

# Life Not Lived due to Disequilibrium in Heterogeneous Age-Structured Populations

ROBERT A. DESHARNAIS AND JOEL E. COHEN

*Laboratory of Populations, The Rockefeller University,  
1230 York Avenue, Box 20, New York, New York 10021-6399*

Received May 27, 1985

Three models of age-structured populations with demographically heterogeneous subpopulations are analyzed. In the first model, each subpopulation has its own age-specific vital rates which are fixed in time. In the second model, the vital rates of each subpopulation are uniformly inhibited by increasing total numbers of individuals. In the third, the vital rates of groups of subpopulations are inhibited by the total numbers of individuals in other groups of subpopulations with an intensity that depends on the interacting pair of groups. Three functions are defined to measure disequilibrium in the subpopulation frequencies, subpopulation age structures, and total population size. For the first model, we show that disequilibrium will shift the trajectory of the total numbers of individuals forward or backward in time by an asymptotic constant that is proportional to the sum of the disequilibrium measures. For the second model, we establish sufficient conditions for the existence of a globally stable equilibrium and we show that disequilibrium will result in a finite loss or gain in life which is proportional to the sum of the disequilibrium measures. For the last model, we show that the loss or gain in life for each group of subpopulations is a linear combination over all groups of the sums of the three disequilibrium measures. We illustrate these results with numerical examples and give possible biological interpretations of the models. We relate these new results to previous work on the cost of natural selection and measures of demographic disequilibrium. © 1986 Academic Press, Inc.

## 1. INTRODUCTION

Heterogeneity exists in all populations of living organisms. Often, large populations can be divided into subpopulations based upon differences in rates of reproduction and mortality. Human populations are heterogeneous in vital rates, among other characteristics (e.g. Vaupel *et al.*, 1979; Vaupel and Yashin, 1985). Natural populations of the parthenogenetic cockroach *Pycnoscelus surinamensis* are composed of different genotypic clones (Parker *et al.*, 1977). Predicting the effects of heterogeneity is a problem common to demographic and evolutionary theory.

The purpose of this paper is to describe the effects of demographic

heterogeneity on total population size. Our models consider a population that is initially composed of two or more subpopulations with different age-specific vital rates. In Section 2, we define two measures of disequilibrium—one for subpopulation frequencies and one for age distributions—and we show how these measures can be used to predict the asymptotic time lag due to disequilibrium when the population growth rate is density independent. In Section 3, for a simple model of density dependence, we show that the time-integrated number of individuals not realized by the population (the "life not lived") due to disequilibrium can be predicted using the measures defined in Section 2. In Section 4, we extend the results of Section 3 to several interacting populations. We illustrate our results with numerical examples in Section 5. In Section 6, we relate our results to the cost of natural selection and earlier measures of demographic disequilibrium and we indicate possible examples where our models might be applied.

## 2. DENSITY-INDEPENDENT POPULATION GROWTH

### 2.1. Notation and Background

Consider a large demographically heterogeneous age-structured population which can be subdivided into a finite set  $S$  of demographically homogeneous noninteracting subpopulations. Assume that each subpopulation grows independently without migration of any kind. Let the age structure of the  $i$ th subpopulation at time  $t$  be described by a column vector  $K_i(t)$  of length  $n_i$ . If the vital rates of each subpopulation remain constant through time, and time and age are measured in the same discrete units, then the age structure at time  $t + 1$  can be computed from the age structure at time  $t$  using

$$K_i(t+1) = M_i K_i(t), \quad i \in S, \quad (1)$$

where  $M_i$  is an  $n_i \times n_i$  projection matrix. Then  $K_i(t) = M_i^t K_i(0)$ ,  $i \in S$ .

Suppose each  $M_i$  is nonnegative and primitive. (This assumption holds for human populations if  $M_i$  has the form of a Leslie matrix and age classes beyond the last age of reproduction are excluded.) Also suppose  $K_i(0) \neq 0$ ,  $i \in S$ . The Perron-Frobenius theorem shows that each  $M_i$  has a simple real root  $\lambda_i$ , which exceeds in modulus all other roots and that

$$\lim_{t \rightarrow \infty} M_i^t \lambda_i^{-t} = u_i v_i^T, \quad i \in S, \quad (2)$$

where  $u_i$  and  $v_i$  are positive right and left eigenvectors with eigenvalue  $\lambda_i$ ,

and  $v_i^T u_i = 1, i \in S$ . The superscript  $T$  indicates transposition.  $\lambda_i$  is the asymptotic growth rate of the  $i$ th subpopulation.

If  $w$  is a nonnegative vector, let  $\|w\|$  represent the norm of  $w$  obtained by summing all of its elements. The *age distribution vector* for the  $i$ th subpopulation is defined as

$$q_i(t) = K_i(t) \|K_i(t)\|^{-1}, \quad i \in S. \tag{3}$$

The strong ergodic theorem of demography asserts that

$$\lim_{t \rightarrow \infty} q_i(t) = q_i^* = u_i \|u_i\|^{-1}, \quad i \in S, \tag{4}$$

independent of initial conditions, provided  $K_i(0) \neq 0$ . Thus the vector  $u_i$  is proportional to the *stable age distribution*  $q_i^*$ .

The vector  $v_i$  measures the relative contribution of each initial age class to the growing stable population. The  $j$ th element of  $v_i$  is called the *reproductive value* of an individual of age  $j$  (Fisher, 1930). The total reproductive value of a population grows geometrically for any initial age distribution; that is,

$$v_i^T K_i(t) = v_i^T K_i(0) \lambda_i^t, \quad i \in S. \tag{5}$$

By convention,  $u_i$  and  $v_i$  are scaled so that the first element of  $v_i$  equals one for every  $i \in S$ .

Explicit formulas for  $u_i$  and  $v_i$  are known (Follard, 1973, pp. 46ff) when the projection matrix is a Leslie matrix.

The number of individuals in the  $i$ th subpopulation is given by  $N_i(t) = \|K_i(t)\|, i \in S$ , and the total number of individuals in the population is  $N(t) = \sum_{i \in S} N_i(t)$ . The frequency of the  $i$ th subpopulation is

$$p_i(t) = N_i(t)/N(t), \quad i \in S. \tag{6}$$

We now examine the asymptotic behavior of the subpopulation frequency  $p_i(t)$ . Let  $\lambda_m = \max_{i \in S}(\lambda_i)$ . Divide the set  $S$  into two complementary subsets  $Y$  and  $Z$ , where  $Y = \{i | \lambda_i = \lambda_m, i \in S\}$  and  $Z = S - Y$ . Multiplying the numerator and denominator of (6) by  $\lambda_m^{-t}$  and using (2) gives

$$\begin{aligned} \lim_{t \rightarrow \infty} p_i(t) &= p_i^* = \|u_i v_i^T K_i(0)\| / \left[ \sum_{h \in Y} \|u_h v_h^T K_h(0)\| \right], \quad i \in Y. \\ &= 0, \quad i \in Z. \end{aligned} \tag{7}$$

As is well known, the subpopulations with the largest growth rate come to dominate the population as a whole.

In a single-locus population genetic model, Ginzburg (1972) defined an

entropy function to measure the deviation of the initial frequencies  $p_i(0)$  from equilibrium:

$$H_p = - \sum_{i \in Y} p_i^* \log [p_i(0)/p_i^*]. \quad (8)$$

Let the average reproductive value of a subpopulation be defined as  $V_i(t) = v_i^T q_i(t)$ . At equilibrium,  $V_i^* = v_i^T q_i^*$ . The following function measures the deviation of the initial average reproductive values from equilibrium:

$$H_v = - \sum_{i \in Y} p_i^* \log [V_i(0)/V_i^*]. \quad (9)$$

## 2.2 New Results

How are the dynamics of total population size  $N(t)$  affected by initial conditions?

