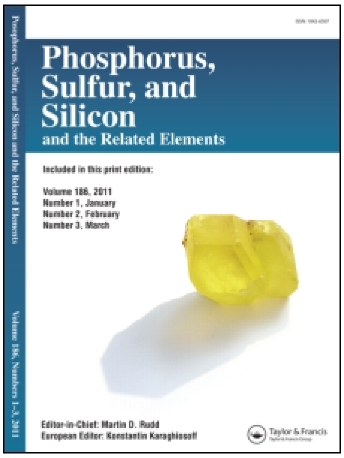

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C. D. Reddy[a]; B. S. Reddy[a]; P. M. Reddy[a]; K. D. Berlin[a]; K. M. Coucj[a]; S. Tyagi[a]; M. B. Houssain[a]; D. Van der Helm[a]
[a] Department of Chemistry, 107 Physical Sciences, Stillwater, OK

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ERRATUM

C. D. Reddy, B. S. Reddy, P. M. Reddy, K. D. Berlin*, K. M. Coucj, S. Tyagi, M. B. Houssain and D. Van der HELM

Department of Chemistry, 107 Physical Sciences, Stillwater, OK 74078-3071

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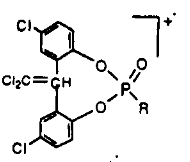
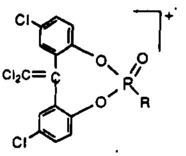
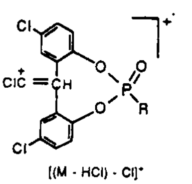
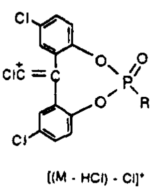
Corrections as follows:

Page	*Line*	*Existing Error*	*To be Corrected as*
152	Scheme	Toluene [2l–2o]	Toluene [2l–2m]
153	Footnote	[a]Data is	[a]Data in
156	Mass Scheme	 [M - HCl]$^{+\cdot}$	 [M - HCl]$^{+\cdot}$
156	Mass Scheme	 [(M - HCl) - Cl]$^{+}$	 [(M - HCl) - Cl]$^{+}$
157	18	P1-O2-07	P1-O2-C7
159	ACKNOWLEDGEMENTS	BSR and PNR	BSR and PMR

Phosphorus, Sulfur, and Silicon and the Related Elements, Vol. **115**, 149–160, C. D. Reddy, B. S. Reddy, P. M. Reddy, K. D. Berlin, K. M. Couch, S. Tyagi, M. B. Houssain, and D. Van der Helm.

*Corresponding author.

where

$$c \doteq \left[w_0 + w_1 p + \ldots + w_{m-1} p^{m-1} + w_m p^m \frac{1}{1-p} \right]^{-1}.$$

and

$$w = f^{-1}\left(\frac{1}{n_0}\right).$$

Since $n'(w) = n_0 f'(w) < 0$, Corollary 1 implies that the positive equilibrium is (locally asymptotically) stable if

$$|n'(w)| x_0 = bc \frac{p^m}{1-p} w |f'(w)|$$

is sufficiently small, i.e. if w is sufficiently small or (by (30)) sufficiently large. (In [26] it is proved that the positive equilibrium $\vec{x}^*$ is stable if $0 > n'(w^*) x^*_0 > -p$.)

6 DISCUSSION

The magnitude of the "inherent" net reproductive number $n(\vec{0})$ (often denoted R_0 in the literature) determines the (local) stability properties of the trivial equilibrium $\vec{x} = \vec{0}$ of the nonlinear matrix equation (13) [5],[7]. At a nontrivial equilibrium $\vec{x}$, however, the net reproductive number $n(\vec{x})$ always equals one and therefore its magnitude cannot be used to determine the stability properties of the equilibrium. In this paper we have investigated the relationship between nontrivial equilibrium stability and the variation of n near the equilibrium. In our main result we showed in Theorem 1, for models in which the nonlinear dependence is through a dependence on a weighted total population size $w = \vec{w}'\vec{x}$, that the inequality $n'(w) \leq 0$ is necessary for the (local asymptotic) stability of a positive equilibrium. Although the converse of this result is false, Theorem 4 gives conditions under which $n'(w) < 0$ implies (local asymptotic) stability of a positive equilibrium.

