THE PERIODIC LIMIT FOR THE LESLIE MODEL

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ABSTRACT

If adjacent fertility rates in the Leslie population model are not assumed to be strictly positive, population distributions need not converge to the so-called stable age distribution. Instead the asymptotic behavior of a distribution may be periodic, taking a form which Bernardelli [1] called "population waves".

Here we state and interpret the main theorems describing this phenomenon and discuss objections which stand in the way of applying it to population studies. This is a continuation of our work done in [2].

In an appendix we prove, after normalization and under reasonable conditions, that asymptotically the period of a population distribution is the same as the period of the total population.

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§1. INTRODUCTION,

When the Leslie model of population growth was first introduced (see Bernardelli [1], Lewis [5], Leslie [4]), attention was given to the possibility that a population distribution might not converge to the stable age distribution but instead might tend to a periodic limit. Leslie proved the so-called Strong Ergodic Theorem: convergence to the stable age distribution must occur for "a species breeding continuously over a large proportion of its total life span". He also discussed a hypothetical example due to Bernardelli of a beetle population with only one non-vanishing fertility rate. The distribution of the beetles oscillated periodically and did not converge to the fixed distribution predicted by Leslie's theorem.

Bernardelli had been very impressed by this periodicity and cited many examples of cyclic phenomena which might be susceptible to an analysis in terms of it. He was particularly hopeful that it might be useful in relating the very brief fertility span of some insects to the violent oscillations in population size that they exhibit.

Lewis likewise noted the periodic case and suggested that it might have importance "for some lower animals with few age groups".

The periodic case has received little attention since these early papers. A number of authors (for example, Lopez [6], Sykes [10], Demetrius [3]) have stated precise mathematical conditions for Leslie's Theorem to hold, and the failure of these conditions sets the stage for periodicity. However, since these conditions are apparently fulfilled in human populations and populations of higher animals, the incentive to study the periodic case has not been strong.

Most recently [2] we have stated and proved theorems concerning the periodic case which generalize Leslie's Theorem.

Our present purpose is to restate these theorems and additional theorems in a formalism similar to that of Parlett [9] and to discuss some of the difficulties which the periodic case faces in applications. Even if the periodic case turns out to have no applications, we still hope to have confronted some of the issues that it raises and to have clarified the mathematical context of Leslie's Theorem.

§2. DEFINITIONS AND LEMMAS.

We take the elements of $\mathbb{R}^n (n \geq 2)$ to be n by 1 column vectors. $E_1, \ldots, E_n$ are the standard basis of column vectors for $\mathbb{R}^n$. A population vector X is a column vector $X = \sum_{j=1}^{n} x_j E_j$ where $x_1, \ldots, x_n \geq 0$. The population distribution of a population vector X is the direction of X in $\mathbb{R}^n$. If X is a column vector in $\mathbb{R}^n$, X^* denotes its transpose, a row vector. The dot product of two column vectors X and Y in $\mathbb{R}^n$ is $X \cdot Y = X^* Y$.

Recall that the Leslie population matrix L is an n by n matrix whose first row consists of fertility rates $F_1, \ldots, F_n$, whose first subdiagonal consists of survival rates $P_1,\ldots,P_{n-1}$, and whose remaining entries are zero. We assume that the survival rates are strictly positive and that the fertility rates are non-negative. In addition, we make the comparatively weak assumption that at least one fertility rate is positive.

As in [2] we define constants $c_1,\ldots,c_n$ and polynomials $g_1(\lambda),\ldots,g_n(\lambda),p(\lambda)$ as follows:

$$c_i = \begin{cases} 1 & \text{if } i = 1 \\ P_1P_2\cdots P_{i-1} & \text{if } 2 \leq i \leq n \end{cases} ; \quad g_i(\lambda) = \sum_{j=i}^{n} c_jF_j\lambda^{n-j} ; \quad 1 \leq i \leq n$$

$$p(\lambda) = \det(\lambda I - L) = \lambda^n - g_1(\lambda).$$

$p(\lambda)$ is up to sign the characteristic polynomial of L. Its roots are the eigenvalues of L. $p(\lambda)$ has one positive root, which we call λ_0. λ_0 is a simple root and dominates all other roots in absolute value.

An elementary estimate for λ_0 may be derived directly from the definition of $p(\lambda)$.

$$\max_{1\leq i\leq n} (c_iF_i)^{1/i} \leq \lambda_0 \leq \max_{1\leq i\leq n} (n\,c_iF_i)^{1/i} .$$

The n in the right-hand parentheses may be replaced by the number of non-vanishing fertility rates. If this number is one, λ_0 is completely determined.

