

Equilibrium and local stability in a logistic matrix model for age-structured populations

Laifu Liu¹ and J. E. Cohen²

¹ Department of Mathematics, Beijing Normal University, Beijing, China

² Department of Mathematics, Rockefeller University, 1230 York Avenue, New York, NY 10021-6399, USA

Abstract. A logistic matrix model for age-structured population dynamics is constructed. This model discretizes a continuous, density-dependent model with age structure, i.e. it is an extension of the logistic model to the case of age-dependence. We prove the existence and uniqueness of its equilibrium and give a necessary and sufficient condition for the local stability of the equilibrium.

1. Introduction

The dynamics of a population with age structure, closed to immigration and emigration, are described by McKendrick (1926) and von Foerster (1959) as

$$\begin{aligned} \partial u / \partial a + \partial u / \partial t &= -\mu(a)u(a, t), \\ u(0, t) &= \int_0^m f(a)u(a, t) da, \end{aligned} \quad (1)$$

where age a and time t are continuous variables, $u(a, t)$ is population density, m is the maximum attainable age, $f(a)$ is fertility and $\mu(a) > 0$ is the force of mortality at age a . The McKendrick–von Foerster equation (1) is equivalent to Lotka’s renewal integral equation model for population dynamics (Lotka (1925)).

Density dependence is a ubiquitous theme in population ecology. In general, fertility and mortality are functions of age a and functionals of density $u(a, t)$. In von Foerster’s model, fertility and mortality may be replaced by $F(u)(a, t)$ and $D(u)(a, t)$, respectively. Fertility and mortality may be specified in other ways as well. In a frequently studied case, these vital rates are functions of the total population

$$N(t) = \int_0^m u(a, t) da,$$

or of a weighted average of the density function with respect to age. This is an example of a nonlinear model for population dynamics.

A significant advance by Gurtin and MacCamy (1974) led to further investigations of nonlinear models. Gurtin and MacCamy (1974, 1979) and Gurney and Nisbet (1980) allow F and D to depend on age and total population. Sinestrari (1980) studies the case in which F and D are functions of age a and current population $u(a, t)$. Rorres (1976, 1979) and Blasio et al. (1982) assume that fertility depends on population size defined as a weighted average of the density function, while mortality depends only on age.

A special case is studied by Marcati (1982) in which D is assumed to be a linear function of the total population. His model is age-dependent with a logistic-type nonlinear death rate. Marcati assumes that different age groups are affected by each age group at different rates. Thus F and D are functionals of density $u(a, t)$. Rotenberg (1975) and Cushing (1984) also investigate this general case. Rotenberg takes the simplest nonlinear example of a death rate that depends on the population to be one in which population enters as a linear functional, such that

$$D(u)(a, t) = \mu(a) + \int_0^m \gamma(a, \xi)u(\xi, t) d\xi,$$

where $\gamma(a, \xi)$ is the density-dependent effect of the population aged ξ on the mortality of the population aged a . This is a natural extension of Marcati's model. Webb (1985, pp. 263–269) reviews an age-structured logistic population model with density-dependent mortality (but linear fertility) and gives extensive references.

To model density-dependent fertility, let

$$F(u)(a, t) = f(a) \exp\left\{-\int_0^m \tilde{\gamma}(a, \xi)u(\xi, t) d\xi\right\},$$

where $\tilde{\gamma}(a, \xi)$ is the density-dependent effect of the population aged ξ on the fertility of the population aged a . Then the model for density dependence is

$$\partial u / \partial a + \partial u / \partial t = -\mu(a)u(a, t) - \left[\int_0^m \gamma(a, \xi)u(\xi, t) d\xi\right]u(a, t), \quad (2)_1$$

$$u(0, t) = \int_0^m f(a) \exp\left\{-\int_0^m \tilde{\gamma}(a, \xi)u(\xi, t) d\xi\right\}u(a, t) da. \quad (2)_2$$

This is a natural extension of the logistic model to the case of age dependence.

It is necessary to extend the logistic model to describe age dependence because the original model fails to take into account the effects of age differences in a population. For example, Lloyd (1965, 1968) showed that, when crowded together, there are complex interactions between flour beetles (*Tribolium castaneum*) that are at different stages in the life cycle. Consequently, he found a rather poor agreement between the counts of adult beetles and the best fitting logistic curve. Varley (1974) concluded: "This experiment suggests that the attempts to explain the adult curve in terms of the Verhulst–Pearl equation fail partly because the equation completely neglects the changing age structure of population The logistic equation, therefore, seems unsuitable to describe the growth of insect populations where the rate of increase is normally high and

the longevity of different age classes is long relative to the time periods considered."

Observed biological data are often presented in discrete form. For this reason, matrix models are very useful for biologists. Moreover, matrix calculations are easy. One of the most famous models in population ecology is the Bernadelli-Lewis-Leslie matrix model developed by Bernadelli (1941), Lewis (1942) and Leslie (1945). This model deals primarily with simple birth and death processes in populations.

The Bernadelli-Lewis-Leslie matrix model has been studied extensively. Leslie (1948) considers cases in which some of the elements of the model are density-dependent. His investigation is limited to cases in which density dependence acts on either survival or fertility, but not both, and requires that these elements be proportional to a given function of the total population size. Ziebur (1984) gives a closed-form solution of a density-dependent age-structured logistic model of Leslie (1948). Pennycuick et al. (1968) and Pennycuick (1969) simulate by computer the trajectory of a population under a density-dependent Bernadelli-Lewis-Leslie matrix model in which the fertility and survival elements are proportional to separate functions of the total population. Cook and Léon (1976) discuss stability for a 2×2 matrix model with density dependence. The behavior of the Bernadelli-Lewis-Leslie matrix model with density-dependent fertility is investigated by Guckenheimer et al. (1977) and by Levin and Goodyear (1980). Fisher and Goh (1984) study the stability of a special matrix model with density-dependent fertility in which only individuals in the oldest age group are reproductive.

The ordinary Bernadelli-Lewis-Leslie matrix model corresponds to a discretization of the continuous model (1). If model (2) is regarded as an age-structured extension of the logistic model, then what kind of matrix model discretizes (2)? Furthermore, what can be said about the equilibrium and stability of such a model? We shall prove the existence and uniqueness of equilibrium, and give a necessary and sufficient condition for local stability.

Much detailed analysis is required here to establish the existence and uniqueness of the equilibrium. It seems likely that the same analytical techniques could be applied to more general nonlinear matrix equations that retain key properties of the nonlinearities we assume, or that our laboriously attained results follow more easily from general facts about iterations of nonlinear maps. Both of these possibilities remain to be explored in future work.

Elsewhere we will give methods to estimate the parameters of this model and apply the model to data.