The nonlinearities in most matrix population models appearing in the literature do in fact arise through a dependence on a weighted total population size w. Some, however, do not and it is natural to ask whether our main result in Theorem 1 can be generalized to the matrix equation (2) when $F = F(\vec{x})$ and P

$= P(\vec{x})$. One natural conjecture for a generalization of Theorem 1 is that $\nabla_{\vec{x}} n(\vec{x}) \leq \vec{0}$ is a necessary condition for the stability of a positive equilibrium $\vec{x}$ of equation (2). The following example shows that this conjecture is, however, false.

Consider the two dimensional, nonlinear Leslie matrix equation with fertility and transition matrices

$$F(x_0,x_1) = \begin{pmatrix} \frac{9}{10}e^{x_0+x_1-2} & \frac{1}{10} \\ 0 & 0 \end{pmatrix}$$

$$P(x_0,x_1) = \begin{pmatrix} 0 & 0 \\ \frac{1}{2}e^{-7(x_0-1)} & \frac{1}{2}e^{-4(x_1-1)} \end{pmatrix}.$$

This matrix equation has the positive equilibrium $(x_0, x_1) = (1, 1)$. The Jacobian evaluated at this equilibrium

$$J(1, 1) = \begin{pmatrix} \frac{9}{5} & 1 \\ -3 & -\frac{3}{2} \end{pmatrix}$$

has eigenvalues $\lambda = \frac{3}{20} \pm \frac{1}{20} i\sqrt{111}$ whose magnitudes

$|\lambda| = |\frac{3}{20} \pm \frac{1}{20} i\sqrt{111}\,| = \frac{1}{10}\sqrt{30}$ are less than one. Thus, the positive equilibrium $(1, 1)$ is locally asymptotically stable. The net reproductive number is given by

$$n(x_0,x_1) = \frac{9}{10}e^{x_0+x_1-2} + \frac{1}{10}e^{-7(x_0-1)}\frac{1}{1-e^{-4(x_1-1)}}$$

from which the gradient at the equilibrium can readily be calculated to be

$$\nabla_{\vec{x}} n(1,1) = \left(\frac{1}{5}, \frac{1}{2}\right).$$

Thus, it is seen that $\nabla_{\vec{x}} n \leq \vec{0}$ is, in general, not necessary for (local asymptotic) stability.

It would be interesting to determine additional conditions under which $\nabla_{\vec{x}} n \leq \vec{0}$ is a necessary condition for equilibrium stability.

As a final remark, we point out a connection between the net reproductive number n and the "population growth rate" $\lambda = \lambda(\vec{x})$, defined as the dominant eigenvalue of the (nonnegative and irreducible) projection matrix $A(\vec{x})$. If $\vec{p} = \vec{q}(\vec{x})$ is the associated eigenvector, a partial differentiation of $A(\vec{x})\vec{q}(\vec{x}) = \lambda(\vec{x})\vec{q}(\vec{x})$ yields

$$\frac{\partial A}{\partial x_i}\vec{q} + A\frac{\partial \vec{q}}{\partial x_i} = \frac{\partial \lambda}{\partial x_i}\vec{q} + \lambda\frac{\partial \vec{q}}{\partial x_i}.$$

When $\vec{x}$ is an equilibrium, $\lambda(\vec{x}) = 1$ and $\vec{q}(\vec{x}) = \vec{x}$, and this equation, after an inner product by the left eigenvector $\vec{u}^T = \vec{u}^T(\vec{x})$ of $A(\vec{x})$, yields

$$\frac{\partial \lambda}{\partial x_i} = \frac{\vec{u}^T \dfrac{\partial A(\vec{x})}{\partial x_i} \vec{x}}{\vec{u}^T \vec{x}}.$$

This formula, together with (11), gives

$$\frac{\partial \lambda}{\partial x_i} = \frac{\vec{u}^T F(\vec{x})\vec{x}}{\vec{u}^T} \frac{\partial n}{\partial x_i}.$$

