sum_{1<i\leqslant n}|D(i)|\sum_{1<i\leqslant n}|D(1,i)| - |D(1)|\sum_{1<i<j\leqslant n}|D(i,j)| \\ &= \textstyle\sum_{1<i\leqslant n}|D(i)|\,|D(1,i)| \\ &\quad + \textstyle\sum_{1<i<j\leqslant n}\left[|D(i)|\,|D(1,j)| + |D(j)|\,|D(1,i)| - |D(1)|\,|D(i,j)|\right]. \end{aligned}$$

In this last expression for b, the first summation is strictly positive by Lemma 2. (When $n = 2$, the first summation reduces to $r - a_{11}$ and the second vanishes, so $b = r - a_{11}$, which may be verified directly.) To show $d^2r/da_{ii}^2 > 0$ it suffices to show that for all i, j satisfying $1 < i < j \leqslant n$ we have

$$|D(i)|\,|D(1,j)| + |D(j)|\,|D(1,i)| - |D(1)|\,|D(i,j)| \equiv g_{ij} \geqslant 0.$$

In terms of the included rows and columns, rather than the excluded rows and columns, $g_{ij} = |D[1,j,P]|\,|D[i,P]| + |D[1,i,P]|\,|D[j,P]| - |D[i,j,P]|\,|D[1,P]|$, where P is the strictly increasing sequence of all positive integers $\leqslant n$ and different from 1, i and j. Now a form due to Stouffer ((9), p. 358), without his restriction that $d_{1m} = 1$, $m = 2, \ldots, n$, gives

$$\begin{aligned} |D[1,i,j]| = |D[1]|\,|D[i,j]| + |D[i]|\,|D[1,j]| + |D[j]|\,|D[1,i]| \\ + d_{1i}d_{ij}d_{j1} + d_{1j}d_{ji}d_{i1} - 2|D[1]|\,|D[j]|\,|D[j]|. \end{aligned}$$

Applying Lemma 3 and noting that $|D[1,i,j,P]| = |D| = 0$ gives

$$\begin{aligned} |D[P]|g_{ij} = {}& 2|D[1,P]|\,|D[i,P]|\,|D[j,P]| \\ & - 2|D[1,P]|\,|D[i,j,P]|\,|D[P]| - |D[1,P|i,P]|\,|D[i,P|j,P]|\,|D[j,P|1,P]| \\ & - |D[1,P|j,P]|\,|D[j,P|i,P]|\,|D[i,P|1,P]|. \end{aligned}$$

By (7), p. 372

$$|D[i,j,P]|\,|D[P]| = |D[i,P]|\,|D[j,P]| - |D[i,P|j,P]|\,|D[j,P|i,P]|.$$

Hence

$$\begin{aligned} |D[P]|g_{ij} = {}& 2|D[i,P|j,P]|\,|D[j,P|i,P]|\,|D[1,P]| \\ & - |D[1,P|i,P]|\,|D[i,P|j,P]|\,|D[j,P|1,P]| \\ & - |D[1,P|j,P]|\,|D[j,P|i,P]|\,|D[i,P|1,P]|. \end{aligned}$$

By Lemma 2 $|D[P]| > 0$ and $D[1,P] > 0$. By Lemma 4, if $i \neq j$, $|D[i,P|j,P]| \leqslant 0$. Hence $g_{ij} \geqslant 0$. Thus $d^2r/da_{11}^2 > 0$ when $A \geqslant 0$ is irreducible.

When $A \geqslant 0$ is reducible, let A_1 be the irreducible square submatrix on the main diagonal in which a_{11} falls in the canonical form of A ((3), p. 75). As in the proof of Corollary 1, there are three cases. If $r(A_1) < r(A)$, then $dr/da_{11} = 0$ and $d^2r/da_{11}^2 = 0$. If $r(A_1) = r(A)$ and A_1 is of order 1×1, then $dr/da_{11} = 1$ and $d^2r/da_{11}^2 = 0$. If $r(A_1) = r(A)$ and A_1 is of order 2×2 or larger, $d^2r/da_{11}^2 > 0$ by applying the proof for the irreducible case to A_1. This proves the theorem.