2. The model

If a population is observed at discrete points in time, spaced one unit apart, then time t and age a are discrete variables. Let both t and a be integers such that $t = k$, $a = i$, $k = 0, 1, 2, \dots$, and $i = 0, 1, \dots, m$. The population size of individuals of age a where $i \leq a < i + 1$ at time t is denoted

$$n_i(t) = \int_0^1 u(i+h, t) dh, \quad i = 0, 1, \dots, m-1, \quad (3)$$

and called the i th age group of the population at time t . Because we are interested in population size only at discrete times $t = k$, we have the approximation

$$n_i(k) \approx n_i(k+h), \quad 0 \leq h < 1. \quad (4)$$

Assume that

1. $\mu(a) = \mu_i$ and $f(a) = f_i$, where $i \leq a < i+1$, $i = 0, 1, \dots, m-1$;
2. $\gamma(a, \xi) = \gamma_{ij}$ and $\tilde{\gamma}(\hat{a}, \xi) = \tilde{\gamma}_{ij}$, where $i \leq a < i+1$, $j \leq \xi < j+1$, $i, j = 0, 1, \dots, m-1$.

Consider model (2) on the characteristic $(a+h, t+h)$ through (a, t) . We have

$$\partial u / \partial a + \partial u / \partial t = \lim_{\Delta h \rightarrow 0} [u(a+h+\Delta h, t+h+\Delta h) - u(a+h, t+h)] / \Delta h.$$

Let $\bar{u}(h) = u(a+h, t+h)$. Then Eq. (2) implies that

$$d\bar{u}/dh = \left[-\mu(a+h) - \int_0^m \gamma(a+h, \xi) u(\xi, t+h) d\xi \right] \bar{u}(h).$$

Integrating this with respect to h on the interval $[0, 1)$ gives

$$u(a+1, t+1) = u(a, t) \exp \left\{ - \int_0^1 \mu(a+h) dh - \int_0^1 \int_0^m \gamma(a+h, \xi) u(\xi, t+h) d\xi dh \right\}.$$

Taking into account assumptions 1 and 2 with $a = i$, $t = k$, we have

$$u(i+1, k+1) = u(i, k) \exp \left\{ -\mu_i - \sum_{j=0}^{m-1} \gamma_{ij} \int_0^1 n_j(k+h) dh \right\},$$

$$i = 0, 1, \dots, m-1 \quad \text{and} \quad k = 0, 1, \dots$$

If, instead of integrating in (3), we replace $u(i+h, t)$ by $u(i, t)$ so that $n_i(t) \approx u(i, t)$, and use this with (4), we have

$$n_{i+1}(k+1) = n_i(k) \exp \left\{ -\mu_i - \sum_{j=1}^m \gamma_{ij} n_j(k) \right\}, \quad i = 1, 2, \dots, m.$$

Let $s_i = e^{-\mu_i}$ be the survival proportion of the population in the i th age group. We assume henceforth that $s_i < 1$. Thus

$$n_{i+1}(k+1) = n_i(k) s_i \exp \left\{ - \sum_{j=1}^m \gamma_{ij} n_j(k) \right\}, \quad i = 1, \dots, m. \quad (5)$$

For the discrete case, we must consider the possibility that reproduction rises throughout the time interval $[t-1, t)$. The boundary condition $(2)_2$ must be changed to

$$\int_0^1 u(h, t) dh = \int_0^1 \left\{ \int_0^m f(a) \exp \left[- \int_0^m \tilde{\gamma}(a, \xi) u(\xi, t-h) d\xi \right] u(a, t-h) da \right\} dh.$$

Taking $t = k$, we have

$$\begin{aligned} n_1(k) &= \int_0^1 \left\{ \sum_{i=0}^{m-1} \int_i^{i+1} f(a) \exp \left[- \sum_{j=0}^{m-1} \int_j^{j+1} \tilde{\gamma}(a, \xi) u(\xi, k-h) d\xi \right] u(a, k-h) da \right\} dh \\ &= \int_0^1 \left\{ \sum_{i=0}^{m-1} f_i \exp \left[- \sum_{j=0}^{m-1} \tilde{\gamma}_{ij} \int_0^1 u(j+\xi, k-h) d\xi \right] \int_0^1 u(i+a, k-h) da \right\} dh \\ &= \int_0^1 \left\{ \sum_{i=0}^{m-1} f_i \exp \left[- \sum_{j=0}^{m-1} \tilde{\gamma}_{ij} n_j(k-h) \right] n_i(k-h) \right\} dh. \end{aligned}$$

Using (4), we have approximately

$$n_1(k+1) = \sum_{i=1}^m f_i \exp \left\{ - \sum_{j=1}^m \tilde{\gamma}_{ij} n_j(k) \right\} n_i(k). \tag{6}$$

Together (5) and (6) are a discrete form of the logistic model (2).

Let $\bar{N}(k) = (n_1(k), \dots, n_m(k))^T$ denote the population vector at time k , where T denotes the transpose. F and S are fertility and survivorship matrices, respectively, as follows:

$$F = \begin{pmatrix} f_1 & f_2 & \cdots & f_m \\ 0 & 0 & \cdots & 0 \\ & & \cdots & \\ 0 & 0 & \cdots & 0 \end{pmatrix}, \quad S = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ & & \cdots & & \\ 0 & 0 & \cdots & s_{m-1} & 0 \end{pmatrix},$$

and $\tilde{E}(\bar{N}(k))$, $E(\bar{N}(k))$ are $m \times m$ diagonal matrices such that $\tilde{E}(\bar{N}(k)) = \text{diag}(\tilde{e}_i(\bar{N}))$, $E(\bar{N}(k)) = \text{diag}(e_i(\bar{N}))$, where

$$\begin{aligned} \tilde{e}_i(\bar{N}(k)) &= \exp \left\{ - \sum_{j=1}^m \tilde{\gamma}_{ij} n_j(k) \right\}, & e_i(\bar{N}(k)) &= \exp \left\{ - \sum_{j=1}^m \gamma_{ij} n_j(k) \right\}, \\ & & & i = 1, \dots, m. \end{aligned}$$

Equations (5) and (6) can be written in matrix form as

$$\bar{N}(k+1) = [F\tilde{E}(\bar{N}(k)) + SE(\bar{N}(k))] \bar{N}(k) = \mathbf{M}(\bar{N}(k)) \bar{N}(k). \tag{7}$$

$\mathbf{M}(\bar{N}(k))$ is also a Bernadelli-Lewis-Leslie-type matrix but its nonzero elements are all functions of the population vector. If $f_m \neq 0$, then we can write

$$\mathbf{M}(\bar{N}(k)) = MD(\bar{N}(k)),$$

where $M = F + S$ is an ordinary Bernadelli-Lewis-Leslie matrix, which is necessarily nonsingular, and $D(\bar{N}(k))$ describes the density dependence, i.e.

$$D(\bar{N}(k)) = M^{-1}(F\tilde{E} + SE) = \begin{pmatrix} e_1 & 0 & \cdots & 0 \\ 0 & e_2 & \cdots & 0 \\ & & \cdots & \\ \mathbf{f}_1(\tilde{e}_1 - e_1) & \mathbf{f}_2(\tilde{e}_2 - e_2) & \cdots & \tilde{e}_m \end{pmatrix},$$

where $\mathbf{f}_i = f_i/f_m$, $i = 1, \dots, m-1$.