Define a *reference population*,  $\bar{N}(t)$ , as a population where (i)  $\bar{p}_i(0) = p_i^*$  for  $i \in S$ , (ii)  $\bar{q}_i(0) = q_i^*$  for  $i \in Y$ , and (iii)  $\bar{N}(0) = N(0)$ . The initial configuration of the reference population is the equilibrium configuration of an evolving population.

**THEOREM 1.** *The trajectories  $\bar{N}(t)$  and  $N(t)$  become separated in time by an asymptotic time lag  $\tau$ , where*

$$\lim_{t \rightarrow \infty} [N(t)/\bar{N}(t)] = \lambda_m^{-\tau} \quad (10)$$

and

$$\tau = r_m^{-1} [H_p + H_v], \quad (11)$$

with  $r_m = \log(\lambda_m)$ .

*Proof.* By definition, the reference age structure for the  $i$ th subpopulation is  $\bar{R}_i(0) = N(0) p_i^* q_i^*$ . Therefore,

$$\bar{N}(t) = N(0) \sum_{i \in Y} p_i^* \|M_i^t q_i^*\| = N(0) \lambda_m^t. \quad (12)$$

Let  $\tau$  be the solution to (10). Such a solution exists and is unique because both  $N(t)$  and  $\bar{N}(t)$  asymptotically grow at the same geometric rate  $\lambda_m$ . Then

$$\begin{aligned} \lim_{t \rightarrow \infty} \log [N(t)/\bar{N}(t)] &= \lim_{t \rightarrow \infty} \log \left[ \sum_{i \in S} p_i(0) \| (M_i^t \lambda_m^{-t}) q_i(0) \| \right] \\ &= \log \left[ \sum_{i \in Y} p_i(0) \| u_i v_i^T q_i(0) \| \right] \\ &= -\tau \log(\lambda_m). \end{aligned} \quad (13)$$

From (7), using  $K_i(0) = q_i(0)p_i(0)N(0)$  for all  $i$ ,

$$\begin{aligned} \sum_{h \in Y} p_h(0) \|u_h v_h^T q_h(0)\| \\ = [p_i(0)/p_i^*] \|u_i v_i^T q_i(0)\|, \quad i \in Y. \end{aligned} \tag{14}$$

Since  $V_i(0) = v_i^T q_i(0)$  and  $V_i^* = v_i^T q_i^* = v_i^T u_i \|u_i\|^{-1} = \|u_i\|^{-1}$ , from (13) and (14) we have

$$\tau \log(\lambda_m) = -\log[p_i(0)/p_i^*] - \log[V_i(0)/V_i^*], \quad i \in Y. \tag{15}$$

Multiplying (15) by  $p_i^*$  for each  $i \in Y$  and summing over  $i$  yields (11). ■

Equation (15) provides an alternate expression for calculating  $\tau$ . Equation (11) facilitates a comparison of our results with those of Ginzburg (1977) (see Subsect. 6.1).

When a single subpopulation with index  $k$  dominates at equilibrium,  $p_k^* = 1$  and  $H_p = -\log[p_k(0)]$ . In this case,  $H_p$  is Haldane's (1957) "cost of natural selection" (see Subsect. 6.1).

### 3. DENSITY-DEPENDENT POPULATION GROWTH

In this section we consider a demographically heterogeneous density-dependent age-structured model. We could allow for density-dependent interactions among the various age classes. However, this type of model would be extremely complex. As a first approximation to density dependence, we assume that every individual, regardless of age, contributes equally and independently to the mortality of other individuals, regardless of their age, and that this extra mortality is independent of all other causes of death. Furthermore, we assume that this extra mortality is distributed evenly throughout each time interval. Since the fecundity terms in the first row of the Leslie projection matrix also include the survivorship of the parents and offspring within each time interval (Keyfitz, 1968, p. 30), all the elements of the projection matrix will experience the same proportional change. This change will be modeled using a negative exponential function:

$$K_i(t+1) = M_i K_i(t) \exp[-a_i N(t)], \quad 0 < a_i < \infty, \quad i \in S. \tag{16}$$

The parameter  $a_i$  measures the per capita density sensitivity. The solution to (16) is

$$K_i(t) = M_i^t K_i(0) \exp \left[ -a_i \sum_{\xi=0}^{t-1} N(\xi) \right], \quad i \in S. \tag{17}$$

As before, let  $\lambda_i$  be the dominant root of the matrix  $M_i$ ,  $i \in S$ , and let  $r_i = \log(\lambda_i)$ . Unlike the previous definition of  $Y$ , here let  $Y = \{i | r_i/a_i = \alpha, i \in S\}$  and  $Z = S - Y$ , where  $\alpha = \max_{i \in S} (r_i/a_i)$ . The following lemma describes the asymptotic behavior of total population size.

LEMMA 1. *If  $0 < r_i < 2$  for  $i \in Y$ , then  $\lim_{t \rightarrow \infty} N(t) = N^* = \alpha$ .*

We prove Lemma 1 in the Appendix.

Let  $H_N(0) = -\log[N(0)/N^*]$ . The following theorem shows how initial conditions affect  $N(t)$ .

THEOREM 2. *If  $0 < r_i < 2$  for  $i$  in the set  $Y$  such that  $r_i/a_i = \alpha$ , then*

$$\begin{aligned} \lim_{t \rightarrow \infty} p_i(t) &= p_i^* > 0, & i \in Y, \\ &= 0, & i \in Z, \end{aligned} \quad (18)$$

and

$$\sum_{t=0}^{\infty} [N^* - N(t)] = (a^*)^{-1} [H_p + H_v + H_N], \quad (19)$$

where  $a^* = \sum_{i \in Y} p_i^* a_i$ .

*Proof.* By definition,

$$\begin{aligned} p_i(t) &= [N(0)/N(t)] p_i(0) \|(M_i^t \lambda_i^{-t}) q_i(0)\| \\ &\quad \times \exp \left[ r_i t - a_i \sum_{\xi=0}^{t-1} N(\xi) \right], \quad i \in S. \end{aligned} \quad (20)$$

Lemma 1 implies  $\lim_{t \rightarrow \infty} t^{-1} \sum_{\xi=0}^{t-1} N(\xi) = \alpha$ . We consider two cases.

Case 1:  $i \in Z$ . From (2) and (20), putting  $b_i = N(0) p_i(0) [V_i(0)/V_i^*]$  gives

$$\lim_{t \rightarrow \infty} p_i(t) = [b_i/\alpha] \exp[(r_i - a_i \alpha) \lim_{t \rightarrow \infty} t]. \quad (21)$$

Since  $r_i/a_i < \alpha$ ,  $\lim_{t \rightarrow \infty} p_i = 0$  for  $i \in Z$ .

Case 2:  $i \in Y$ . Let  $\delta(t) = \alpha - N(t)$  and  $L(t) = \sum_{\xi=0}^{t-1} \delta(\xi)$ . Using (20)

$$\begin{aligned} \delta(t) &= \alpha - \sum_{i \in Z} p_i(t) N(t) \\ &\quad - \sum_{i \in Y} N(0) p_i(0) \|(M_i^t \lambda_i^{-t}) q_i(0)\| \exp[a_i L(t)]. \end{aligned} \quad (22)$$

Consider the function  $f(x) = \sum_{i \in Y} b_i \exp(a_i x)$ . Since Lemma 1 implies  $\lim_{t \rightarrow \infty} \delta(t) = 0$  and  $\lim_{t \rightarrow \infty} p_i(t) = 0$  for  $i \in Z$ , (2) and (22) imply

$$\lim_{t \rightarrow \infty} f(L(t)) = \alpha. \tag{23}$$

Since  $f(x)$  is a continuous monotonic increasing function, (23) implies  $\lim_{t \rightarrow \infty} L(t) = L^*$  where  $f(L^*) = \alpha$ . Using this fact in (20), we get

$$\lim_{t \rightarrow \infty} p_i(t) = p_i^* = [b_i/\alpha] \exp[a_i L^*], \quad i \in Y. \tag{24}$$

Solving this for  $L^*$  gives

$$a_i L^* = -\log[p_i(0)/p_i^*] - \log[V_i(0)/V_i^*] - \log[N(0)/N^*], \quad i \in Y. \tag{25}$$

Multiplying (25) by  $p_i^*$  and summing over  $i \in Y$  gives (19). ■

Equation (25) provides an alternate expression for the cumulative difference between  $N(t)$  and  $N^*$ .