Corollary 3. *If $A \geqslant 0$ is irreducible, an upper bound for d^2r/da_{11}^2 in terms of the principal minors of $D = rI - A$ is*

$$2\left(\textstyle\sum_{i=1}^{n}|D(i)|\right)^{-3}|D(1)|\left(\textstyle\sum_{1<i\leqslant n}|D(i)|\right)\left(\textstyle\sum_{1<i\leqslant n}|D(1,i)|\right).$$

Let $A \geqslant 0$ be primitive, that is, for some m, $A^m > 0$. For $m = 1, 2, \ldots$, let

$$\mathrm{Tr}\,(A^m) = \textstyle\sum_{i=1}^{n} a_{ii}^{(m)},$$

where $a_{ii}^{(m)}$ is the ith diagonal element of A^m, and let $g_m(a_{11}) = (\mathrm{Tr}\,(A^m))^{1/m}$. Kingman (4) uses the fact that $r = \lim_{m\to\infty} g_m$. Since $d^2g_1/da_{11}^2 = 0$ and $d^2r/da_{11}^2 > 0$ by Theorem 3, one might hope that $d^2g_m/da_{11}^2 \leqslant d^2g_{m+1}/da_{11}^2$, or at least that $d^2g_m/da_{11}^2 \geqslant 0$ for $m = 1, 2, \ldots$. However, it is readily checked that there exist 3×3 matrices $A > 0$ such that $d^2g_3/da_{11}^2 < 0$.

The proof of Theorem 3 by direct calculation yields little insight into why the main diagonal elements of a non-negative matrix play a special role. It may be relevant to note that $\mathrm{Tr}(A^m)$ is a polynomial of degree m in a_{ii}, all other diagonal and off diagonal elements of A held constant, in which the coefficient of a_{ii}^{m-1} is 0, $m = 1, 2, \ldots$. As a function of a_{ij}, $i \neq j$, all other elements held constant, $\mathrm{Tr}(A^{2m})$ is a polynomial of degree m and $\mathrm{Tr}(A^{2m-1})$ is a polynomial of degree $m-1$, $m = 1, 2, \ldots$.

5. *Frobenius normal form*

Theorem 4. *Let A be a non-negative matrix in Frobenius normal form, i.e. $a_{1i} = a_i \geqslant 0$, $i = 1, \ldots, n$, $a_{i+1,i} = 1$, $i = 1, \ldots, n-1$, and all other elements 0. Assume that $a_n > 0$, $a_{n-1} > 0$ and if $n > 2$, then also $a_k > 0$ where $k < n-1$ and $\gcd(k, n-1) = 1$. Then $d^2r/da_1^2 > 0$ and $d^2r/da_n^2 < 0$.*

Proof. We calculate d^2r/da_i^2 for $i = 1, \ldots, n$, using equation (2) with a_i replacing a_{11}, and show the claimed inequalities when $i = 1$ and $i = n$. The assumptions about the first row of A ensure that A and $A(n)$ are irreducible, in fact, primitive. Since

$$0 = f(r, a_i) = |rI - A| = r^n - a_1 r^{n-1} - a_2 r^{n-2} - \ldots - a_n,$$

we have

$$\begin{aligned}\partial f/\partial r &= nr^{n-1} - \textstyle\sum_{j=1}^{n-1}(n-j)\,a_j\,r^{n-1-j},\\ \partial^2 f/\partial r^2 &= n(n-1)\,r^{n-2} - \textstyle\sum_{j=1}^{n-2}(n-j)\,(n-j-1)\,a_j\,r^{n-2-j},\\ \partial f/\partial a_i &= -r^{n-i}, \quad \partial^2 f/\partial a_i^2 = 0, \quad \partial^2 f/\partial r\,\partial a_i = -(n-i)\,r^{n-i-1}.\end{aligned}$$

Since r is the largest real root of f and $\lim_{x\to\infty} f(x, a_i) = +\infty$, we have $\partial f/\partial r > 0$. Because $\partial f/\partial a_i < 0$, the sign of d^2r/da_i^2 is the opposite of the sign of

$$\alpha \equiv 2(\partial f/\partial r)\,(\partial^2 f/\partial r\,\partial a_i) - (\partial^2 f/\partial r^2)\,(\partial f/\partial a_i).$$

(If a_{11} is replaced by a_i in the definition of b in equation (3), then $\alpha = -2b$.) After substitution and rearrangement

$$\alpha = n(-n-1+2i)\,r^{2(n-1)-i} + \textstyle\sum_{j=1}^{n-1}(n-j)\,(n+1+j-2i)\,a_j\,r^{2(n-1)-i-j}. \tag{4}$$

When $i = 1$,

$$\alpha = -r^{n-2}[n(n-1)\,r^{n-1} - \textstyle\sum_{j=1}^{n-1}(n-j)\,(n-1+j)\,a_j\,r^{n-1-j}] = -r^{n-2}n(n-1)\,F(r),$$

where

$$F(r) = r^{n-1} - [n(n-1)]^{-1}\textstyle\sum_{j=1}^{n-1}(n-j)\,(n-1+j)\,a_j\,r^{n-1-j} = |rI_{(n-1)\times(n-1)} - B|.$$

Here $B = (b_{ij}) \geqslant 0$ is a matrix of order $(n-1)\times(n-1)$ in Frobenius normal form with with $b_{1j} = [n(n-1)]^{-1}(n-j)(n-1+j)a_j, j = 1,\ldots,n-1$. Since

$$0 < (n-j)(n-1+j) \leqslant n(n-1)$$

for $j = 1,\ldots,n-1$, $B \leqslant A(n)$, $B \neq A(n)$, so $r(B) < r(A(n)) < r = r(A)$. Therefore $F(r) > 0$, $\alpha < 0$, and $d^2r/da_1^2 > 0$.