Equation (7) is the logistic matrix model we shall study. It is a discrete analogue of the logistic model with age structure (2). If $\gamma(a, \xi) = \tilde{\gamma}(a, \xi) = 0$, then model

(2) reduces to model (1), which describes the case of density independence. In the same way, if $\gamma_{ij} = \tilde{\gamma}_{ij} = 0$, then E and \tilde{E} in model (7) are identity matrices and (7) is an ordinary Bernadelli-Lewis-Leslie matrix model.

We now consider some simplifications of model (7). Let (7) in full generality be referred to as case 1.

Case 2. If the density-dependent sensitivity is the same for both survivorship and fertility, then $\gamma_{ij} = \tilde{\gamma}_{ij}$, $i, j = 1, \dots, m$. In this case, $\tilde{E}(\bar{N}) = E(\bar{N}) = D(\bar{N})$ where $D(\bar{N}(k)) = \text{diag}(e_i(\bar{N}(k)))$.

Case 3. If the density-dependent sensitivity of each age group i to each other age group j is the same for all j , i.e. $\gamma_{ij} = \gamma_i$, $i, j = 1, \dots, m$, then the diagonal elements of $D(\bar{N}(k))$ are $e_i(\bar{N}(k)) = \exp\{-\gamma_i N(k)\}$, where $N(k) = \sum_{i=1}^m n_i(k)$ is the total population at the time k .

Case 4. In case 3, assume that $\gamma_i = \gamma$, $i = 1, \dots, m$. This means that the density-dependent sensitivity of every age group is the same. Model (7) can then be written as

$$\bar{N}(k+1) = M e^{-\gamma N(k)} \bar{N}(k).$$

This is the simplest case of a matrix model of density-dependent population dynamics. Desharnais and Cohen (1986) discuss this model.

If $m = 1$ (without age structure), the matrix M is a scalar. Let $M = \lambda = e^r$. Then model (7) becomes

$$N(k+1) = \exp\{r - \gamma N(k)\} N(k),$$

which is the well-known difference equation analogous to the logistic differential equation (May (1974)).

3. Equilibria

If there exists a population $\bar{N}^* = (n_1^*, \dots, n_m^*)^T$ that satisfies the relation

$$\bar{N}^* = \mathbf{M}(\bar{N}^*) \bar{N}^*,$$

then its size and age structure remain constant, according to model (7). Such \bar{N}^* is defined to be an equilibrium population.

At an equilibrium \bar{N}^* , the matrix $\mathbf{M}(\bar{N}^*)$ must have a dominant eigenvalue of 1 and the equilibrium \bar{N}^* must be an eigenvector corresponding to this eigenvalue.

In this section, the existence and uniqueness of the equilibrium will be described by Theorems 1 and 2. The proofs of Theorems 1 and 2 will be deferred to the last section of the paper.

The characteristic equation of the matrix $\mathbf{M}(\bar{N})$ is

$$\lambda^m - f_1 d_1 \tilde{e}_1 \lambda^{m-1} - f_2 d_2 e_1 \tilde{e}_2 \lambda^{m-2} - \dots - f_m d_m e_1 \dots e_{m-1} \tilde{e}_m = 0,$$

where

$$d_1 = 1, \quad d_{i+1} = \prod_{k=1}^i s_k, \quad i = 1, \dots, m-1,$$

$$e_i = \exp\left\{-\sum_{j=1}^m \gamma_{ij}n_j\right\}, \quad \tilde{e}_i = \exp\left\{\sum_{j=1}^m \tilde{\gamma}_{ij}n_j\right\}.$$

Define

$$F(e_1, \dots, e_{m-1}, \tilde{e}_1, \dots, \tilde{e}_m) = 1 - f_1d_1\tilde{e}_1 - f_2d_2e_1\tilde{e}_2 - \dots - f_md_me_1 \dots e_{m-1}\tilde{e}_m,$$

which is just the left side of the characteristic equation when $\lambda = 1$.

We write $\ln x$ for the real natural logarithm of a positive number x . Since we shall have no occasion to take the logarithm of any numbers other than positive reals, no questions can arise about multiple branches of a function involving \ln .

Theorem 1. *Finding the equilibrium of model (7) is equivalent to solving the following set of non-linear equations:*

$$\begin{aligned} c(\gamma_{11}d_1 + \gamma_{12}d_2x_1 + \gamma_{13}d_3x_1x_2 + \dots + \gamma_{1m}d_mx_1 \dots x_{m-1}) &= -\ln x_1, \\ c(\gamma_{i1}d_1 + \gamma_{i2}d_2x_1 + \gamma_{i3}d_3x_1x_2 + \dots + \gamma_{im}d_mx_1 \dots x_{m-1}) &= -\ln x_i, \end{aligned} \quad (8)_1$$

$$\begin{aligned} c(\gamma_{m-1,1}d_1 + \gamma_{m-1,2}d_2x_1 + \gamma_{m-1,3}d_3x_1x_2 + \dots + \gamma_{m-1,m}d_mx_1 \dots x_{m-1}) &= -\ln x_{m-1}, \\ F(x_1, \dots, x_{m-1}, \tilde{x}_1, \dots, \tilde{x}_m) &= 0, \end{aligned} \quad (8)_2$$

for $c \geq 0$ and $0 < x_i \leq 1$, $i = 1, \dots, m-1$, where

$$\tilde{x}_i = \exp[-c(\tilde{\gamma}_{i1}d_1 + \tilde{\gamma}_{i2}d_2x_1 + \tilde{\gamma}_{i3}d_3x_1x_2 + \dots + \tilde{\gamma}_{im}d_mx_1 \dots x_{m-1})]. \quad (9)$$

Theorem 2. *If*

$$\tilde{\gamma}_{i1} = \tilde{\gamma}_{i1}d_1 > \left[\sum_{j=2}^m \tilde{\gamma}_{ij}d_j\right] e^{-2}, \quad x_0(c) = c, \quad i = 1, \dots, m,$$

and the matrix M has a dominant eigenvalue $\lambda > 1$, then the equilibrium of model (7) is unique.

In case 4, when $\gamma_i = \gamma$, $i = 1, \dots, m$, we have $x_i = x = e^{-\gamma N}$, $i = 1, \dots, m$. Then (8)₂ simplifies to

$$1 - \sum_{j=1}^m f_j d_j e^{-j\gamma N} = 0.$$

If we multiply this equality by $e^{m\gamma N}$ and we let $\lambda = e^{\gamma N}$, we obtain the characteristic equation of M . Suppose λ is the dominant eigenvalue of M . Then $N^* = \ln \lambda / \gamma$ solves this characteristic equation. The equilibrium population satisfies

$$n_1^* = c^*d_1, n_2^* = c^*d_2\lambda^{-1}, \dots, n_m^* = c^*d_m\lambda^{-(m-1)}$$

The parameter c^* is selected such that the total population at equilibrium is N^* . So we have

$$c^* = \left\{\sum_{j=1}^m d_j \lambda^{-j+1}\right\}^{-1} N^* = \left\{\sum_{j=1}^m d_j \lambda^{-j+1}\right\}^{-1} \ln \lambda / \gamma.$$

When $m = 1$, the equilibrium population size is $N^* = r/\gamma$, where $r = \ln \lambda$.