In the case of dependence on weighted total population size $\lambda = \lambda(w)$, this formula in turn yields the relationship

$$\lambda'(w) = \frac{\vec{u}^T F(w)\vec{x}}{\vec{u}^T\vec{x}} n'(w)$$

between the derivatives $\lambda'(w)$ and $n'(w)$ at equilibrium. Thus, these two derivatives have the same sign and $\lambda'(w)$ *can replace* $n'(w)$ *in our theorems*. For example, by Theorem 1, $\lambda'(w) \leq 0$ is a necessary condition for equilibrium stability. One advantage of working with the net reproductive rate n is that explicit formulas can often be obtained for it in terms of the entries in the fertility and transition (e.g. see (17) for nonlinear Usher models)[7]; such formulas for λ are unavailable.

7 APPENDIX

7.1 The proof of Theorem 1

The positive equilibrium $\vec{x}$ is a right eigenvector belonging to the eigenvalue 1 of the irreducible projection matrix $A(\vec{x})$. Thus, 1 is dominant and simple; thus, if $\vec{v}$ satisfies $A(\vec{x})\vec{v} = \vec{v} \neq \vec{0}$, then $\vec{v} = c\vec{x}$ for some constant $c \neq 0$. The irreducibility of the matrix A also implies that there exists a positive left eigenvector $\vec{u}^{T}$, such that $\vec{u}^{T} A = \vec{u}^{T}$. If a vector $\vec{y}^{T} \neq \vec{0}$ satisfies the equation $\vec{y}^{T} A = \vec{y}^{T}$, then there exists a nonzero constant d, such that $\vec{y}^{T} = d\vec{u}^{T}$.

Define the column vectors $\vec{r}_i = (s_{i0},s_{i1},\ldots,s_{im})^{T}$ for $i = 0,1,\ldots,m$. The vector $\vec{r}_i$ is the transpose of the i^{th} row vector of the cofactor matrix S. By using the properties of determinants it is readily verified that, if nonzero, the vector $\vec{r}_i$ is a right eigenvector belonging to eigenvalue 1 of the matrix A. Similarly, if nonzero, the row vectors $\vec{l}_j = (s_{0j},s_{1j},\ldots,s_{mj})$ for $j = 0,1,\ldots,m$ are left eigenvectors belonging to the eigenvalue 1 of the matrix A. The vector $\vec{l}_j$ is the transpose of the j^{th} column vector of the matrix S.

By the assumption that $s_{ii} > 0$ for all i it follows that both $\vec{r}_i$ and $\vec{l}_j$ are nonzero and are eigenvectors. Thus, $\vec{r}_i = c_i\vec{x}$ and $\vec{l}_j = d_j\vec{u}$. From the first components, we obtain $c_i = \dfrac{s_{i0}}{x_0}$ and $d_j = \dfrac{s_{0j}}{u_u}$ and hence

$$\vec{r}_i = \frac{s_{i0}}{x_0}\vec{x}, \qquad \vec{l}_j = \frac{s_{0j}}{u_0}\vec{u}.$$

Thus,

$$\vec{w}^{T}\vec{r}_i = \frac{w}{x_0}s_{i0}.$$

By using appropriate column operations a straight forward calculation shows

$$\det(I - J) = \det(I - A) + \sum_{k=0}^{m} w_k \det A'_k$$

where A'_k is a $(m + 1) \times (m + 1)$ matrix $I - A$ with its k^{th} column replaced by the column vector $-\vec{h} = -A'\vec{x}$. Using the fact that at equilibrium, $\det(I - A) = 0$ and by expanding the determinant $\det A'_k$ by its k^{th} column, we obtain

$$\det(I - J) = -\sum_{k=0}^{m} w_k \sum_{j=0}^{m} h_j s_{jk} = -\sum_{j=0}^{m} \left(\sum_{k=0}^{m} w_k s_{jk} \right) h_j$$
$$= -\sum_{j=0}^{m} \vec{w}^T \vec{r}_j h_j = -\frac{w}{x_0} \sum_{j=0}^{m} s_{j0} h_j$$
$$= -\frac{w}{x_0} \vec{l}^T \vec{h} = -\frac{w}{x_0} \vec{l}_0^T A' \vec{x}$$
$$= -\frac{w}{x_0} \frac{s_{00}}{u_o} \vec{u} A' \vec{x}.$$