The equilibrium frequencies depend upon the initial conditions and can be computed easily. The unique real solution  $x$  of  $f(x) = \alpha$  equals the cumulative difference  $L^*$ . One can then compute  $p_i^*$  from (24).

Consider the special case when  $a_i = a$  for  $i \in Y$ . Using (24),  $N_i^* = p_i^* x = b_i \exp[aL^*]$  for  $i \in Y$  which implies  $p_i^* = b_i / \sum_{h \in Y} b_h$ . Since  $b_i = \|u_i v_i^T K_i(0)\|$ , (7) provides an exact expression for  $p_i^*$ ,  $i \in S$ .

Let  $\bar{N}(t)$  be a reference population as defined in the previous section and assume  $a_i = a$  for  $i \in Y$ . Since  $\bar{p}_i(0) = 0$  for  $i \in Z$ , the exponential factor cancels in (3) and (6) yielding  $\bar{p}_i(t) = p_i^*$  and  $\bar{q}_i(t) = q_i^*$  for  $i \in S$  and all  $t \geq 0$ . The dynamics of  $\bar{N}(t)$  are given by

$$\bar{N}(t+1) = \bar{N}(t) \exp[r - a\bar{N}(t)], \tag{26}$$

where  $r = \alpha x$ . This difference equation is a discrete-time analog of the logistic model of population growth. The following corollary relates the dynamics of  $N(t)$  and  $\bar{N}(t)$ .

COROLLARY 1. *If  $a_i = a$  for  $i \in Y$  and  $0 < r < 2$ , then*

$$\sum_{t=0}^{\infty} [\bar{N}(t) - N(t)] = a^{-1} [H_p + H_v]. \tag{27}$$

*Proof.* From the definition of a reference population,  $\bar{H}_p = \bar{H}_v = 0$  and  $\bar{N}(0) = N(0)$ . From Lemma 1,  $\bar{H}_N = H_N$ . Applying Theorem 2 to the reference population and subtracting the cumulative difference from (19) yields (27). ■

In particular, when a single subpopulation survives at equilibrium, the set  $Y$  is a singleton and Corollary 1 is applicable.

Desharnais and Costantino (1982) applied Ginzburg's entropy  $H_p$  to the continuous-time logistic model of density-dependent natural selection. Their "selective difference area" is analogous to the sum in (27) (see Subsect. 6.1).

The cumulative differences in (19) and (27) have several interesting properties. First, they are independent of the vital rates of those subpopulations which go extinct at equilibrium ( $p_i^* = 0$ ). Thus the magnitude of the differences between the dominant roots of the projection matrices for  $i \in Y$  and  $i \in Z$  has no effect on the cumulative differences in life lived. To illustrate, let  $S = \{1, 2\}$  and  $a_1 = a_2 = a$ . If  $q_1(0) = q_1^*$  and  $q_2(0) = q_2^*$ , then  $H_p = 0$  and from Corollary 1,

$$\begin{aligned} \sum_{t=0}^{\infty} [\bar{N}(t) - N(t)] &= -a^{-1} \log[p_1(0)] \quad \text{when } \lambda_1 > \lambda_2. \\ &= 0 \quad \text{when } \lambda_1 = \lambda_2. \\ &= -a^{-1} \log[p_2(0)] \quad \text{when } \lambda_1 < \lambda_2. \end{aligned} \quad (28)$$

As this example shows, the magnitude of  $|\lambda_1 - \lambda_2|$  has no effect. A second property of the cumulative differences in life lived is that they are independent of the initial age distributions of the subpopulations which go extinct. This is because  $H_p$  in (9) depends on  $q_i(0)$  for  $i \in Y$  only. Third, the relative frequencies among the subpopulations which belong to set  $Z$  are unimportant since these are also eliminated from the calculation of  $H_p$ . These results are surprising, since every subpopulation contributes to the total population size.

#### 4. SEVERAL INTERACTING POPULATIONS

In this section, we extend the analysis to a *community* of several interacting populations. We define a population as a group of individuals with the same sensitivity in mortality rates to the numbers of individuals in the same and every other population. We assume that each population is composed of one or more demographically heterogeneous subpopulations. All other assumptions concerning the way in which the total size of a population affects mortality are the same as in (16).

Let  $C$  represent the set of indices  $c$  for populations in the community and let  $S_c$  represent the set of indices  $i$  for subpopulations within the population  $c$  ( $c \in C$ ).  $K_{ci}(t)$  is the (nonzero) age structure vector for the  $i$ th subpopulation within population  $c$  and  $M_{ci}$  is its (primitive) projection matrix.



For each matrix  $M_{ci}$ ,  $\lambda_{ci}$  is the dominant eigenvalue, and  $u_{ci}$  and  $v_{ci}$  are the right and left eigenvectors, respectively, associated with  $\lambda_{ci}$ . For each population  $c \in C$ ,  $\lambda_{cm} = \max_{i \in S_c}(\lambda_{ci})$ ,  $Y_c = \{i | \lambda_{ci} = \lambda_{cm}, i \in S_c\}$ , and  $Z_c = S_c - Y_c$ . We also have  $N_{ci}(t) = \|K_{ci}(t)\|$ ,  $q_{ci}(t) = K_{ci}(t)/N_{ci}(t)$ , and  $p_{ci}(t) = N_{ci}(t)/N_c(t)$ , where  $N_c(t)$  is the total number of individuals in the  $c$ th population. The difference equations are given by

$$K_{ci}(t+1) = M_{ci}K_{ci}(t) \exp \left[ - \sum_{j \in C} a_{cj} N_j(t) \right], \quad i \in S_c, c \in C, \quad (29)$$

where  $a_{cj} \geq 0$  measures the per capita effect of population  $j$  on the mortality rate of population  $c$  ( $c, j \in C$ ). This model has the solution

$$K_{ci}(t) = M_{ci}^t K_{ci}(0) \exp \left[ - \sum_{j \in C} a_{cj} \sum_{\zeta=0}^{t-1} N_j(\zeta) \right], \quad i \in S_c, c \in C. \quad (30)$$

Now we introduce some matrix notation. Let  $N(t)$  be the vector obtained by catenating the variables  $N_c(t)$  for  $c \in C$ . Let the vector  $r_m$  have elements  $r_{cm} = \log(\lambda_{cm})$ ,  $c \in C$ , and let  $A = (a_{cj})$ ,  $c, j \in C$ . For each subpopulation  $i \in S_c$  and  $c \in C$ , the age distribution vector  $q_{ci}(t)$  and the frequency  $p_{ci}(t)$  go through the same sequence as they would in the density-independent model with identical initial conditions. Therefore,  $p_{ci}(t) \rightarrow p_{ci}^*$  and  $q_{ci}(t) \rightarrow q_{ci}^*$ ,  $i \in S_c$ ,  $c \in C$ . For each population  $c \in C$ , the entropies  $H_{cp}$  and  $H_{cv}$  are computed using (8) and (9), respectively, with  $p_i^*$  replaced by  $p_{ci}^*$ ,  $V_i(0)$  by  $v_{ci}^T q_{ci}(0)$ , and  $V_i^*$  by  $v_{ci}^T q_{ci}^*$ . Let  $H_{cN} = -\log[N_c(0)/N_c^*]$ . The scalars  $H_{cp}$ ,  $H_{cv}$ , and  $H_{cN}$  are the elements of vectors  $H_p$ ,  $H_v$ , and  $H_N$ , respectively.