Cases 2 and 3 are discussed at the end of the last section.

4. Stability of the equilibrium

In this section, using standard techniques, we give criteria for local stability based on the eigenvalues of the linearized matrix.

To study the local stability of the equilibrium population, we consider the perturbation $\bar{\xi}(k)$ at time $k = 0, 1, 2, \dots$ in the neighborhood of the equilibrium \bar{N}^* and write $\bar{N}(k) = \bar{N}^* + \bar{\xi}(k)$. In model (7) we have

$$\bar{N}(k+1) = \bar{N}^* + \bar{\xi}(k+1) = \mathbf{M}(\bar{N}(k))\bar{N}(k) = \mathbf{M}(\bar{N}^* + \bar{\xi}(k))[\bar{N}^* + \bar{\xi}(k)].$$

Expansion of the right side of this in a Taylor series about $\bar{N}^* = \mathbf{M}(\bar{N}^*)\bar{N}^*$ gives

$$\bar{N}^* + \bar{\xi}(k+1) = \mathbf{M}(\bar{N}^*)\bar{N}^* + A\bar{\xi}(k) + O(\bar{\xi}(k)\bar{\xi}(k)^T).$$

Here A denotes the $m \times m$ matrix (a_{ij}) ,

$$a_{ij} = [(\partial/\partial n_j)n_i(k+1)]_{\bar{N}^*}.$$

$O(\bar{\xi}(k)\bar{\xi}(k)^T)$ represents higher order terms in the quantities $\xi_i(k)$ which can be neglected when $\bar{\xi}(k)$ is sufficiently small. It can be seen from (7) that

$$\begin{aligned} A &= \mathbf{M}(\bar{N}^*) - [F\tilde{E}(\bar{N}^*)\mathbf{N}^*\tilde{\Gamma} + SE(\bar{N}^*)\mathbf{N}^*\Gamma] \\ &= F\tilde{E}(\bar{N}^*)(I - \mathbf{N}^*\tilde{\Gamma}) + SE(\bar{N}^*)(I - \mathbf{N}^*\Gamma) \end{aligned}$$

where I is an $m \times m$ unit matrix and \mathbf{N}^* , $\tilde{\Gamma}$, and Γ are $m \times m$ matrices such that

$$\mathbf{N}^* = \text{diag}(n_i^*), \quad \tilde{\Gamma} = (\tilde{\gamma}_{ij}), \quad \Gamma = (\gamma_{ij}).$$

The behavior of the population in the neighborhood of the equilibrium is determined by A according to

$$\bar{\xi}(k+1) = A\bar{\xi}(k) = A^{k+1}\bar{\xi}(0).$$

Let $|\lambda_i|$ denote the modulus of the eigenvalue λ_i of A . By conventional arguments, we have a standard result:

Theorem 3. *Equilibrium is locally stable if and only if $\max_{i=1, \dots, m} |\lambda_i| < 1$.*

In case 2, $\gamma_{ij} = \tilde{\gamma}_{ij}$, for $i, j = 1, \dots, m$, and $\Gamma = \tilde{\Gamma}$. Hence

$$A = \mathbf{M}(\bar{N}^*)(I - \mathbf{N}^*\Gamma).$$

When $f_m \neq 0$,

$$A = MD(\bar{N}^*)(I - \mathbf{N}^*\Gamma).$$

In case 3, when $\gamma_{ij} = \gamma_i$, $j = 1, \dots, m$ we obtain $\mathbf{N}^\Gamma = \text{diag}(\gamma_i n_i^*)\mathbf{1}^T$, where $\mathbf{1}$ is an $m \times 1$ matrix with all elements equal to 1.*

In case 4,

$$\mathbf{N}^*\Gamma = \gamma\bar{N}^*\mathbf{1}^T.$$

When $m = 1$, without age structure, we have $\mathbf{N}^*\Gamma = \gamma N^*$. Matrix A is a scalar; $A = \lambda e^{-\gamma N^*}(1 - \gamma N^*)$. If we put $r = \ln \lambda$, then $\bar{N}^* = r/\gamma$ and $\lambda e^{-\gamma N^*} = 1$. In this case, the necessary and sufficient condition for local stability of the equilibrium is that $|A| = |1 - r| < 1$ or $0 < r < 2$. Lewontin (1958) and May (1974) give this same result for the difference equation analogue of the logistic differential equation.

5. Proofs of Theorems 1 and 2 (from Sect. 3) and auxiliary results

Proof of Theorem 1. Let $\bar{N}^* = (n_1^*, \dots, n_m^*)^T$ be an equilibrium of model (7). Then a solution of (8) is $c = n_1^*$, $x_i = n_{i+1}^*/s_i n_i^*$, $i = 1, \dots, m-1$, as we now show. In fact, from (7) we know that

$$n_{i+1}^* = s_i e_i^* n_i^*, \quad i = 1, \dots, m-1, \tag{10}$$

where

$$e_i^* = e_i(\bar{N}^*) = \exp\left\{-\sum_{j=1}^m \gamma_{ij} n_j^*\right\}.$$

Hence

$$x_i \equiv n_{i+1}^*/s_i n_i^* = e_i^*, \quad i = 1, \dots, m-1. \tag{11}$$

From (10) and (11) we obtain

$$n_{i+1}^* = s_i e_i^* n_i^* = \left[\prod_{k=1}^i s_k \right] e_1^* \cdots e_i^* n_1^* = c d_{i+1} x_1 \cdots x_i, \tag{12}$$

$$x_i = e_i^* = \exp\{-c(\gamma_{i1} d_1 + \gamma_{i2} d_2 x_1 + \cdots + \gamma_{im} d_m x_1 \cdots x_{m-1})\}, \quad i = 1, \dots, m-1. \tag{13}$$

Taking the logarithm of (13), we get the first $m-1$ Eqs. (8)₁. If we take into account the functions in (9), (12) and (13), then Eq. (8)₂ is just the characteristic equation of the matrix $MD(\bar{N}^*)$ when $\lambda = 1$. So c, x_1, \dots, x_{m-1} , is a solution of (8).

Conversely, if c, x_1, \dots, x_{m-1} , is a solution of (8), and

$$n_1^* = c, \quad n_{i+1}^* = c d_{i+1} x_1 \cdots x_i, \quad i = 1, \dots, m-1,$$

then $\bar{N}^* = (n_1^*, \dots, n_m^*)^T$ is an equilibrium of model (7). To see this, we obtain from (8)₁

$$\begin{aligned} \sum_{j=1}^m \gamma_{ij} n_j^* &= -\ln x_i, \quad i = 1, \dots, m-1, \\ x_i &= \exp\left\{-\sum_{j=1}^m \gamma_{ij} n_j^*\right\} = e_i^*, \quad i = 1, \dots, m-1, \\ \tilde{x}_i &= \exp\left\{-\sum_{j=1}^m \tilde{\gamma}_{ij} n_j^*\right\} = \tilde{e}_i^*, \quad i = 1, \dots, m. \end{aligned}$$

Because $d_{i+1} = s_i d_i$, it follows that

$$n_{i+1}^* = s_i x_i n_i^* = s_i e_i^* n_i^*, \quad i = 1, \dots, m-1.$$

Multiplying Eq. (8)₂ by c , we have

$$\begin{aligned} n_1^* &= c = f_1 \tilde{x}_1 c + f_2 \tilde{x}_2 c d_2 x_1 + \cdots + f_m \tilde{x}_m c d_m x_1 \cdots x_{m-1} \\ &= f_1 \tilde{e}_1^* n_1^* + f_2 \tilde{e}_2^* n_2^* + \cdots + f_m \tilde{e}_m^* n_m^*. \end{aligned}$$

In summary, for the model

$$\bar{N}^* = \mathbf{M}(\bar{N}^*) \bar{N}^*,$$

there is a one-to-one correspondence between an equilibrium and a solution of (8).