From the formula in (14) we obtain finally that

$$\det(I - J) = -\frac{w s_{00} \vec{u}^T F(w) \vec{x}}{x_0 u_0} n'(w) \qquad (32)$$

The characteristic equation $\det(\lambda I - J)$ of the linearized model (18) is a polynomial of degree $m + 1$, and the coefficient of the highest term λ^{m+1} is 1. Therefore, if $n'(w) > 0$, (32) implies that $\det(I - J) < 0$ and consequently there exists at least one real eigenvalue λ which is larger than 1. This proves that the positive equilibrium $\vec{x}$ of (13) is unstable.

7.2 Proof of Theorem 2

Assume that $n'(w) > 0$. Then the dominant eigenvalue $n((1 + \varepsilon)w)$ of the matrix $R(\varepsilon) \doteq (I - P((1 + \varepsilon)w))^{-1} F((1 + \varepsilon)w)$ is greater then 1 if $\varepsilon > 0$ is sufficiently small. Therefore, the dominant eigenvalue $\lambda(\varepsilon)$ of $A(\varepsilon) = F((1 + \varepsilon)w) + P((1 + \varepsilon)w)$ is also greater than 1 when $\varepsilon > 0$ is sufficiently small.[7] Let $\vec{v}(\varepsilon)$ be the corresponding eigenvalue to $\lambda(\varepsilon)$, i.e.

$$A(\varepsilon)\vec{v}(\varepsilon) = \lambda(\varepsilon)\vec{v}(\varepsilon).$$

If in this equation we substitute the expansions

$$\lambda(\varepsilon) = 1 + \lambda_1 \varepsilon + \cdots$$
$$\vec{v}(\varepsilon) = \vec{x} + \vec{v}_1 \varepsilon + \cdots$$
$$A(\varepsilon) = A(w) + wA'(w)\varepsilon + \cdots$$

and equate the first order ε coefficients, we obtain

$$(A(w) - I)\,\vec{v}_1 = \lambda_1\vec{x} - wA'(w)\vec{x}$$

which has a solution if and only if the right hand side is orthogonal to the left eigenvector $\vec{x}^T$ of $A(w)$. Without loss in generality we assume that $\vec{x}$ is a unit vector, i.e. $\vec{u}^T\vec{u} = 1$. Thus,

$$\lambda_1 = w\,\frac{\vec{u}^T A'(w)\vec{x}}{\vec{u}^T \vec{x}}.$$

The fact that $\lambda(\varepsilon) > 1$ for small $\varepsilon > 0$ implies that $\theta \doteq \vec{u}^T A'(w)\vec{x} > 0$. From the formula $J(w) \doteq A(w) + A'(w)\vec{x}\vec{w}^T$ for the Jacobian we obtain

$$\vec{u}J = \vec{u}A + \vec{u}A'\vec{x}\vec{w}^T = \vec{u}^T = \theta\vec{w}^T$$

and

$$\vec{u}^T JJ^T\vec{u} = 1 + 2\theta\vec{w}^T\vec{u} + \theta^2\vec{w}^T\,\vec{w} > 1. \qquad (33)$$

The normality of the matrix J implies that the matrix J^TJ is symmetric and therefore has real eigenvalues (and a complete set of orthogonal eigenvectors).[12] It follows form (33) that the matrix JJ^T has at least one eigenvalue $\lambda_0 > 1$. If we let $\vec{z}(0)$ be the eigenvector corresponding to λ_0 of matrix $J^T J$, then the resulting solution of the linearized equation $\vec{z}(t + 1) = J\vec{z}(t)$ is exponentially unbounded; specifically

$$\lim_{t\to\infty} \vec{z}(t)^T\vec{z}(t) = \lim_{t\to\infty} \lambda_0^t\vec{z}^T(0)\vec{z}(0) = +\infty.$$

Thus, the positive equilibrium of (13) is unstable.