**THEOREM 3.** Suppose  $\lim_{t \rightarrow \infty} N(t) = N^*$ , where every element of  $N^*$  is positive, and  $\det(A) \neq 0$ . Then  $N^* = A^{-1} r_m$  and

$$\sum_{t=0}^{\infty} [N^* - N(t)] = A^{-1} [H_p + H_v + H_N]. \quad (31)$$

*Proof.* The difference equations for total population size can be written in the form

$$N_c(t+1) = N_c(t) [1 - \omega_c(t)] \exp \left[ r_{cm} - \sum_{j \in C} a_{cj} N_j(t) \right], \quad c \in C. \quad (32)$$

where

$$\omega_c(t) = 1 - \sum_{i \in S_c} p_{ci}(t) \|M_{ci} q_{ci}(t) \lambda_{cm}^{-1}\|, \quad c \in C. \quad (33)$$

Since, for  $i \in S_c$  and  $c \in C$ ,  $p_{ci}(t) \rightarrow p_{ci}^*$ ,  $q_{ci}(t) \rightarrow q_{ci}^*$ ,  $M_{ci} q_{ci}^* = \lambda_{ci} q_{ci}^*$ , and  $p_{ci}^* = 0$  when  $\lambda_{ci} \neq \lambda_{cm}$ ,  $\lim_{t \rightarrow \infty} \omega_c(t) = 0$  for every  $c \in C$ . If  $N^*$  is strictly positive, then it is obvious from (32) that  $\lim_{t \rightarrow \infty} N(t) = N^*$  implies  $r_m - AN^* = 0$ . If  $\det(A) \neq 0$ , then  $N^* = A^{-1}r_m$ .

Let  $\delta(t) = N^* - N(t)$  and  $L(t) = \sum_{j \in C}^{-1} \delta(\xi_j)$ . Using (30) with  $\lambda'_{cm} = \exp[r_{cm}t] = \exp[\sum_{j \in C} a_{cj} \sum_{j \in C}^{-1} N_j^*]$ ,

$$\begin{aligned} \lim_{t \rightarrow \infty} N_c(t) &= \lim_{t \rightarrow \infty} N_c(0) \exp \left[ \sum_{j \in C} a_{cj} L_j(t) \right] \sum_{i \in S_c} p_{ci}(0) \| (M_{ci} \lambda_{cm}^{-1})' q_{ci}(0) \| \\ &= N_c(0) \exp \left[ \lim_{t \rightarrow \infty} \sum_{j \in C} a_{cj} L_j(t) \right] \sum_{i \in S_c} p_{ci}(0) \| u_{ci} v_{ci}^T q_{ci}(0) \| = N_c^*. \end{aligned} \quad (34)$$

Substituting into (34) from (14), multiplying by  $p_{ci}^*$ , and summing over all  $i \in S_c$  gives

$$\lim_{t \rightarrow \infty} \sum_{j \in C} a_{cj} L_j(t) = H_{cp} + H_{cV} + H_{cN}, \quad c \in C. \quad (35)$$

Hence  $\lim_{t \rightarrow \infty} A \sum_{j \in C}^{-1} [N^* - N(t)] = H_p + H_V + H_N$ .

Now we examine the rate of convergence of  $\delta(t)$  to zero. Let  $\Omega(t) = \sum_{c \in C} |\omega_c(t)|$  and  $d(t) = \sum_{c \in C} |\delta_c(t)|$ . Expanding the exponential term of (32) to second order in a Taylor series gives

$$\begin{aligned} \delta_c(t+1) &= \delta_c(t) - N_c^* \sum_{j \in C} a_{cj} \delta_j(t) + N_c^* \omega_c(t) \\ &\quad + O[\omega_c(t) d(t)] + O[d^2(t)], \quad c \in C. \end{aligned} \quad (36)$$

Let  $J = I - \text{diag}(N^*)A$ , where  $I$  is the identity matrix and  $\text{diag}(N^*)$  is a diagonal matrix. In matrix notation, (36) gives, after dropping the last two terms,

$$\delta(t+1) = (J + O[\Omega(t)/d(t)]) \delta(t). \quad (37)$$

Since each  $M_{ci}$  is primitive, as  $t \rightarrow \infty$ ,

$$M_{ci}^t = \lambda_{ci}^t u_{ci} v_{ci}^T + O[t^{m_{ci}-1} \theta_{ci}^t], \quad i \in S_c, c \in C. \quad (38)$$

Here  $\theta_{ci} < \lambda_{ci}$  is the largest modulus of the subdominant eigenvalues of  $M_{ci}$  and  $m_{ci}$  is one less than the greatest multiplicity of the eigenvalues with modulus  $\theta_{ci}$  (Seneta, 1981, p. 9). If  $q_{ci}(0) \neq q_{ci}^*$ , then, as  $t \rightarrow \infty$ ,

$$q_{ci}(t) = q_{ci}^* + O[t^{m_{ci}} (\theta_{ci}/\lambda_{ci})^t], \quad i \in S_c, c \in C. \quad (39)$$

Let  $b_{ci} = N_c(0) p_{ci}(0) [V_{ci}(0)/V_{ci}^*]$ . Using (38),

$$p_{ci}(t) = \frac{b_{ci} \lambda'_{ci} + O[t^{m\alpha} \theta'_{ci}]}{\sum_{h \in S_c} (b_{ch} \lambda'_{ch} + O[t^{m\alpha} \theta'_{ch}])}, \quad i \in S_c, c \in C. \quad (40)$$

Multiplying the numerator and denominator of (40) by  $\lambda_{cm}^{-1}$ ,

$$\begin{aligned} p_{ci}(t) &= p_{ci}^* + O[\beta'_c] \quad \text{for } i \in Y_c, c \in C, \\ &= O[\beta'_c] \quad \text{for } i \in Z_c, c \in C, \end{aligned} \quad (41)$$

where  $\beta_c = \max_{i \in Z_c} (\lambda_{ci}/\lambda_{cm})$ . Substituting (39) and (41) into (33) gives

$$\begin{aligned} \omega_c(t) &= 1 - \sum_{i \in Y_c} (p_{ci}^* + O[\beta'_c]) (1 + O[t^{m\alpha} (\theta_{ci}/\lambda_{cm})']) \\ &\quad - \sum_{i \in Z_c} O[\beta'_c] (1 + O[t^{m\alpha} (\theta_{ci}/\lambda_{ci})']) = O[\beta'_c]. \end{aligned} \quad (42)$$

Therefore, as  $t \rightarrow \infty$ ,  $\Omega(t) = O[\beta']$ , where  $\beta = \max_{c \in C} (\beta_c) < 1$ . If  $d(t) = O[\beta']$  as  $t \rightarrow \infty$ , then  $|\lim_{t \rightarrow \infty} L_c(t)| < \infty$  for  $c \in C$ . Otherwise,  $d(t)$  decays slower than  $\beta'$ , and by (42),  $\lim_{t \rightarrow \infty} [\Omega(t)/d(t)] = 0$ . From (37), for large  $t$ ,  $\delta(t) = O[\mu']$ , where  $\mu$  is the largest modulus of the eigenvalues of  $J$ . By assumption of the theorem,  $\lim_{t \rightarrow \infty} \delta(t) = 0$ , which implies  $\mu < 1$ . Therefore,  $|\lim_{t \rightarrow \infty} L_c(t)| < \infty$  for every  $c \in C$ . This allows us to take the limit on the left-hand side of (35) inside the summation, yielding the desired result (31).  $\blacksquare$

Finding the necessary and sufficient conditions for the vector  $N(t)$  to approach a finite positive limit remains an open problem.