Lemma 1. For any value of $c \geq 0$, there exists a solution $x_1(c), \dots, x_{m-1}(c)$ of $(8)_1$ with $0 < x_i \leq 1$, $i = 1, \dots, m-1$. This solution is a continuous, differentiable, monotonically decreasing function of c .

Proof. Fix $c \geq 0$. The (single-valued) functions $-\ln x_i$, $i = 1, \dots, m-1$, which are on the right side of $(8)_1$, decrease monotonically from $+\infty$ to 0 as x_i increase in the interval $0 < x_i \leq 1$. On the other hand, regarding the left side of $(8)_1$, the functions

$$c(\gamma_{i1}d_1 + \gamma_{i2}d_2x_1 + \dots + \gamma_{im}d_mx_1 \cdots x_{m-1}), \quad i = 1, \dots, m-1$$

increase monotonically with every x_j in the interval $0 < x_j \leq 1$, $j = 1, 2, \dots, m-1$; the i th such function increases from $c\gamma_{i1}d_1 \geq 0$ when every $x_j = 0$ to $c \sum_{i=1}^m \gamma_{ij}d_j < +\infty$ when every $x_j = 1$. Furthermore, the above functions are monotonically increasing as a function of $x = (x_1, \dots, x_{m-1})$ in this sense: if $x^1 = (x_1^1, \dots, x_{m-1}^1)$ and $x^2 = (x_1^2, \dots, x_{m-1}^2)$ and $x_j^1 \geq x_j^2$ for all $j = 1, \dots, m-1$, then the i th function above evaluated with $x = x^1$ is greater than or equal to the i th function above evaluated with $x = x^2$, for $i = 1, \dots, m-1$.

The first equation (for $i = 1$) of $(8)_1$ gives a function from the unit $(m-2)$ -cube, $0 < x_i \leq 1$, $i = 2, \dots, m-1$, into the interval $0 < x_1 \leq 1$:

$$x_1 = x_1(x_2, \dots, x_{m-1}). \quad (14)$$

Under the constraint (14), the second equation (for $i = 2$) of $(8)_1$ also has a right side that decreases monotonically, and a left side that increases monotonically, as x_2 increases in the interval $0 < x_2 \leq 1$. Therefore a function

$$x_2 = x_2(x_3, \dots, x_{m-1}), \quad (15)$$

from the unit $(m-3)$ -cube, $0 < x_i \leq 1$, $i = 2, \dots, m-1$, into the interval $0 < x_2 \leq 1$ is determined. Hence both (14) and (15) are determined simultaneously by the first two equations of $(8)_1$. Continuing to the last equation of $(8)_1$, we obtain recurrence relations

$$x_1 = x_1(x_2, \dots, x_{m-1}),$$

$$x_2 = x_2(x_3, \dots, x_{m-1}),$$

$$x_{m-2} = x_{m-2}(x_{m-1}),$$

$$x_{m-1} = V,$$

determined by $(8)_1$. Because V is determined, the solution $x = (x_1, \dots, x_{m-1})$ of $(8)_1$ is also determined. Since x depends on c , we write $x = x(c)$.

It is evident from the form of the Eqs. $(8)_1$ that a small change in c will lead to a small change in $x(c)$; further, by implicit differentiation, that $x(c)$ is a differentiable (vector-valued) function of c .

Let $x_i(c_1)$, $i = 1, \dots, m-1$, be a solution of $(8)_1$ for $c = c_1$. If $c_2 > c_1$, it is obvious that

$$c_2[\gamma_{i1}d_1 + \gamma_{i2}d_2x_1(c_1) + \dots + \gamma_{im}d_mx_1(c_1) \cdots x_{m-1}(c_1)] > -\ln x_i(c_1),$$

$$i = 1, \dots, m-1.$$

Hence

$$x_i(c_2) < x_i(c_1) \quad \text{for } c_2 > c_1.$$

Corollary 1. For the solution $x_i(c)$, $i = 1, \dots, m-1$ of (8)₁, the functions of c ,

$$F_i(c) = c[\gamma_{i1}d_1 + \gamma_{i2}d_2x_1(c) + \dots + \gamma_{im}d_mx_1(c) \cdots x_{m-1}(c)],$$

$i = 1, \dots, m-1$, increase monotonically with c .

Proof. Obvious from (8)₁ and Lemma 1.

Corollary 2. Let x_i^* and x_i^{**} , $i = 1, \dots, m-1$, be solutions of (8)₁ for given c^* and c^{**} , respectively. Let $x_0^* = c^*$, $x_0^{**} = c^{**}$. If $x_i^* = x_i^{**}$, $i = 0, 1, \dots, p-2$, but $x_{p-1}^* \neq x_{p-1}^{**}$, then

$$\left[\left(\sum_{j=p}^m \gamma_{ij}d_j \prod_{k=0}^{j-1} x_k^* \right) - \left(\sum_{j=p}^m \gamma_{ij}d_j \prod_{k=0}^{j-1} x_k^{**} \right) \right] / (x_{p-1}^* - x_{p-1}^{**}) > 0, \quad (16)$$

$$i = p, \dots, m-1; \quad p = 1, \dots, m-1.$$

Proof. Equation (16) follows directly from Corollary 1 when $p = 1$. Suppose $p > 1$.

If $x_i^* = x_i^{**}$, $i = 1, \dots, p-2$, we can regard the two sets of functions x_i^* and x_i^{**} , $i = p, \dots, m-1$, as solutions of the equations

$$A_i + B_p x_{p-1} [\gamma_{ip}d_p + \gamma_{i,p+1}d_{p+1}x_p + \dots + \gamma_{im}d_mx_p \cdots x_{m-1}] = -\ln x_i, \quad (17)$$

$$i = p, \dots, m-1,$$

corresponding to the parameters x_{p-1}^* and x_{p-1}^{**} respectively. Here

$$A_i = \sum_{j=1}^{p-1} \gamma_{ij}d_j \prod_{k=0}^{j-1} x_k^*, \quad i = p, \dots, m-1,$$

and

$$B_p = \prod_{k=0}^{p-2} x_k^*$$

are regarded as constants (depending on $x_i^* = x_i^{**}$, $i = 1, \dots, p-2$).