We define the <u>index of L</u> to be the greatest common integral divisor of the set of indices i such that $F_i > 0$. Denoting this index hereafter by k, we observe that $1 \leq k \leq n$.

<u>Lemma 1</u>: L has a one-dimensional column eigenspace corresponding to the eigenvalue λ_0. This space is spanned by the vector $U_{\lambda_0} = U_1 + \ldots + U_k$ where

$$U_j = \sum_{\substack{i=1 \\ i \equiv j, \bmod k}}^{n} \frac{c_i}{\lambda_0^i} E_i \qquad 1 \leq j \leq k.$$

The vectors $U_1, \ldots, U_k$ are mutually orthogonal and $L\,U_j = \lambda_0 U_{j+1, \bmod k}$ for $1 \leq j \leq k$.

<u>Lemma 2</u>: L has a one-dimensional row eigenspace corresponding to the eigenvalue λ_0. This space is spanned by the vector $V^*_{\lambda_0} = V^*_1 + \ldots + V^*_k$ where

$$V_j = \frac{1}{p'(\lambda_0)} \sum_{\substack{i=1 \\ i \equiv j, \bmod k}}^{n} \frac{g_i(\lambda_0)\lambda_0^{i-1}}{c_i} E_i \qquad 1 \leq j \leq k.$$

The vectors $V_1, \ldots, V_k$ are mutually orthogonal and $V^*_j L = \lambda_0 V^*_{j-1, \bmod k}$ for $1 \leq j \leq k$.

In **Lemma** 2 $p'(\lambda_0)$ is the first derivative of $p(\lambda)$ evaluated at λ_0.

Lemma 3: $V_{]} \bullet U_{1} = V^{*}U_{-]}{}_{1}^{i} \equiv \frac{1}{K} 6_{1J}$ for $1 \leq i, j \leq k$.

Let $U = \text{span}\{U_1, \ldots, U_k)$ and $V = \text{spanf}v\wedge \ldots, V_k)$. By the preceding lemmas $U\wedge, \ldots, U_k$ and $V\text{-}\wedge \ldots, V_k$ are orthogonal bases for the subspaces U and V respectively.

Lemma 4: $IR^n = U © \backslash s^x$. That is, for any X in $3R^n$, there exist unique scalars >V • • • * Tv and a uni<3ue vector W in \s such that $X = \sum_{j=l}^{k} y_J U_3 + W$. In fact, $y_J = k(X\text{-}V_J)$ for $l \leq j \leq k$.

Let $P: 2R^n \to U$ be the canonical projection from $3R^n$ into U guaranteed by Lemma 4. Thus, $P(X) = \sum_{j=l}^{k} k(X - V_j)U_j$. Let $I_u : U \to U$ be the identity map of U. Let $T: U \to U$ be the unique linear map of U into U which permutes the basis elements of U cyclically according to the formula $FU_j = U_{j+1, \text{mod } k}$ for $l\wedge.j\wedge,k$.

Lemma 5: i) $r(U_{AO}) = U_{A_O}$;

ii) $\frac{1}{k}\left[I_u + \Gamma + \Gamma^2 + \ldots \wedge^{\text{II}} *^1\right] X = (X \cdot V_{\lambda_0})U_{\lambda_0}$

for each vector X in U;

iii) $P^3 = 1\wedge$ if and only if j is a multiple of k.

§3. THEOREMS AND INTERPRETATIONS;

Let X be a population vector at time 0 (the initial population vector). Then, in accordance with the Leslie model,

L^{fc}(X) is the population vector at time t = 0,1,2... . To obtain information on *1^* (X) for t large, we examine L^{t} or, more precisely, the normalized matrix (L/A$_{O}$) ˘. The following theorem generalizes Leslie^{1}s theorem.

Theorem 1; Let index L = K. Then

lim \l'L/'X$_{rs}$\$^{t}$ - P(t)"l = 0

where P(t) = k $\overset{k}{E}$ U.Vf . -, $_{n}$ is a matrix-valued function
J•=±i j j-t,mod k
of the integer variable t.

The limit in Theorem 1 is relative to any of the (equivalent) norms on the set of n by n matrices. If k = 1, P(t) has the constant value U$_{^O}$ V*$_{\lambda O}$: this is Leslie's Theorem. In general, the situation is described by Theorem 2.

Theorem 2; P(t) has the following properties:

i) period (P(t)) = k;

ii) i$_{K}$ [$_{L}$ $\overset{k}{E}_{t=l}$ P(t)$_{J}$l = U$_{^A0}$ V*$_{^A0}$;

iii) as an operator, P(t) = $\overset{t}{I}$P : 3$\overset{n}{R}$ —> U.