## 5. NUMERICAL EXAMPLES

We illustrate our results using the census data and demographic projection matrices of Keyfitz and Flieger (1968) for Mexico, the United States, and Canada in the year 1962. We imagine that all females under the age of 45 in these three nations form a single population and each nation represents a subpopulation. Mexico, the U.S., and Canada are labeled as subpopulations 1, 2, and 3, respectively. To simplify matters, we collapse the census data into age classes of 0-14, 15-29, and 30-44 years. Using 1962 as time zero, the initial age structures of each subpopulation are given by the vectors  $K_1(0) = (8.646, 4.913, 3.003)^T \times 10^6$ ,  $K_2(0) = (28.592, 18.775, 18.382)^T \times 10^6$ , and  $K_3(0) = (2.929, 1.845, 1.788) \times 10^6$ . We condensed the Leslie matrices from the 5-year time unit adopted by Keyfitz and Flieger

into a 15-year time unit, using the method described by Keyfitz (1968, pp. 37-40). We obtained the following primitive projection matrices:

$$M_1 = \begin{pmatrix} 0.5433 & 1.6225 & 0.5299 \\ 0.9627 & 0 & 0 \\ 0 & 0.9470 & 0 \end{pmatrix},$$

$$M_2 = \begin{pmatrix} 0.5022 & 1.0126 & 0.1472 \\ 0.9923 & 0 & 0 \\ 0 & 0.9829 & 0 \end{pmatrix},$$

$$M_3 = \begin{pmatrix} 0.4425 & 1.1336 & 0.2235 \\ 0.9928 & 0 & 0 \\ 0 & 0.9870 & 0 \end{pmatrix}.$$

The dominant eigenvalues of these matrices are  $\lambda_1 = 1.6598$ ,  $\lambda_2 = 1.3353$ , and  $\lambda_3 = 1.3760$ , respectively. The corresponding left eigenvectors are  $v_1 = (1, 1.1597, 0.3193)^T$ ,  $v_2 = (1, 0.8395, 0.1103)^T$ , and  $v_3 = (1, 0.9403, 0.1624)^T$ . The corresponding right eigenvectors are  $u_1 = (0.5623, 0.3262, 0.1861)^T$ ,  $u_2 = (0.5934, 0.4413, 0.3248)^T$ , and  $u_3 = (0.5674, 0.4094, 0.2936)^T$ . The logarithms of the eigenvalues give  $r_1 = 0.5067$ ,  $r_2 = 0.2891$ , and  $r_3 = 0.3192$  for the intrinsic rates of increase. From the initial census vectors we have  $q_1(0) = (0.5221, 0.2966, 0.1813)^T$ ,  $q_2(0) = (0.4349, 0.2855, 0.2796)^T$ ,  $q_3(0) = (0.4463, 0.2812, 0.2725)^T$ ,  $p_1(0) = 0.1864$ ,  $p_2(0) = 0.7398$ ,  $p_3(0) = 0.0738$ , and  $N(0) = 88.8737 \times 10^6$ .

Assume (contrary to reality) that all vital rates remain constant through time. The solid curve in Fig. 1 gives a projection of the total population size for 20 time units (300 years) using the observed initial conditions. Since  $\lambda_1 > \lambda_3 > \lambda_2$ , subpopulation 1 comes to dominate the population as a whole. Using (7) with  $Y = \{1\}$  and  $Z = \{2, 3\}$ , we have  $p_1^* = 1$  and  $p_2^* = p_3^* = 0$ . From (4), the stable age distribution for subpopulation 1 is  $q_1^* = (0.5233, 0.3035, 0.1732)^T$ .

To evaluate the effects of the initial disequilibrium, we compare the trajectory of total population size with the observed initial conditions to the trajectory that would occur if the subpopulation frequencies and age distributions were equal to their equilibrium values at time zero. This reference trajectory is given by the dashed line in Fig. 1. As Fig. 1 illustrates, the two trajectories become separated in time by a constant asymptotic value  $\tau$ . Theorem 1 allows us to calculate  $\tau$  from the initial conditions. From (8),  $H_p = -\log[p_1(0)] = 1.6801$ . From (9),  $H_V = -\log[V_1(0)/V_1^*] = 0.007163$ , where  $V_1(0) = v_1^T q_1(0) = 0.9239$  and  $V_1^* = v_1^T q_1^* = 0.9306$ . With  $r_m = r_1$ , (11) gives  $\tau = 3.33$ . The effect of disequilibrium is to delay the growth of the population by 3.33 time units, or

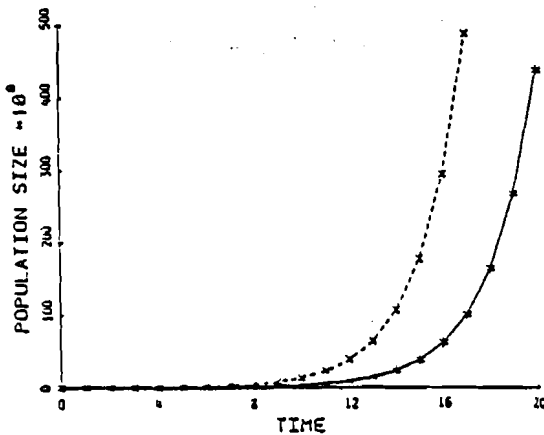


FIG. 1. A hypothetical numerical example of the density-independent model. Total population size is plotted as a function of time. The solid line is the trajectory for the observed nonequilibrium initial conditions. The dashed line is the trajectory of the equilibrium reference population. The asymptotic time lag between these two trajectories equals  $\tau$  (see the text for details).

approximately 50 years. If the vital rates and age distributions of females in the U.S. and Canada had, in 1962, matched those of Mexico in 1962, then the total census projections of these three nations would have been advanced asymptotically by 50 years.

An illustration of the density-dependent model requires values of the density-sensitivity parameters  $a_1$ ,  $a_2$ , and  $a_3$ . As an artificial example, we will fix  $\alpha$  at  $250 \times 10^6$  and set  $a_1 = r_1/\alpha = 2.027 \times 10^{-9}$ ,  $a_2 = r_2/\alpha = 1.157 \times 10^{-9}$ , and  $a_3 = 0.5(r_3/\alpha) = 2.554 \times 10^{-9}$ . In this case  $Y = \{1, 2\}$  and  $Z = \{3\}$ . The solid curve in Fig. 2 is a projection of the total population size for the model (16). In this simulation, the subpopulation frequencies approached limiting values  $p_1^* = 0.3477$ ,  $p_2^* = 0.6523$ , and  $p_3^* = 0$  and total population size approached  $\alpha$ .

Theorem 2 can be used to predict the life not lived due to disequilibrium. From (8),  $H_p = -p_1^* \log[p_1(0)/p_1^*] - p_2^* \log[p_2(0)/p_2^*] = 0.13471$ . From (9),  $H_v = -p_1^* \log[V_1(0)/V_1^*] - p_2^* \log[V_2(0)/V_2^*] = 0.0296$ , where  $V_1(0) = 0.9239$ ,  $V_1^* = 0.9306$ ,  $V_2(0) = 0.7054$ , and  $V_2^* = 0.7354$ .  $H_N = -\log[N(0)/N^*] = 1.0342$  and  $a^* = p_1^* a_1 + p_2^* a_2 = 1.459 \times 10^{-9}$ . Using (19),  $\sum_{t=0}^{\infty} [N^* - N(t)] = 821.49 \times 10^6$  individual-time units. Since one time unit equals 15 years, the population fails to realize 12,322 million female-years of life due to disequilibrium. This "life not lived" is represented by the total area lying between the solid curve and the dashed line in the upper left corner of Fig. 2.