Now regard x_{p-1} as a parameter in (17). As in Lemma 1, for $i = p, \dots, m-1$, the solutions x_i of (17) are decreasing as functions of x_{p-1} . Therefore, again as in Lemma 1,

$$B_p x_{p-1} [\gamma_{ip}d_p + \gamma_{i,p+1}d_{p+1}x_p + \dots + \gamma_{im}d_mx_p \cdots x_{m-1}], \quad i = p, \dots, m-1,$$

are increasing monotonically with x_{p-1} . Hence (16) holds for $x_{p-1}^* \neq x_{p-1}^{**}$.

Lemma 2. If

$$\tilde{\gamma}_{i1} = \tilde{\gamma}_{i1}d_1 > \left[\sum_{j=2}^m \tilde{\gamma}_{ij}d_j \right] e^{-2}, \quad x_0(c) = c, \quad i = 1, \dots, m, \quad (18)$$

then $\tilde{x}_i(c)$ given by (9) are monotonically decreasing functions of c , $i = 1, \dots, m$.

Proof. According to Lemma 1, if $x_i(c)$, $i = 1, \dots, m-1$, solve (8)₁, then the

functions on the right, and therefore also the left, of

$$[-\ln x_i(c)]/c = \gamma_{i1}d_1 + \gamma_{i2}d_2x_1(c) + \cdots + \gamma_{im}d_mx_1(c) \cdots x_{m-1}(c),$$

$$i = 1, \dots, m-1$$

are monotonically decreasing in c . Then

$$d/dc \{[\ln x_i(c)]/c\} = [cx'_i(c) - x_i(c) \ln x_i]/[c^2x_i(c)] > 0,$$

$$cx'_i > x_i \ln x_i, \quad i = 1, \dots, m-1. \quad (19)$$

Therefore, from (9), recalling that $x_0(c) \equiv c$,

$$d/dc \tilde{x}_i(c) = -\tilde{x}_i(c) \left\{ \sum_{j=1}^m \tilde{\gamma}_{ij}d_j \prod_{k=0}^{j-1} x_k(c)/c + c[\tilde{\gamma}_{i2}x'_1 + \cdots + \tilde{\gamma}_{im}d_m(x_1 \cdots x_m)'] \right\}.$$

From (19), we have

$$d/dc \tilde{x}_i(c) < -\tilde{x}_i(c) \left\{ \tilde{\gamma}_{i1}d_1 + \tilde{\gamma}_{i2}d_2x_1(1 + \ln x_1) + \cdots + \tilde{\gamma}_{im}d_m \left[\prod_{k=1}^{m-1} x_k \right] \right. \\ \left. \times \left[1 + \ln \prod_{k=1}^{m-1} x_k \right] \right\}.$$

Using the elementary inequality

$$\left(\prod_{k=1}^i x_k \right) \left(1 + \ln \prod_{k=1}^i x_k \right) \geq -e^{-2}, \quad i = 1, \dots, m-1,$$

in combination with condition (18), we have

$$\tilde{\gamma}_{i1}d_1 + \tilde{\gamma}_{i2}d_2x_1(1 + \ln x_1) + \cdots + \tilde{\gamma}_{im}d_m \left[\prod_{k=1}^{m-1} x_k \right] \left(1 + \ln \prod_{k=1}^{m-1} x_k \right) \\ \geq \tilde{\gamma}_{i1} - \left(\sum_{j=2}^m \tilde{\gamma}_{ij}d_j \right) e^{-2} > 0.$$

Then $\tilde{x}'_i(c) < 0$.

Corollary 3. Let $S_1(c) = d_1c + d_2cx_1(c)$, where $x_1(c)$ solves (8)₁. Then $S_1(c)$ increases monotonically in c .

Proof. From (9), it is evident that $S_1(c) = -\ln \tilde{x}_1$ if we take $\tilde{\gamma}_{i1} = \tilde{\gamma}_{i2} = 1$ and $\tilde{\gamma}_{ij} = 0$, $j = 3, \dots, m$. With this assumption, and recalling that $d_1 > d_2$, it is obvious that (18) is satisfied. Thus, from Lemma 2, $\tilde{x}_1(c) = \exp\{-S_1(c)\}$ decreases monotonically and $S_1(c)$ increases monotonically as functions of c .

Corollary 4. For x_i^* and x_i^{**} , $i = 0, 1, \dots, m-1$, as in Corollary 2, with $x_i^* = x_i^{**}$, $i = 0, 1, \dots, p-2$, we have

$$[(d_p x_{p-1}^* + d_{p+1} x_{p-1}^* x_p^*) - (d_p x_{p-1}^{**} + d_{p+1} x_{p-1}^{**} x_p^{**})](x_{p-1}^* - x_{p-1}^{**}) \geq 0. \quad (20)$$

Equality holds if and only if $x_{p-1}^* = x_{p-1}^{**}$.

Proof. When $p = 1$, (20) follows directly from Corollary 3. Corollary 4 extends Corollary 3 to the case $p > 1$.

Using the notation introduced after (17), define

$$y_i = \exp(A_i)x_i, \quad i = p, \dots, m-1.$$

Equation (17) could be written as

$$B_p x_{p-1} [\gamma_{ip} \mathbf{d}_p + \gamma_{i,p+1} \mathbf{d}_{p+1} y_p + \dots + \gamma_{im} \mathbf{d}_m y_p \dots y_{m-1}] = -\ln y_i, \quad (21)$$

$$i = p, \dots, m-1,$$

where $\mathbf{d}_p = d_p$, $\mathbf{d}_i = d_i \exp\{-\sum_{k=p}^{i-1} A_k\}$, $i = p+1, \dots, m-1$, and x_{p-1} is a parameter. Because $A_i > 0$, we have the inequalities $\mathbf{d}_{i+1} < \mathbf{d}_i$, $i = p, \dots, m-2$.

For a solution of (21) corresponding to x_{p-1} , we consider the function of x_{p-1}

$$S_p(x_{p-1}) = d_p x_{p-1} + d_{p+1} x_{p-1} x_p(x_{p-1}) = \mathbf{d}_p x_{p-1} + \mathbf{d}_{p+1} x_{p-1} y_p(x_{p-1}).$$

It is clear from Corollary 3 that $S_p(x_{p-1})$ increases monotonically with x_{p-1} . x_i^* and x_i^{**} , $i = p, \dots, m-1$, are solutions of (21) corresponding to x_{p-1}^* and x_{p-1}^{**} respectively. Therefore (20) holds.

Lemma 3. For given c , there is only one solution of $(8)_1$ in the unit $(m-1)$ -cube.

Proof. According to Theorem 1, the solution of Eq. $(8)_1$ corresponds to the equilibrium of a special model of population dynamics,

$$n_{i+1}(t+1) = s_i \exp\left\{-\sum_{j=1}^m \gamma_{ij} n_j(t)\right\} n_i(t), \quad i = 1, \dots, m-1, n_1(t) = c. \quad (22)$$

in which reproduction measured by $n_1(t)$ is a constant independent of the population size. To prove the uniqueness of the solution of $(8)_1$, we have only to prove the uniqueness of the equilibrium of model (22) for a given c .