P(t) is a periodic function with period k and its average value over one period is the matrix tL$_{^A0}$ V:*$_{\lambda 0}$. Acting on a vector X, P(t) projects it into the subspace U and then "rotates" it in U by a power of the transformation *T.* P(t) suppresses all information except the projection of a vector in the k-dimensional subspace U. Hence, an (n-k)-dimensional family of vectors X gives rise to the same vector-valued function $P(t)X$ of the variable t. If the projections of X and Y in $\mathfrak{U}$ differ by a power of the transformation Γ, then the functions $P(t)X$ and $P(t)Y$ are the same except for a change of phase.

Theorem 3: If X is in $\mathbb{R}^n$, then

$$P(t)X = \sum_{j=1}^{k} \gamma_X(j-t)U_j$$

where $\gamma_X(t) = k(X \cdot V_{t,\mathrm{mod}\ k})$ is a scalar-valued function of the integer variable t.

Theorem 4: γ_X has the following properties:

i) period $(\gamma_X(t))$ = period$(P(t)X)$ = period of the distribution of $P(t)X$, and each is an integral divisor of period $(P(t)) = k$;

ii) $\frac{1}{k}\left(\sum_{t=1}^{k} \gamma_X(t)\right) = X \cdot V_{\lambda_0}$.

Theorems 3 and 4 show that the vector-valued function $P(t)X$ is completely determined by the scalar-valued function $\gamma_X(t)$. In particular, the period of $\gamma_X(t)$ is the same as that of $P(t)X$, which is the same as that of the distribution of $P(t)X$. Note that this period need not be equal to k. For example, if $X = U_{\lambda_0}$, we have $\gamma_X(t) \equiv 1$ and $P(t)X \equiv U_{\lambda_0}$.

Theorem 5; For a population vector X the following statements are equivalent:

i) l^X converges to a time-independent distribution;

ii) period $(y_v(t))$ = period $(P(t)X) = 1$;

iii) X is in spanfu$._{\wedge_0}$) © lr^x;

iv) $\lim_{t \to \infty}$ ^V^ $_{A^}$ = (X • V$._{A_0}$)IL$_{A_0}$ •

The only subtlety in Theorem 5 arises from the possibility that $P(t)X = 0$ for some time t. In this case X is in lr^x and so X • V-v$_{\wedge_0}$ = 0 . If X is a population vector,, we can conclude as in [2] that X has its population concentrated in the ages beyond fertility. Hence, $L^t X = 0$ for t large.

When $k = 1$, span{U$._{\wedge_0}$ } © V^x = U © V^x = HR^n and Theorem 5 reduces to Leslie^{1}s theorem.

The direction of U$._{A_0}$ in]R^n is the stable age distribution. Let p = period (P(t)X). Then, using Theorem 2 and the fact that p is a divisor of k, we obtain:

$$\frac{i}{P} \left(\sum_{t=l}^{p} P(t)x \right) = \frac{i}{K} \left(\sum_{t=l}^{k} P(t)x \right) = U_{\lambda_0} V^*_{\lambda_0} X = (X.V_{\lambda_0})U_{\lambda_0} .$$

Thus the stable age distribution arises in the periodic case as an average value (in a suitable sense) of the asymptotic distributions over one period.

Let Pop:]R^n —* IR denote the total population function. If X is in IR^n, $\mathrm{Pop}(X) = \sum_{j=1}^{n} x_j$.

Theorem 6: Let X be in $\mathbb{R}^n$. If $\lambda_0 > \max\{P_1,\ldots,P_{n-1}\}$, then period $(P(t)X) = \text{period}(\text{Pop}(P(t)X))$.

A more general statement of Theorem 6 together with a proof may be found in the Appendix.

Theorem 6 facilitates the search for the periodic case. Supposing that the Leslie model with index greater than one describes a species in nature, we need not tabulate the population vectors of the species to observe periodicity. It suffices to tabulate the total population function $\text{Pop}(L^t X)$, normalize it by an exponential multiplier of the form $c\,\lambda_0^{-t}$, and read off the period.

The hypothesis $\lambda_0 > \max\{P_1,\ldots,P_{n-1}\}$ follows from the stronger hypothesis $\lambda_0 \geq 1 > \max\{P_1,\ldots,P_{n-1}\}$. If the survival rates are strictly less than one in each age group and if the population does not vanish asymptotically $(\lambda_0 \geq 1)$, the latter hypothesis holds.