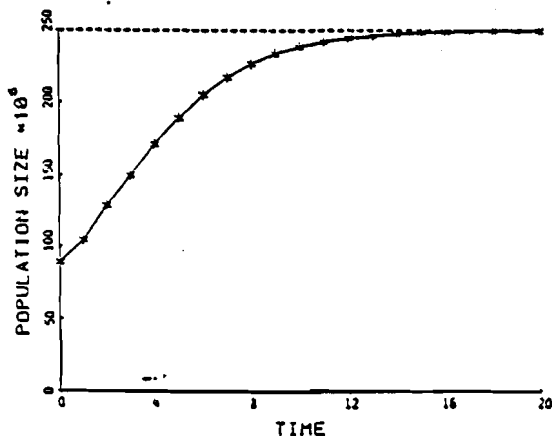


FIG. 2. A hypothetical numerical example of the density-dependent model. Total population size is plotted as a function of time. The solid line is the trajectory for the observed nonequilibrium initial conditions. The dashed line is the equilibrium constant  $N^*$ . The total area between these two lines is the life not lived due to disequilibrium (see the text for details).

## 6. DISCUSSION

We have analyzed three models of age-structured populations with demographically heterogeneous subpopulations. All three models ignore nonlinear interactions between sexes. The models are therefore most naturally interpreted as applying to a single sex, or to a two-sex population in which the sex not described is present in abundance. In the first model, each subpopulation has its own age-specific vital rates, fixed in time, and grows independently of all others. In the second, each subpopulation has its own age-specific vital rates, and these are all uniformly inhibited by increasing total numbers of individuals. In the third, each subpopulation has its own age-specific vital rates, but the vital rates of groups of these subpopulations are inhibited by the total numbers of individuals in other groups of subpopulations with an intensity that depends on the interacting pair of groups of subpopulations.

We have described how disequilibrium affects total population size. We defined three functions,  $H_p$ ,  $H_v$ , and  $H_N$ , which measure disequilibrium in the subpopulation frequencies, subpopulation age structures, and total population size, respectively. For the first model, we showed that disequilibrium will shift the trajectory of the total numbers of individuals forward or backward in time by an amount that is asymptotically constant and that this constant is proportional to the sum of the disequilibrium measures  $H_p$  and  $H_v$ . For the second model, we established sufficient con-

ditions for the existence of a globally stable equilibrium and we showed that disequilibrium will result in a finite loss or gain in life, which can be measured in units of individual-time (e.g., person-years or animal-hours). This "life not lived" or "extra life lived" is also proportional to the sum of the disequilibrium measures  $H_p$  and  $H_v$  plus the disequilibrium measure  $H_N$ . For the last model, we extended the results of the second model to two or more interacting populations. In this case the life not lived for each population is a linear combination over all populations of the sums of the three disequilibrium measures. In all three models,  $H_p$ ,  $H_v$ , and  $H_N$  partition the effects of disequilibrium into three components: heterogeneity in vital rates, deviations from a stable age structure, and a nonequilibrium total population size, respectively.

### 6.1. $H_p$ as a Measure of Genetic Disequilibrium

In an age-structured population of asexually reproducing organisms, natural selection occurs through the differential survival and reproduction of genotypic clones. Each clone can be viewed as a subpopulation and  $H_p$  measures *genetic* disequilibrium. In population genetics, the overall effect of genetic disequilibrium has been called the "cost of natural selection" (Haldane, 1957; Crow, 1970). This section relates our results to previous work in this area.

Haldane (1957) considered a population in an environment subjected to a sudden change, for example, by pollution or migration. The population is less adapted to the new environment and its reproductive capacity becomes lowered. Initially rare genotypes now become favored. Haldane defined the cost of selection as the total reduction in reproductive capacity that occurs as the population adapts to the environmental change. For an asexual population with two genotypes, he showed that the cost of selection is  $-\log(p_0)$ , where  $p_0$  is the initial frequency of the newly favored genotype. Haldane assumed that generations are discrete and that the total population size remains constant. His cost of selection is measured in units of total population size.

In the diploid single-locus continuous-time model of natural selection with constant genotype fitnesses and no age structure, Ginzburg (1977, 1983) included total population size as a dynamic variable. He also considered the effects of genetic disequilibrium and introduced  $H_p$  into population genetics. Ginzburg showed that  $H_p = W^* \tau$ , where  $W^*$  is the asymptotic exponential rate of population growth and  $\tau$  is the asymptotic time lag separating a reference population in genetic equilibrium from an evolving population with nonequilibrium initial allele frequencies. Our Theorem 1 extends his result to age-structured populations with asexual reproduction.

Desharnais and Costantino (1982) also considered the diploid single-

locus continuous-time model of natural selection without age structure. They allowed the genotypic fitnesses to decrease linearly with population size, i.e.,  $W_{ij}(N) = r_{ij} - aN$ , where  $W_{ij}$  is the genotypic fitness,  $r_{ij}$  is the intrinsic rate of increase, and  $a$  measures density sensitivity. Defining  $\bar{N}(t)$  as the trajectory of a reference population which is in genetic equilibrium at time zero, Desharnais and Costantino showed that  $\int_0^\infty [\bar{N}(t) - N(t)] dt = a^{-1}H_p$ . Our Corollary 1 extends their result to age-structured populations with asexual reproduction.

## 6.2. $H_v$ as a Measure of Disequilibrium in Age Structure

Keyfitz (1968) and Keyfitz and Flieger (1968) measured the dissimilarity between an observed age distribution  $q$  and its limiting stable age distribution  $q^*$  by

$$D = 50 \sum_{j=1}^n |q_j - q_j^*|,$$

where  $q_j$  is the  $j$ th element of the  $n$  vector  $q$ . For a given  $q$ ,  $D$  is the same for any two projection matrices with the same stable age distribution  $q^*$ .

Cohen (1979) showed that, for any nonnegative primitive projection matrix  $M$  and observed age distribution  $q$ , if  $\lambda$  is the dominant eigenvalue of  $M$ ,  $B = uv^T$ ,  $u$  and  $v$  are the right and left eigenvectors of  $M$  corresponding to  $\lambda$  and  $I$  is the identity matrix,

$$\sum_{i=0}^{\infty} (\lambda^{-i} M^i - B) q = (Z - B) q,$$

where

$$Z = (I + B - M/\lambda)^{-1}.$$

The  $n$  vector  $(Z - B)q$  represents the cumulative distance between the observed  $q$  and its stable age distribution  $q^*$ . As an alternative measure of demographic disequilibrium, Cohen (1979) suggested using

$$D_1 = 50 \sum_{j=1}^n |([Z - B] q)_j|,$$

where  $([Z - B] q)_j$  is the  $j$ th element of the  $n$  vector  $[Z - B] q$ . The advantage of  $D_1$  over  $D$  is that  $D_1$  takes into account the trajectory of the population as it approaches stability.

Demetrius (1974) introduced the use of entropy measures in studying age-structured populations [for recent developments, see Demetrius and Ziehe (1984) and Goldman and Lord (1986)].