7.3 Proof of Theorem 3

The Jacobian J of the linearized model at $\vec{x}$ has the form (18)

$$J(w) = A(w) + A'(w)\vec{x}\vec{w}^T$$

Let $\vec{u}^T$ be the unit left positive eigenvector corresponding to eigenvalue 1 of matrix $A(w)$) and define $\varepsilon \doteq |A'(w)\vec{x}|$. Recall from (14) that

$$n'(w) = \frac{\vec{u}^{\mathsf{T}} A'(w)\vec{x}}{\vec{u}^{\mathsf{T}} F(w)\vec{x}}.$$

The positive equilibrium $\vec{x}$ is an eigenvector of $A(w)$ associated with eigenvalue 1. The irreducibility and primitivity of matrix $A(w)$ implies that 1 is a strictly dominant, simple eigenvalue [13]. From the formula for J it follows that if ε is sufficiently small J has a strictly dominant, simple eigenvalue λ_b near 1. Let $\vec{y}^{\mathsf{T}}$ be the left unit eigenvector of matrix J corresponding to λ_b; that is

$$\vec{y}^{\mathsf{T}} A(w) + \vec{y}^{\mathsf{T}} A'(w)\vec{x}\vec{w}^{\mathsf{T}} = \lambda_b \vec{y}^{\mathsf{T}}.$$

As $\varepsilon \to 0$, note that $J \to A$ and $\vec{y} \to \vec{u}^{\mathsf{T}}$. From this equation subtract

$$\vec{u}^{\mathsf{T}} A(w) = \vec{u}^{\mathsf{T}}$$

to obtain

$$(\vec{y}^{\mathsf{T}} - \vec{u}^{\mathsf{T}})\, A(w) + \vec{y}^{\mathsf{T}} A'(w)\vec{x}\vec{w}^{\mathsf{T}} = \lambda_b \vec{y}^{\mathsf{T}} - \vec{y}^{\mathsf{T}} + \vec{y}^{\mathsf{T}} - \vec{u}$$

or

$$(\vec{y}^{\mathsf{T}} - \vec{u}^{\mathsf{T}})\,(A(w) - I) = (\lambda_b - 1)\, \vec{y}^{\mathsf{T}} - \vec{y}^{\mathsf{T}} A'(w)\vec{x}\vec{w}^{\mathsf{T}}.$$

The singularity of $A(w) - I$ requires that the right hand side by orthogonal to the right nullspace of $A(w) - I$, i.e. orthogonal to the equilibrium $\vec{x}$. This yields

$$(\lambda_b - 1)\, \vec{y}^{\mathsf{T}} \vec{x} = \vec{y}^{\mathsf{T}} A'(w)\vec{x}\vec{w}^{\mathsf{T}} \vec{x}$$

or

$$\lambda_b - 1 = \frac{\vec{y}^{\mathsf{T}} A'(w)\vec{x}\vec{w}^{\mathsf{T}} \vec{x}}{\vec{y}^{\mathsf{T}} \vec{x}}.$$

Thus, for ε sufficiently small

$$\lambda_b - 1 \approx \frac{\vec{u}^{\mathsf{T}} A'(w)\vec{x}\vec{w}^{\mathsf{T}} \vec{x}}{\vec{u}^{\mathsf{T}} \vec{x}} = n'(w)\, \frac{\vec{u}^{\mathsf{T}} F(w)\vec{x}\vec{w}^{\mathsf{T}}\vec{x}}{\vec{u}^{\mathsf{T}} \vec{x}}$$

and the sign of $\lambda_b - 1$ is the same as that of $n'(w)$. If $n'(w) > 0$ then $\lambda_b > 1$ and the equilibrium $\bar{x}$ is unstable. On the other hand if $n'(w) < 0$ then the dominant eigenvalue λ_b of the Jacobian J is less than 1 and the equilibrium $\bar{x}$ is (locally asymptotically) stable. This proves the theorem.

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