Suppose there are two equilibria, n_i^* and n_i^{**} , $i = 1, \dots, m$ for a given c . If we prove that $n_i^* = n_i^{**}$, $i = 1, \dots, p$ ($p \geq 1$) implies $n_{p+1}^* = n_{p+1}^{**}$, then, since $n_1^* = n_1^{**} = c$, Lemma 3 is proved.

To prove this, using the mean value theorem, we have

$$(n_{p+1}^* - n_{p+1}^{**}) - (n_p^* - n_p^{**}) = s_p \exp\left\{-\sum_{j=1}^m \gamma_{pj} n_j^*\right\} n_p^* - s_p \exp\left\{-\sum_{j=1}^m \gamma_{pj} n_j^{**}\right\} n_p^{**}$$

$$- (n_p^* - n_p^{**})$$

$$= -A(n_p^* - n_p^{**}) - B\left\{\sum_{j=1}^m \gamma_{pj}(n_j^* - n_j^{**})\right\},$$

where

$$A = 1 - s_p \exp\left\{-\sum_{j=1}^m \gamma_{pj} n_j^*\right\} > 0,$$

$$B = s_p \exp\left\{-\sum_{j=1}^m \gamma_{pj}[n_j^* + \theta(n_j^{**} - n_j^*)]\right\} n_p^{**} > 0, \quad 0 \leq \theta \leq 1.$$

Hence

$$(n_{p+1}^* - n_{p+1}^{**})^2 - (n_p^* - n_p^{**})^2$$

$$= [(n_{p+1}^* - n_{p+1}^{**}) - (n_p^* - n_p^{**})][(n_p^* + n_{p+1}^*) - (n_p^{**} + n_{p+1}^{**})]$$

$$= -\left\{A(n_p^* - n_p^{**}) + B\left[\sum_{j=1}^m \gamma_{pj}(n_j^* - n_j^{**})\right]\right\} [(n_p^* + n_{p+1}^*) - (n_p^{**} + n_{p+1}^{**})].$$

If the solutions x_i^* and x_i^{**} of (8)₁ correspond respectively to the equilibria n_i^* and n_i^{**} of (22), then

$$n_{i+1}^* = d_{i+1} \prod_{k=0}^i x_k^*, \quad n_{i+1}^{**} = d_{i+1} \prod_{k=0}^i x_k^{**}, \quad i = 0, \dots, m-1. \quad (23)$$

When $p = 1$, we have

$$\begin{aligned} (n_2^* - n_2^{**})^2 - (n_1^* - n_1^{**})^2 &= -A(n_1^* - n_1^{**})[(n_1^* + n_2^*) - (n_1^{**} + n_2^{**})] \\ &\quad - B \left[\sum_{j=1}^m \gamma_{1j} n_j^* - \sum_{j=1}^m \gamma_{1j} n_j^{**} \right] [(n_1^* + n_2^*) - (n_1^{**} + n_2^{**})]. \end{aligned}$$

From (23) we get

$$\begin{aligned} n_1^* - n_1^{**} &= x_0^* - x_0^{**}, \quad (n_1^* + n_2^*) - (n_1^{**} + n_2^{**}) = (x_0^* + d_1 x_0^* x_1^*) - (x_0^{**} + d_1 x_0^{**} x_1^{**}), \\ \sum_{j=1}^m \gamma_{1j} n_j^* - \sum_{j=1}^m \gamma_{1j} n_j^{**} &= \sum_{j=1}^m \gamma_{1j} d_j \prod_{k=0}^{j-1} x_k^* - \sum_{j=1}^m \gamma_{1j} d_j \prod_{k=0}^{j-1} x_k^{**}. \end{aligned}$$

Using Corollaries 1 and 3, we have

$$(n_2^* - n_2^{**})^2 - (n_1^* - n_1^{**})^2 \leq 0$$

hence

$$|n_2^* - n_2^{**}| \leq |n_1^* - n_1^{**}|.$$

When $p > 1$, suppose that $n_i^* = n_i^{**}$, $i = 1, \dots, p-1$. These equalities hold if and only if $x_i^* = x_i^{**}$, $i = 1, \dots, p-2$. Because

$$n_p^* - n_p^{**} = d_p \left[\prod_{k=0}^{p-2} x_k^* \right] (x_{p-1}^* - x_{p-1}^{**}),$$

we have

$$\begin{aligned} (n_p^* + n_{p+1}^*) - (n_p^{**} + n_{p+1}^{**}) &= \left[\prod_{k=0}^{p-1} x_k^* \right] [(d_p x_{p-1}^* + d_{p+1} x_{p-1}^* x_p^*) \\ &\quad - (d_p x_{p-1}^{**} + d_{p+1} x_{p-1}^{**} x_p^{**})], \\ \sum_{j=1}^m \gamma_{pj} n_j^* - \sum_{j=1}^m \gamma_{pj} n_j^{**} &= \sum_{j=p}^m \gamma_{pj} n_j^* - \sum_{j=p}^m \gamma_{pj} n_j^{**} \\ &= \sum_{j=p}^m \gamma_{pj} d_j \prod_{k=0}^{j-1} x_k^* - \sum_{j=p}^m \gamma_{pj} d_j \prod_{k=0}^{j-1} x_k^{**}. \end{aligned}$$

From Corollaries 2 and 4, it follows that

$$(n_{i+1}^* - n_{i+1}^{**})^2 - (n_i^* - n_i^{**})^2 \leq 0, \quad i = 2, \dots, m-1,$$

hence

$$|n_{i+1}^* - n_{i+1}^{**}| \leq |n_i^* - n_i^{**}|.$$

If $n_p^* = n_p^{**}$, then $n_{p+1}^* = n_{p+1}^{**}$.

Proof of Theorem 2. According to Lemmas 1 and 2, $x_i(c)$ in (8)₂ and $\tilde{x}_i(c)$

in (9) are monotonically decreasing functions of c . Therefore $F(x_1, \dots, x_{m-1}, \tilde{x}_1, \dots, \tilde{x}_m)$ is a monotonically increasing function of c . Because $x_i(0) = \tilde{x}_i(0) = 1$, and $\lim_{c \rightarrow +\infty} x_i(c) = 0$, we have

$$\lim_{c \rightarrow +\infty} F(x_1, \dots, x_{m-1}, \tilde{x}_1, \dots, \tilde{x}_m) = 1 > 0,$$

$$F(0) = F(x_1(0), \dots, x_{m-1}(0), \tilde{x}_1(0), \dots, \tilde{x}_m(0)) = 1 - \sum_{i=1}^m f_i d_i.$$

Here $\sum_{i=1}^m f_i d_i$ is the net rate of reproduction (NRR) when the population is density-independent. If $\text{NRR} > 1$, i.e. $F(0) < 0$, then Eq. (8)₂ must have a unique and positive solution c . Hence (8) has a unique solution, and the equilibrium for model (7) exists and is unique.

It is known (e.g. Keyfitz 1968, p. 102) that the matrix M has a dominant eigenvalue $\lambda > 1$ if and only if $\text{NRR} > 1$.

On the basis of Lemma 1, in case 2, where we assume $\tilde{\gamma}_{ij} = \gamma_{ij}$, we do not need the conditions of (18) for the first $m - 1$ age groups but impose them only on γ_{mj} .