We now propose  $H_V$ , defined in (9), as another measure of demographic disequilibrium. Our theorems suggest that  $H_V$  may be more appropriate than  $\Delta$  or  $D_1$  for assessing the effects of age-structure disequilibrium on the future trajectory of the total population size. As an example, consider a single homogeneous age-structured population, so that  $H_p = 0$  in our first model. Using the 1962 data for the United States from Section 5 of this paper, we have  $q = (0.4349, 0.2855, 0.2796)^T$  and  $q^* = (0.4366, 0.3245, 0.2389)^T$ . The three measures of demographic disequilibrium are  $\Delta = 4.07$ ,  $D_1 = 3.29$ , and  $H_V = 0.0416$ . As a hypothetical age structure consider  $q' = (0.1831, 0.6338, 0.1831)^T$ . Now we have  $\Delta' = 30.94$ ,  $D_1' = 21.66$ , and  $H_V' = 0$ . Although  $q'$  looks less similar to  $q^*$  than the observed  $q$ , Theorem 1 tells us that, since  $H_V' = 0$ , the trajectory of the hypothetical population starting from  $q'$  will be asymptotically indistinguishable from the stable reference population ( $\tau' = 0$ ), whereas the projection for the observed population lags behind the reference population by 2.16 years ( $\tau = 0.144$ ). For measuring deviations of the age structure from stability at a given time or over time,  $\Delta$  or  $D_1$  appears to be more appropriate.

### 6.3. Possible Examples

We are not aware of any field studies that would make it possible to estimate all the parameters of any of these models. The purpose of this section is to indicate some demographic and biological examples that might be investigated quantitatively in terms of these models. Whether any of the models actually describes any of the examples remains to be determined.

A first example is national populations of humans with different age-specific vital rates and negligible migration among countries. Our use, as a numerical example, of the United States, Canada, and Mexico ignores international migration. In applying any of our models to such populations, either males or females are ignored and assumed to be available in excess, as is usual in demographic applications of single-sex models.

A second example is populations of asexually reproducing clones. Such populations arise among vertebrates and invertebrates.

Cole (1979) estimates that about 30 of the world's 3000 species of lizards have all-female populations that reproduce by true parthenogenesis (that is, without any physiological or genetic contribution from male gametes). He and colleagues (e.g., Cole, 1975; Cole and Townsend, 1977; Hardy and Cole, 1981) have investigated in detail the New World whiptail lizard *Cnemidophorus exsanguis* and established parthenogenesis in the laboratory. Vrijenhoek and colleagues (e.g., Vrijenhoek, 1984) have established ecological differences among clones of all-female populations of the fish *Poeciliopsis monacha*, which reproduce gynogenetically (that is, with a physiological but no genetic contribution from male gametes). Since

these clones differ genetically and ecologically, they may also differ demographically. Other examples of naturally occurring unisexual vertebrates include the salamanders (e.g., Uzzell, 1970).

Among invertebrates, examples of populations of asexually reproducing clones include such medically important parasites as the protozoa of the genera *Leishmania* and *Trypanosoma*. Here the parasites of each human host that is infected by a single clone might be interpreted as one subpopulation, with demographic parameters determined by the interaction of the parasite's genotype and the host's defenses. These and other examples are described by Allee *et al.* (1949, p. 628).

A third and final example includes "cyclomorphic" populations (Allee *et al.*, 1949, pp. 685-686) in which the form of the population varies periodically among two or more alternate states. For example, human malarial parasites (genus *Plasmodium*) reproduce asexually in humans, passing through a number of different forms. The parasites switch to sexual reproduction and still other forms when ingested along with blood by a mosquito. Our models may apply to the often prolonged phase of asexual reproduction. The primitive matrices  $M_i$  in our models would not have Leslie form but would describe the asexual life stages of malarial parasites.

These examples give a diversity of possible applications of our models. Some of these applications have potential practical interest.

## 7. APPENDIX

*Proof of Lemma 1.* Using (17) to compute the age distribution vector  $q_i(t)$  defined by (3), the exponential factor cancels. As a result, the vector  $q_i(t)$  goes through the same sequence as it would in the density-independent model (1) with identical initial conditions. Therefore, (4) still holds.

Now we show that  $N_i(t)$  is bounded. It is obvious from (17) that  $N_i(t) \geq 0$  for  $i \in S$ . Let  $c_i(t) = \|M_i q_i(t)\|$ . Since  $\lim_{t \rightarrow \infty} c_i(t) = \lambda_i$  for  $i \in S$ , the sequence  $c_i(t)$  has a least upper bound  $c_i' \geq \lambda_i$ . Hence,

$$\begin{aligned} N_i(t+1) &= c_i(t) N_i(t) \exp[-a_i N(t)] \\ &\leq c_i' N_i(t) \exp[-a_i N_i(t)] \leq c_i' (a_i e)^{-1}, \quad i \in S. \end{aligned} \quad (A1)$$

The last inequality comes from the fact that the function  $x e^{-ax}$ ,  $x \geq 0$ , has a maximum when  $x = 1/a$ .

Let  $d_i(t) = N_i(0) \|(M_i \lambda_i^{-1})^t q_i(0)\|$  and  $\eta(t) = t^{-1} \sum_{s=0}^{t-1} N_i(s)$ . From (A1), we can choose a constant  $\gamma_i$  which is an upper bound of  $N_i(t)$ ,  $i \in S$ . For  $t > 0$ ,

$$N_i(t) = d_i(t) \exp[t(r_i - a_i \eta(t))] \leq \gamma_i, \quad i \in S, \quad (A2)$$

implies

$$\eta(t) \geq (r_i/a_i) + (a_i t)^{-1} \log [d_i(t)/\gamma_i], \quad i \in S. \tag{A3}$$

Since  $\lim_{t \rightarrow \infty} d_i(t) = N_i(0)[V_i(0)/V_i^*]$ , the sequence  $d_i(t)$  has a least upper bound  $d'_i \geq N_i(0)[V_i(0)/V_i^*]$ . If we choose  $\gamma_i > d'_i$ , then for any  $\varepsilon > 0$  and every  $i \in S$ ,  $\eta(t) > (r_i/a_i) - \varepsilon$  whenever  $t > t_i^0(\varepsilon) = (a_i \varepsilon)^{-1} \log [\gamma_i/d'_i]$ . Let  $t^0(\varepsilon) = \max_{i \in S} [t_i^0(\varepsilon)]$  and  $\alpha = \max_{i \in S} (r_i/a_i)$ . Clearly,  $\eta(t) > \alpha - \varepsilon$  for  $t > t^0$ . This implies

$$\begin{aligned} 0 \leq N_i(t) &= d_i(t) \exp [t(r_i - a_i \eta(t))] \\ &< d'_i \exp [t(r_i - a_i(\alpha - \varepsilon))] \end{aligned} \tag{A4}$$

whenever  $t > t^0$ . For  $i \in Z$ , we can choose  $\varepsilon < \alpha - (r_i/a_i)$ . Therefore,

$$\lim_{t \rightarrow \infty} N_i(t) = 0, \quad i \in Z. \tag{A5}$$

Let  $N_Y(t) = \sum_{i \in Y} N_i(t)$ ,  $N_Z(t) = \sum_{i \in Z} N_i(t)$ , and  $\rho_i(t) = N_i(t)/N_Y(t)$  for  $i \in Y$ . We can write

$$N_Y(t+1) = N_Y(t) \sum_{i \in Y} \rho_i(t) \exp [r_i - a_i(N_Y(t) + \omega_i(t))], \tag{A6}$$

where

$$\omega_i(t) = N_Z(t) - a_i^{-1} \log [\|M_i q_i(t) \lambda_i^{-1}\|], \quad i \in Y. \tag{A7}$$

Equations (4) and (A5) imply

$$\lim_{t \rightarrow \infty} \omega_i(t) = 0, \quad i \in Y. \tag{A8}$$

We employ a Liapunov function used by Fisher and Goh (1980) for the discrete-time analog of the logistic equation.