We close this section with one final theorem.

Theorem 7: $\lim\limits_{t\to\infty} \frac{1}{t}\left[\sum\limits_{j=1}^{t} \left(\frac{L}{\lambda_0}\right)^j\right] = U_{\lambda_0} V^*_{\lambda_0}$

Theorem 7 is an ergodic theorem and demonstrates that Leslie matrices can be analyzed by ergodic methods. Indeed, the matrix (L/λ_0) is similar to a stochastic matrix and consequently Leslie's Theorem as well as our theorems fall within the ergodic theory of stochastic matrices.

§4. THE APPLICABILITY OF THE PERIODIC LIMIT.

Despite the attractive mathematical theory of the previous sections, there are both empirical and theoretical reasons for questioning whether the Leslie model with index greater than one is an appropriate descriptive tool for real populations.

Empirically it has been found that Leslie matrices used in studying human populations have adjacent fertility rates positive. If F_{j_0} and F_{j_0+1} are two such rates, then index $L = \text{g.c.d.}\{j: F_j > 0\} = \text{g.c.d.}\{j_0, j_0+1\} = 1$. $(V/\lambda_0)^t$ converges to the constant matrix $U_{\lambda_0} V^*_{\lambda_0}$ and periodicity does not occur.

Theoretical reasons suggest that this same reduction may hold generally.

To see this we examine the Leslie model in greater detail. Let n be a positive integer ≥ 2 representing an age nobody lives to. With $i = 1, \ldots, n$ and $t \geq 0$, we define:

$x_i(t)$ = number of females[1] whose ages are in the interval $[i-1,i)$ at time t;

$x_1^i(t)$ = number of females whose ages are in the interval $[0,1)$ at time t and whose mothers had ages in the interval $[i-1,i)$ at time $t-1$;

$\delta(t)$ = number of females whose ages are in the interval $[0,1)$ at time t and whose mothers were not yet born at time $t-1$.

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[1] We consider only females for traditional reasons. Such a distinction may be unnecessary and/or impractical for lower animals and insects.

It follows from these definitions that $x_1(t) = \delta(t) + \sum_{i=1}^{n} x_1^i(t)$.
In addition, we hypothesize that there exist constants $P_1,\dots,P_{n-1}$ and $F_1,\dots,F_n$ such that:

$$\text{I.}\quad x_{i+1}(t+1) = P_i x_i(t) \qquad i = 1,\dots,n-1 \qquad t \geq 0;$$

$$\text{II.}\quad x_1^i(t+1) = F_i x_i(t) \qquad i = 1,\dots,n \qquad t \geq 0;$$

$$\text{III.}\quad \delta(t+1) = 0 \qquad t \geq 0.$$

In the interest of simplicity (and ignoring the question of whether the data we discuss is in fact accessible), we interpret Equations I and II as <u>defining equations</u> for the survival and fertility rates and also as axioms asserting their constancy. Thus, to compute these rates we solve Equations I and II using experimental values of $x_1(0),\dots,x_n(0),x_1(1),\dots,x_n(1)$, $x_1^1(1),\dots,x_1^n(1)$. This method will give unique solutions if $x_1(0),\dots,x_n(0) > 0$. These solutions will be consistent with the earlier theory (i.e., positive survival rates and at least one positive fertility rate) provided $x_1(1),\dots,x_n(1) > 0$ and $\delta(1) = 0$.

Our model is then as strong as the axioms of constancy and Equation III. These can be checked individually at different times. If they are confirmed, we put credence in the theorems deduced from the model. If they are not confirmed, the theorems still tell us what would have happened if fertility and mortality schedules had remained constant--hypothetical information which sometimes has a preventive use.

Incidentally, the time t need not vary over a continuum. If fertility and mortality vary seasonally, t should be restricted to integers and the unit of time chosen so that the passage of one unit brings us back to the same season. The requirements that $\delta(t) = 0$ and that some females survive to age $\geq n-1$ also influence the choice of a unit of time.

We return now to the subject of periodicity. Suppose that females may give birth at any age in the interval (α,β) where α and β are real numbers and $1 \leq \alpha < \beta \leq n$. ($1 \leq \alpha$ to conform with $\delta(t) = 0$.) If females may give birth at any age in this interval, then presumably females of age in (α,β) at time t (if there are any) make a positive contribution to $x_1(t+1)$. In fact, females of age in $(\alpha-1,\beta)$ at time t (if there are any) make a positive contribution to $x_1(t+1)$ since their ages will fall in (α,β) at some time in the interval $(t,t+1)$.