When $i = n$, $\alpha = +n(n-1)r^{-1}G(r)$ where

$$G(r) = r^{n-1} - [n(n-1)]^{-1}\textstyle\sum_{j=1}^{n-1}(n-j)(n-1-j)a_j r^{n-1-j} = |rI_{(n-1)\times(n-1)} - C|.$$

Here $C = (c_{ij}) \geqslant 0$ is a matrix of order $(n-1)\times(n-1)$ in Frobenius normal form with $c_{1j} = [n(n-1)]^{-1}(n-j)(n-1-j)a_j$. For $j = 1,\ldots,n-1$, $0 \leqslant (n-j)(n-1-j) < n(n-1)$ so $C \leqslant A(n)$, $C \neq A(n)$ and $r(C) < r(A(n)) < r$. Therefore $G(r) > 0$, $\alpha > 0$, and $d^2r/da_n^2 < 0$. This proves Theorem 4.

COROLLARY 4. *Under the assumptions of Theorem* 4, $d^2r/da_{n-1}^2 < 0$ *for* $n = 3$ *and* $n = 4$.

Proof. When $n = 3$ and $n = 4$, $i = n-1$, $\alpha > 0$ in equation (4).

6. *Demographic applications.* Demographic models often employ the Leslie (6) matrix

$$L = \begin{pmatrix} b_1 & b_2 & \ldots & b_{n-1} & b_n \\ s_1 & 0 & \ldots & 0 & 0 \\ 0 & s_2 & \ldots & 0 & 0 \\ & & \ldots & & \\ 0 & 0 & \ldots & s_{n-1} & 0 \end{pmatrix},$$

where s_i is the proportion of individuals in age class i who survive from one discrete time-point to the next, and b_i is the birth rate per individual in age class i, adjusted for the survival of newborn individuals to the next time-point.

COROLLARY 5. *Let L be a Leslie matrix of order $n \times n$, $n \geqslant 2$, with $s_i > 0$, $i = 1,\ldots,n-1$ and $b_i \geqslant 0$ satisfying the assumptions made in Theorem 4 regarding the a_i, $i = 1,\ldots,n$. Then $r(L)$ is a strictly convex function of b_1, all other elements of L held constant. $r(L)$ is a strictly concave function of $(s_{n-1}b_n)$, all other elements of L held constant. When $n = 3$ and $n = 4$, $r(L)$ is a strictly concave function of b_{n-1}, all other elements of L held constant.*

Proof. By the Danilevsky algorithm ((2), p. 167), L is similar to a matrix A in Frobenius normal form with $a_1 = b_1$, $a_i = b_i\prod_{j=1}^{i-1}s_j$, $i = 2,\ldots,n$. This matrix A satisfies the assumptions of Theorem 4, and has the same spectrum as L.

Some interpretations of Corollary 5 are immediate. $r(L)$ is the long-run growth rate per unit time of a closed age-structured population with constant vital rates given by L. If a population adjusts its vital rates, equal successive increments in b_1 will yield successively increasing increments in $r(L)$, while equal successive increments in $s_{n-1}b_n$ will yield positive but successively decreasing increments in $r(L)$. Conversely, each successive reduction by a fixed amount in b_1 will result in successively smaller reductions in $r(L)$, while each successive reduction by a fixed amount in $s_{n-1}b_n$ will result in successively larger reductions in $r(L)$. These observations do not bear on comparing the effect on $r(L)$ of a given change in b_1 with a given change in $s_{n-1}b_n$.

Corollary 5 also provides useful bounds in the framework of a stochastic population model. If, at each point in discrete time, a population's vital rates are given by one of k Leslie matrices $L^{(i)}$, $i = 1, \ldots, k$, chosen with probability π_i, $\sum_{i=1}^{k}\pi_i = 1$, independently of the Leslie matrix occurring at any other time, and if each $L^{(i)}$ satisfies the assumptions of Corollary 5, then the long-run rate of growth r^* of the population is (1)

$$r^* = r(\textstyle\sum_{i=1}^{k}\pi_i L^{(i)}).$$

If the $L^{(i)}$ are all identical except for $b_1^{(i)}$, then by Corollary 5 and Jensen's inequality, $r^* < \sum_{i=1}^{k}\pi_i r(L^{(i)})$. If the $L^{(i)}$ are all identical except for $s_{n-1}^{(i)}b_n^{(i)}$, then $r^* > \sum_{i=1}^{k}\pi_i r(L^{(i)})$.

This work was supported in part by the U.S. National Science Foundation grant BMS74-13276.

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