In case 3, when $\gamma_{ij} = \gamma_i$, $i, j = 1, \dots, m$, (8)₁ becomes

$$c\gamma_i(d_1 + d_2x_1 + d_3x_1x_2 + \dots + d_mx_1 \dots x_{m-1}) = -\ln x_i.$$

Now replace the parameter c by the new parameter N (which turns out to be just the total population size) according to the transformation

$$N = c(d_1 + d_2x_1 + d_3x_1x_2 + \dots + d_mx_1 \dots x_{m-1}).$$

Then (8)₁ simplifies to $x_i = e^{-\gamma_i N}$. Because of the special form of $x_m = e^{-\gamma_m N}$, Lemma 2 holds without (18). Equation (8)₂ is changed to

$$1 - f_1 d_1 e^{-\gamma_1 N} - \dots - f_m d_m e^{-(\gamma_1 + \dots + \gamma_m)N} = 0. \tag{24}$$

If N^* is the unique solution of (24), let $e_i^* = e^{-\gamma_i N^*}$ and $c^* = N^*/(d_1 + d_2e_1^* + \dots + d_me_1^* \dots e_{m-1}^*)$. The equilibrium must be $\bar{N}^* = (n_1^*, \dots, n_m^*)^T$, where

$$n_1^* = c^* d_1, n_2^* = c^* d_2 e_1^*, n_3^* = c^* d_3 e_1^* e_2^*, \dots, n_m^* = c^* d_m e_1^* \dots e_{m-1}^*.$$

From this, it is evident that the solution N^* of (24) is simply the total population at equilibrium.

Acknowledgments. L. L. was supported in part by U.S. National Science Foundation grant BSR 84-07461, the Sibyl and William T. Golden Foundation, and the Esther A. and Joseph Klingenstein Fund, Inc. J.E.C. was supported in part by U.S. National Science Foundation grant BSR 84-07461, a Fellowship to J.E.C. from the John D. and Catherine T. MacArthur Foundation, and the hospitality of Mr. and Mrs. William T. Golden.

References

Bernadelli, H.: Population waves. *J. Burma Res. Soc.* **31**, 1-18 (1941)
 Blasio, G. D., Iannelh, M., Sinestrari, E.: Approach to equilibrium in age structured populations with an increasing recruitment process. *J. Math. Biol.* **13**, 371-382 (1982)
 Cook, D., Léon, J. A.: Stability of population growth determined by 2×2 Leslie matrix model with density-dependent elements. *Biometrics* **32**, 435-442 (1976)

- Cushing, J. M.: Existence and stability of equilibria in age-structured population dynamics. *J. Math. Biol.* **20**, 259-276 (1984)
- Desharnais, R. A., Cohen, J. E.: Life not lived due to disequilibrium in heterogeneous age-structured populations. *Theor. Popul. Biol.* **29**, 385-406 (1986)
- Fisher, M. E., Goh, B. S.: Stability results for delayed-recruitment models in population dynamics. *J. Math. Biol.* **19**, 147-156 (1984)
- Guckenheimer, J., Oster, G., Ipaktchi, A.: The dynamics of density dependent population models. *J. Math. Biol.* **4**, 101-147 (1977)
- Gurney, W. S., Nisbet, R. M.: Age- and density-dependent population dynamics in static and variable environments. *Theor. Popul. Biol.* **17**, 321-344 (1980)
- Gurtin, M. E., MacCamy, R. C.: Non-linear age-dependent population dynamics. *Arch. Rat. Mech. Anal.* **54**, 281-300 (1974)
- Gurtin, M. E., MacCamy, R. C.: Some simple models for nonlinear age-dependent population dynamics. *Math. Biosci.* **43**, 199-211 (1979)
- Keyfitz, N.: Introduction to the mathematics of population. Reading, MA: Addison-Wesley 1968
- Leslie, P. H.: On the use of matrices in certain population mathematics. *Biometrika* **39**, 183-212 (1945)
- Leslie, P. H.: Some further notes on the use of matrices in population mathematics. *Biometrika* **35**, 213-245 (1948)
- Levin, S. A., Goodyear, C. P.: Analysis of an age-structured fishery model. *J. Math. Biol.* **9**, 245-274 (1980)
- Lewis, E. G.: On the generation and growth of a population. *Sankhya* **6**, 93-96 (1942)
- Lewontin, R. C.: A general method for investigating the equilibrium of gene frequency in a population. *Genetics* **43**, 419-434 (1958)
- Lloyd, M.: Laboratory studies with confined cannibalistic population of flour beetles (*Tribolium castaneum*) in a cold-dry environment. I. Data for 24 unmanipulated populations. *Tribolium Info. Bull.* **8**, 98-123 (1965)
- Lloyd, M.: Self-regulation of adult numbers by cannibalism in two laboratory strains of flour beetles (*Tribolium castaneum*). *Ecology* **49**, 245-259 (1968)
- Lotka, A. J.: Elements of physical biology. Baltimore: Williams and Wilkins 1925 (Republished as: Elements of mathematical biology. New York: Dover 1956)
- Marcati, P.: On the global stability of the logistic age-dependent population growth. *J. Math. Biol.* **15**, 215-226 (1982)
- May, R. M.: Biological populations obeying difference equations: stable points, stable cycles and chaos. *J. Theor. Biol.* **51**, 511-524 (1974)
- McKendrick, A. G.: Applications of mathematics to medical problems. *Proc. Edinburgh Math. Soc.* **44**, 1, 98-130 (1926)
- Pennycuik, C. J., Compton, R. M., Beckingham, L.: A computer model for simulating the growth of a population or of two interacting populations. *J. Theor. Biol.* **18**, 316-329 (1968)
- Pennycuik, L.: A computer model of the Oxford great tit population. *J. Theor. Biol.* **22**, 381-400 (1969)
- Rorres, C.: Stability of an age specific population with density dependent fertility. *Theor. Popul. Biol.* **10**, 26-46 (1976)
- Rorres, C.: Local stability of a population with density-dependent fertility. *Theor. Popul. Biol.* **16**, 283-300 (1979)
- Rorres, C.: A nonlinear model of population growth in which fertility is dependent on birth rate. *SIAM J. Appl. Math.* **37**(2), 423-432 (1979)
- Rotenberg, M.: Equilibrium and stability in populations whose interactions are age-specific. *J. Theor. Biol.* **54**, 207-224 (1975)
- Sinestrari, E.: Nonlinear age-dependent population growth. *J. Math. Biol.* **9**, 331-345 (1980)
- Varley, G. C., Gradwell, G. R., Hassell, M. P.: Insect population ecology: An analytical approach, 15-18. University of California Press (1974)
- Von Foerster, H.: Some remarks on changing populations. In: Stohlman, F. Jr. (ed.) The kinetics of cellular proliferation, pp. 382-407. New York: Grune and Stratton 1959
- Webb, G. F.: Theory of nonlinear age-dependent population dynamics. New York and Basel: Marcel Dekker 1985
- Ziebur, A. D.: Age-dependent models of population growth. *Theor. Popul. Biol.* **26**, 315-319 (1984)

Received April 17, 1986/Revised November 6, 1986