Let j_0 be the least integer such that $\alpha-1 < j_0 < \beta$. The intervals $[j_0-1,j_0)$ and $[j_0,j_0+1)$ each overlap with $(\alpha-1,\beta)$. We can expect that at some time t $x_{j_0}(t)$ is positive and some of the female population counted in $x_{j_0}(t)$ have their ages at time t in the overlap of $[j_0-1,j_0)$ and $(\alpha-1,\beta)$. Hence they contribute to making $x_1^{j_0}(t+1)$ positive. Since $x_1^{j_0}(t+1) = F_{j_0} x_{j_0}(t)$, we conclude that $F_{j_0} > 0$. Similarly, we can expect that at some time t $x_{.}$ .. (t) is positive and some of the female population counted in $x_{.+1}(t)$ have their ages in the overlap of $[JQ^{'}JQ^{*1})$ and (cc-1,/3) . They thereby contribute to making x_l (t+1) positive. Since $x_1^{j\theta+1}$ (t+1) = F. ,x. $_n$(t) , F. $_{+1}$ > 0. Thus, two adjacent fertility rates F. and F. $_{+n}$ are positive and the index of L is one.

This reasoning can be modified to apply to versions of the Leslie model which compute the fertility rates more indirectly (i.e., from life tables). In fact, the plausible ideas in the argument are similar to those used by demographers in practical work. One consequence of this is that demographic calculations from the beginning force adjacent fertility rates to be positive, leaving no room for the periodic case. Leslie himself appears to have been partially aware of this difficulty since he expressed reservations about the conceptual significance of the "fertility rates" in Bernardelli's oscillating beetle population.

Still, Leslie granted that "the ... matrix with only a single element in the first row does correspond to the reproductive biology of certain species" and in this spirit we suggest some directions for future research on the periodic case.

Suppose that we are given a population which does exhibit periodic behavior. Without worrying about the interpretation of the matrix entries, we might try to fit the data for this population to a Leslie matrix. In effect, this means replacing

Equations II and III by:

$$\text{II}' \qquad x_1(t+1) = \sum_{i=1}^{n} F_i x_i(t) \qquad t \geq 0.$$

The constants $F_1,\ldots,F_n$ are labelled fertility parameters rather than fertility rates. A priori some of these parameters may even be negative (violating the hypotheses of our theorems). To compute the survival rates and fertility parameters, we solve Equations I and II' using experimental values of $x_1(t),\ldots,x_n(t)$ for $t = 0,1,\ldots,n$. (If some of the fertility parameters are expected to vanish, t may take on fewer values.)

If the resultant matrix is a Leslie matrix with index greater than one and if the model so constructed has predictive value, we will be forced to seek a theoretical justification of the fertility parameters.

One possible explanation goes back to our earlier argument. If $\alpha = \beta =$ an integer, the argument breaks down irretrievably. To exploit this fact we would need a species whose females give birth only at discrete times $j_1,\ldots j_m$ where each j_i is an integral multiple of the unit of time and $\text{g.c.d.}\{j_1,\ldots,j_m\} = k > 1$. Such a quantized process might be more suitable for describing non-organic growth than biological reproduction.

Another possibility is that members of the species pass through some kind of filter. At each integer time t females whose ages are outside the interval $[j_0-1, j_0)$ are temporarily sterilized: they are rendered incapable of maternity for one time unit. At time t 4-1 the sterilization is repeated. This leads to F. as the only non-zero fertility rate and a Leslie matrix with index equal to $j_{\underline{Q}}$.

Both of these possibilities make delicate use of the unit of time. For this reason, among others,, we emphasize the need for empirical research to determine whether the periodic limit has applications. If a Leslie matrix with periodic limit does describe some species, subtle, and possibly radical, refinements will be needed in our understanding of fertility--at least in the relevant species.

APPENDIX

This appendix is devoted to a proof of the theorem stated below, which generalizes Theorem 6 of the text. All notation is the same as that in the text. At the end of the appendix we state a significant corollary of the theorem. We also list examples of Leslie matrices which violate both the premises and the conclusion of the theorem.

Theorem: If either of the following two conditions hold:

i) $\lambda_0 \geq \max\{P_1,\dots,P_{n-1}\}$ and $\text{g.c.d.}(\{j: \lambda_0 > P_j\} \cup \{k\} \cup \{n\}) = 1$;

or ii) $\lambda_0 \leq \min\{P_1,\dots,P_{n-1}\}$ and $\text{g.c.d.}(\{j: \lambda_0 < P_j\} \cup \{k\} \cup \{n\}) = 1$;

then period $(P(t)X)$ = period$(\text{Pop}(P(t)X))$ for any vector X in $\mathbb{R}^n$.