Let  $K(t)$  represent a catenation of the vectors  $K_i(t)$  for  $i \in S$ . Let  $V[K(t)] = V(t) = [N_Y(t) - \alpha]^2$ ,  $g_i[K(t)] = g_i(t) = \exp [r_i - a_i(N_Y(t) + \omega_i(t))]$ , and  $g[K(t)] = g(t) = \sum_{i \in Y} \rho_i(t) g_i(t)$ . We have

$$\begin{aligned} \Delta V[K(t)] &= \Delta V(t) = V(t+1) - V(t) \\ &= [N_Y(t) g(t) - \alpha]^2 - [N_Y(t) - \alpha]^2 \\ &= N_Y(t) [g(t) - 1] h(t), \end{aligned} \tag{A9}$$

where  $h(t) = h[K(t)] = \sum_{i \in Y} \rho_i(t) h_i(t)$  and  $h_i(t) = h_i[K(t)] = N_Y(t) g_i(t) + N_Y(t) - 2\alpha$ . We would like to know the sign of (A9) as a function of  $N_Y(t)$ .

First consider the function  $g_i(t)$ . Since  $r_i/a_i = \alpha$  for  $i \in Y$ ,

$$\begin{aligned} g_i(t) &< 1 && \text{when } N_Y(t) > \alpha + |\omega_i(t)|, \\ &> 1 && \text{when } N_Y(t) < \alpha - |\omega_i(t)|. \end{aligned} \quad (\text{A10})$$

Now consider the function  $h_i(t)$ . For  $i \in Y$ ,  $h_i(t) < 0$  when  $N_Y(t) = 0$  and  $h_i(t) > 0$  when  $N_Y(t) \geq 2\alpha$ . If  $N_Y(t) \in (0, 2\alpha)$ , then  $h_i(t) = 0$  implies

$$r_i - a_i [N_Y(t) + \omega_i(t)] = \log[(2\alpha)/N_Y(t) - 1], \quad i \in Y. \quad (\text{A11})$$

Let  $x(t) = [1 - N_Y(t)/\alpha]^{-1}$  for  $N_Y(t) \in (0, \alpha)$ . Substituting into (A11), we get

$$\begin{aligned} r_i - a_i x(t) \omega_i(t) &= x(t) \log([1 + x(t)^{-1}]/[1 - x(t)^{-1}]) \\ &= 2 \sum_{n=0}^{\infty} [x(t)^{-2n}]/[2n+1] > 2, \quad i \in Y \end{aligned} \quad (\text{A12})$$

(cf. Fisher and Goh, 1980). From (A12), we get

$$(r_i - 2)[1 - N_Y(t)/\alpha] > a_i \omega_i(t), \quad i \in Y. \quad (\text{A13})$$

If  $r_i < 2$  for  $i \in Y$ , then  $h_i(t) = 0$  implies

$$N_Y(t) > \alpha - |\omega_i(t)| [r_i/(2 - r_i)], \quad i \in Y. \quad (\text{A14})$$

Similarly, if we let:  $x(t) = [N_Y(t)/\alpha - 1]^{-1}$  for  $N_Y \in (\alpha, 2\alpha)$ , then (A11) gives

$$r_i + a_i x(t) \omega_i(t) = 2 \sum_{n=0}^{\infty} [x(t)^{-2n}]/[2n+1] > 2, \quad i \in Y. \quad (\text{A15})$$

If  $r_i < 2$  for  $i \in Y$ , then  $h_i(t) = 0$  also implies

$$N_Y(t) < \alpha + |\omega_i(t)| [r_i/(2 - r_i)], \quad i \in Y. \quad (\text{A16})$$

Let  $r_m = \max_{i \in Y} (r_i)$  and

$$\begin{aligned} \omega(t) &= \max_{i \in Y} |\omega_i(t)| && \text{if } r_m \leq 1, \\ &= [r_m/(2 - r_m)] \max_{i \in Y} |\omega_i(t)| && \text{if } r_m > 1. \end{aligned} \quad (\text{A17})$$

It follows from (A8) that  $\lim_{t \rightarrow \infty} \omega(t) = 0$ . Let  $I_\omega(t)$  denote the closed interval  $[\alpha - \omega(t), \alpha + \omega(t)]$ . Since  $\rho_i(t) > 0$  and  $\sum_{i \in Y} \rho_i(t) = 1$ , (A9), (A10), (A14), and (A16) imply

$$\Delta V(t) < 0 \quad \text{whenever } N_Y(t) \notin I_\omega(t). \quad (\text{A18})$$

Let  $T = \{t | N_Y(t) \in I_w(t), t = 0, 1, 2, \dots\}$ . We consider two possibilities for the set  $T$ .

*Case 1:  $T$  is finite.* Let  $t_m = \max(T)$ . From (A18),  $V(t)$  is a strictly decreasing sequence for  $t > t_m$ . Since  $V(t) \geq 0$ ,  $V(t)$  is a convergent sequence. This implies  $\lim_{t \rightarrow \infty} \Delta V(t) = 0$ . Let  $K^*$  be any of the accumulation points of the bounded vector sequence  $K(t)$ , and let  $N_Y^*$  and  $\omega^*$  be computed from  $K^*$ . Since  $\Delta V[K(t)]$  is a continuous function of the elements of  $K(t)$ , every  $K^*$  is a solution to  $\Delta V[K^*] = 0$ . From (A18),  $\Delta V[K^*] = 0$  implies  $N_Y^* \in [\alpha - \omega^*, \alpha + \omega^*]$ . Since  $\lim_{t \rightarrow \infty} \omega(t) = 0$ ,  $\omega^* = 0$  and  $N_Y^* = \alpha$  for every possible  $K^*$ , or, equivalently,  $\lim_{t \rightarrow \infty} N_Y(t) = \alpha$ .

*Case 2:  $T$  is infinite.* Let  $a_m = \max_{t \in T} a_i$ . Since  $|N_Y(t) - \alpha| \leq \omega(t)$  when  $t \in T$ , and  $|\omega_i(t)| \leq \omega(t)$  for  $i \in Y$ ,

$$\begin{aligned} \exp[-2a_m \omega(t)] &\leq \exp[-a_i(N_Y(t) - \alpha + \omega_i(t))] \\ &\leq \exp[2a_m \omega(t)], \quad i \in Y, \end{aligned} \quad (\text{A19})$$

whenever  $t \in T$ . Multiplying (A19) by  $N_Y(t)$  and summing over  $i \in Y$  gives, from (A6),

$$\begin{aligned} N_Y(t) \exp[-2a_m \omega(t)] &\leq N_Y(t+1) \\ &\leq N_Y(t) \exp[2a_m \omega(t)], \quad t \in T. \end{aligned} \quad (\text{A20})$$

Replacing  $N_Y(t)$  in (A20) with the endpoints of the interval  $I_w(t)$ ,

$$\begin{aligned} [\alpha - \omega(t)] \exp[-2a_m \omega(t)] &\leq N_Y(t+1) \\ &\leq [\alpha + \omega(t)] \exp[2a_m \omega(t)], \quad t \in T. \end{aligned} \quad (\text{A21})$$

Since  $\lim_{t \rightarrow \infty} \omega(t) = 0$  and  $T$  is infinite, for any  $\varepsilon > 0$  there exists a time  $t^0(\varepsilon) \in T$ , such that  $|N_Y(t+1) - \alpha| < \varepsilon$  for all  $t > t^0(\varepsilon)$ , provided  $t \in T$ . However, when  $t \notin T$ , (A18) implies  $|N_Y(t+1) - \alpha| < |N_Y(t) - \alpha|$ . Therefore,  $|N_Y(t+1) - \alpha| < \varepsilon$  for all  $t > t^0(\varepsilon)$ , whether or not  $t \in T$ , proving  $\lim_{t \rightarrow \infty} N_Y(t) = \alpha$ . ■

#### ACKNOWLEDGMENTS

This work was supported in part by U.S. National Science Foundation Grants DEB 80-11026 and BSR 84-07461 and U.S. Environmental Protection Agency Grant R-81223901-0. J.E.C. is grateful for the hospitality of Mr. and Mrs. William T. Golden during this work.

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