We preface the proof of the theorem with several lemmas of some interest in themselves.

Let $a_1,\dots,a_k$ be real numbers and let $C(a_1,\dots,a_k)$ denote the matrix

$$\begin{bmatrix} a_1 & a_2 & \cdots & a_k \\ a_k & a_1 & \cdots & a_{k-1} \\ \vdots & & \ddots & \vdots \\ a_2 & a_3 & \cdots & a_1 \end{bmatrix}$$

obtained by permuting the elements $a_1,\dots,a_k$ cyclically from one row to the next. Such a matrix is called a circulant matrix and has been extensively studied in classical matrix theory.

If a_{ij}. is the entry in the i^{th} row and j^{th} column of $C(a_1,...,a_k)$, then $a_{\pm j}$ = a^.$_{i+1,\mathrm{mod}\ k}$.

Lemma 1: C (a^ . . .$_3$ a$_{fc}$) is non-singular if and only if the polynomials a_x + a^. . .+$a_k z^{k*"X}$ and $z^k - 1$ have no root in common.

•Shis lemma was first proved by W. Spottiswoode. A proof may be found in [7], pp. 407-408.

Lemma 2; Let g(z) = Bj^ + $B_2 z$ + . . .+$B_k z^{k-1}$ where B_1, ...,B_k > 0. Then if ^ is a root of g(z),

(i) |£| 1 7 = $\max\{B_1/B_2, B_2/B_3,...,B_{k-1}/B_k\}$;

and (ii) |£| < y provided g.c.d.({j: B_j < yB_{j+1})U{k}) = 1.

Lemma 2 is due to Enestrom, Kakeya, and Ostrowski. For a proof see [8], pp. 105-106.

Lemma 3 : C (a-,,...,, a,) is non-singular provided a., + . . .+a_v ⁄ 0, a_k 1 a_{k-1} 1 ... 1 a_x, and g.c.d. ({j: a^^$_n$ < a^ } U {k}) = 1.

Proof; By Lemma 1 it suffices to prove that the polynomial f(z) = ^{a}i + ^{a}9^z +---+CUZk""$^{k-1}$ has no root in common with z^k -1. Choose a > a^^ and let g(z) = (a - a_1) + (a - a_2) z + . . .+(a - a^) z^{k-1}. g(z) satisfies the hypotheses of Lemma 2 with

$$\gamma = \max\left\{ ^{\alpha -a}! \ \ldots, \frac{a"a_{kl}}{\alpha - a_k} \right\} \leq 1$$

and

g.c.d. ({j: a- a_j. < a- a_{j+1}) U (k)) = g.c.d. ({j: $a_{j+1} < a_j$} U (k)) = 1.

Thus any root £ of <?(^{z}) has « \£\ < !• Since g(z) = ot($\frac{z^k-1}{z-1}$)- f(z),

we conclude that f(z) has no root in common with z -1 except possibly z = 1. However,, f(l) = a_1-f...+a_k ^ 0.

The following variations on Lemma 3 will be useful later.

Lemma 4: C(a_1,...,aQ is non-singular provided a_1+...+$a_k \neq 0$ and one of the following conditions holds:

(4a) a_x £ a_2 £ . • .£ a_{fc} and **g.c.d.** ({j: a^ < a_{j+1}} U {k}) = 1;

or

(4b) there is an index $j_0 \leq$ k-1 such that

a_{i+1} <• • -1 a < a- <. . .£ a . and

g.c.d. ({j: $a_j < a_{j+1}$) U {j_Q} U {k}) = 1.

Proof: To prove the (4a) version let $c_j = a_{k+i-j}$ for 1 1 j 1 k. Then det C(a_1^...,a_k) = det C(c_k,...,c_1) = ±; det C(c_1,...jc_k) since the third matrix can be obtained from the second by reversing the columns and permuting the rows appropriately afterwards. Thus we need only confirm that c_1'###J>c_k fulfiH the hypotheses of Lemma 3. Clearly,

$c_{fc} \leq c_{k-1} \leq$ ... £ c^ and c_1+. . -+c_k ^ 0. Moreover, g.c.d. ({j : $c_{j+1} < c_j$ } U {k}) = g-c.d. ({j : $a_{k-j} < a_{k+1-j}$} U {k}) = g.c.d • ({k-j: $a_{k-j} < a_{k-j+1}$} U {k}) = g.c.d. ({j: $a_j < a_{j+1}$} U {k})=l, which completes the proof.

If (4b) holds, let $c_j = a_{j_0+k+1-j,\mathrm{mod}\ k}$ for $1 \le j \le k$. Then $\det C(a_1,\dots,a_k) = \det C(c_{j_0},\dots,c_1,c_k,\dots,c_{j_0+1}) = \pm \det C(c_1,\dots,c_k)$, and again we confirm that $c_1,\dots,c_k$ fulfill the hypotheses of Lemma 3. Two of the hypotheses are obviously fulfilled. For the third, note that $c_{j_0+1} = a_k < a_1 = c_{j_0}$. Thus

$$\begin{aligned} &\text{g.c.d.}(\{j: c_{j+1} < c_j\} \cup \{k\}) \\ &= \text{g.c.d.}(\{j: a_{j_0+k-j,\mathrm{mod}\ k} < a_{j_0+k-j+1,\mathrm{mod}\ k}\} \cup \{j_0\} \cup \{k\}) \\ &= \text{g.c.d.}(\{j: a_j < a_{j+1}\} \cup \{j_0\} \cup \{k\}) = 1, \end{aligned}$$

and we are done.

<u>Proof of the theorem</u>: Let $p = \mathrm{period}(\mathrm{Pop}(P(t)X))$. Then p is a divisor of $\mathrm{period}(P(t)X)$. Hence we need only verify that $P(t)X = P(t+p)X$ for all t or, equivalently, that $\gamma_X(t) = \gamma_X(t+p)$ for all t.

$\mathrm{Pop}: \mathbb{R}^n \to \mathbb{R}$ is a linear function. So $\mathrm{Pop}(P(t)X) = \mathrm{Pop}(\sum_{j=1}^{k} \gamma_X(j-t)U_j) = \sum_{j=1}^{k} \gamma_X(j-t)\,\mathrm{Pop}\,U_j$. Expressing this relation in matrix form for different values of t and using the fact that all periods are divisors of $k = \mathrm{period}\ (P(t))$, we obtain:

$$C(\mathrm{Pop}\,U_1,\dots,\mathrm{Pop}\,U_k)\begin{bmatrix}\gamma_X(1)\\ \vdots\\ \gamma_X(k)\end{bmatrix} = \begin{bmatrix}\mathrm{Pop}(P(k)X)\\ \vdots\\ \mathrm{Pop}(P(1)X)\end{bmatrix} = \begin{bmatrix}\mathrm{Pop}(P(k-p)X)\\ \vdots\\ \mathrm{Pop}(P(1-p)X)\end{bmatrix}$$

$$= C(\mathrm{Pop}\,U_1,\dots,\mathrm{Pop}\,U_k)\begin{bmatrix}\gamma_X(1+p)\\ \vdots\\ \gamma_X(k+p)\end{bmatrix}.$$

Thus $\gamma_X(t) = \gamma_X(t+p)$ for all t and the theorem is proved provided we can establish that $C(\text{Pop}\,U_1,\ldots,\text{Pop}\,U_k)$ is non-singular.

Suppose hypothesis (i) of the theorem is fulfilled. Without loss of generality we may suppose that $\lambda_0 = 1$. (This is equivalent to replacing each survival rate P_i by P_i/λ_0.) Then $1 \geq \max\{P_1,\ldots,P_{n-1}\}$ and for $1 \leq j \leq k-1$ $c_{j+1} = c_j P_j \leq c_j$. Hence, $\text{Pop}\,U_j = \sum_{i\equiv j,\text{mod } k} c_i \geq \sum_{i\equiv j,\text{mod } k} c_{i+1} = \sum_{i\equiv j+1,\text{mod } k} c_i = \text{Pop}\,U_{j+1}$. In addition if $n = j_0 + \alpha k$ for $1 \leq j_0 \leq k-1$, then

$$\begin{aligned}\text{Pop}\,U_{j_0} &= c_{j_0} + \ldots + c_{j_0+(\alpha-1)k} + c_n > c_{j_0+1} + \ldots + c_{j_0+1+(\alpha-1)k} \\ &= \text{Pop}\,U_{j_0+1}\,.\end{aligned}$$

Thus we have

$$\begin{aligned}&\text{g.c.d.}(\{j\colon \text{Pop}\,U_{j+1} < \text{Pop}\,U_j\} \cup \{k\}) \\ &= \text{g.c.d.}(\{j\colon \text{ there is an } i \equiv j,\text{mod } k \text{ with } c_{i+1} < c_i\} \\ &\qquad \cup \{j_0\} \cup \{k\}) = \text{g.c.d.}(\{i\colon c_{i+1} < c_i\} \cup \{n\} \cup \{k\}) \\ &= \text{g.c.d.}(\{j\colon p_j < 1\} \cup \{k\} \cup \{n\}) = 1.\end{aligned}$$

The hypotheses of Lemma 3 are fulfilled, and $C(\text{Pop}\,U_1,\ldots\ \text{Pop}\,U_k)$ is therefore non-singular.

Suppose hypothesis (ii) of the theorem holds. Again without loss of generality we take λ_0 to be 1. Choose j_0 such that $n = j_0 + \alpha k$ where $1 \leq j_0 \leq k$. Since $1 \leq \min\{P_1,\ldots,P_{n-1}\}$, we have $c_{j+1} = c_1 > c_j$. If $j_0 = k$, it follows that $\text{Pop}\,U_1 \le \text{Pop}\,U_2 \le \dots \le \text{Pop}\,U_k$ and an argument analogous to that of the last paragraph shows that the hypothesis (4a) of Lemma 4 is fulfilled. If $j_0 < k$,

$$\text{Pop}\,U_{j_0+1} \le \dots \le \text{Pop}\,U_k < \text{Pop}\,U_1 \le \dots \le \text{Pop}\,U_{j_0}$$

since the number of terms drops by one as we move from $\text{Pop}\,U_j$ to $\text{Pop}\,U_{j+1}$ and since

$$\text{Pop}\,U_k = c_k + \dots + c_{\alpha k} < c_1 + c_{1+k} + \dots c_{1+\alpha k} = \text{Pop}\,U_1 .$$

Furthermore, g.c.d.$(\{j: \text{Pop}\,U_j < \text{Pop}\,U_{j+1}\} \cup \{j_0\} \cup \{k\})$ = g.c.d. $(\{j:$ there is an $i \equiv j \bmod k$ with $c_{i+1} > c_i\} \cup \{n\} \cup \{k\})$ = g.c.d. $(\{i: c_{i+1} > c_i\} \cup \{k\} \cup \{n\})$ = g.c.d. $(\{j : 1 < P_j\} \cup \{k\} \cup \{n\}) = 1$.

Hence, hypothesis (4b) of Lemma 4 is fulfilled, and our proof is complete.

Corollary: Let hypothesis (i) or (ii) of the theorem be fulfilled. If the Leslie matrix of a population is known and $\text{Pop}(P(t)X)$ is known for all t, then $P(t)X$ can be determined.

Proof; If the Leslie matrix is known, $C(\text{Pop}\,U_1, \dots, \text{Pop}\,U_k)$ and its inverse can be explicitly computed. Then the matrix equation in the proof of the theorem can be solved for ${}_k\gamma_x(t)$ in terms of $\text{Pop}(P(1)X), \dots, \text{Pop}(P(k)X)$, and $P(t)X = \sum_{j=1} \gamma_x(j-t)U_j$.

<u>Examples</u>: In each example $\lambda_0 = 1$.

1. Let $L = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$. This is the only possible 2 by 2 counterexample to the theorem. $P(t) = L^t$ in this case and period $(P(t)X) = 2$ in general while period $(\mathrm{Pop}(P(t)X)) = 1$ always. Note that $\lambda_0 = P_1$ and g.c.d.$(\{k\} \cup \{n\}) =$ g.c.d.$\{2,2\} = 2$.

2. Let $L = \begin{bmatrix} 0 & \alpha & 0 \\ 1/\alpha & 0 & 0 \\ 0 & 1-\alpha & 0 \end{bmatrix}$ where $1 > \alpha > 0$. Then $P(t) = L^t$, period $(P(t)X) = 2$ in general, but period $(\mathrm{Pop}(P(t)X)) = 1$ always. Here $P_1 > \lambda_0 > P_2$.

3. Let $L = \begin{bmatrix} 0 & u & 0 & \frac{1-u}{c} \\ 1 & 0 & 0 & 0 \\ 0 & c & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix}$ with $1 > u > 0$ and $c > 0$. Period $(P(t)X) = 2$ in general but period $(\mathrm{Pop}(P(t)X)) = 1$ always. If $c \leq 1$, $\lambda_0 = \max\{P_1, P_2, P_3\}$ and g.c.d.$(\{j: P_j < \lambda_0\} \cup \{k\} \cup \{n\}) = 2$. If $c \geq 1$, $\lambda_0 = \min\{P_1, P_2, P_3\}$ and g.c.d.$(\{j: P_j > \lambda_0\} \cup \{k\} \cup \{n\}) = 2$.

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