A Method for Computing the Elements of the Leslie Matrix

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SUMMARY

We give formulas for the computation of the age-class-specific fecundities F_n and survival probabilities P_n of the Leslie matrix. These formulas are intended primarily for use with populations such as insects in which survivorship depends on life stage but is independent of age within a given stage. The Leslie matrix elements are computed by subdividing each age class into a collection of subclasses and then allowing the number of subclasses to tend to infinity. The matrix elements computed in this way provide a relatively accurate representation of the dynamics of the population even when only a few age classes are used to subdivide the population.

1. Introduction

The Leslie matrix model (Lewis, 1942; Leslie, 1945) is frequently used to describe the dynamics of an age-structured population. In this model the population is divided into age classes of equal duration. In the case of a population with two sexes, ordinarily only the females are considered. Let $u_n(t)$ denote the number of females in age class n at time t—that is, of age $n\Delta$ to $(n + 1)\Delta$, where Δ is the age class duration. Assume that any individuals surviving past age class N play a negligible role in the reproduction of the population. The conditional survivorship P_n gives the fraction of the population of age class n that survive to reach age class $n + 1$. Therefore,

$$u_{n+1}(t + \Delta) = P_n u_n(t), \quad n = 0, \ldots, N - 1. \tag{1.1}$$

All females born between times t and $t + \Delta$ enter age class zero. The fecundity F_n of the nth age class is defined to be the number of females born (or female eggs laid) per female in age class n during a time interval of length Δ that survive to the end of the interval. Therefore,

$$u_0(t + \Delta) = \sum_{n=0}^{N} F_n u_n(t). \tag{1.2}$$

If the vector $\mathbf{u}(t)$ is defined by $\mathbf{u}(t) = [u_0(t) \ldots u_N(t)]^T$ then equations (1.1) and (1.2) become

$$\mathbf{u}(t + \Delta) = \mathbf{L}\mathbf{u}(t), \tag{1.3}$$

where $\mathbf{L}$ is the *Leslie matrix*. The first row of $\mathbf{L}$ contains the F_n and the first lower subdiagonal contains the P_n. Throughout this paper we shall assume that the F_n and P_n are fixed for any given n.

Although other formalisms have been suggested (e.g., Blythe, Nisbet, and Gurney, 1984), the Leslie matrix model is a particularly convenient, simple device for the simulation of

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Key words: Age-structured population; Leslie matrix.

populations whose life history parameters depend only on age. The properties of Leslie matrix models have been thoroughly studied and a summary may be found, for example, in Pollard (1973). The elements F_n and P_n of the Leslie matrix are generally computed in terms of functions commonly denoted l_x and m_x. In this paper we shall write these functions $l(x)$ and $m(x)$. The function $m(x)$, called the age-specific fecundity, describes the female birthrate per female of age x to $x + dx$. If the population breeds continuously then $m(x)$ is a continuous function, whereas if the population breeds only at discrete times then $m(x)$ is nonzero only at discrete values of t (at which it is proportional to a delta function). The function $l(x)$, called the age-specific survivorship, represents the fraction of a cohort surviving to age x. It will also be convenient to use the intrinsic death rate $\mu(x)$, defined by

$$\mu(x) = -\frac{d}{dx} \ln l(x). \tag{1.4}$$

This function represents the mortality rate of females between the ages of x and $x + dx$.

In his original paper, Leslie (1945) gives formulas for computing the F_n and P_n in terms of the life history parameters. The most commonly used formulas, however, are those found, for example, in Emlen (1984):

$$P_n = \frac{l[(n + 1)\Delta]}{l(n\Delta)},$$
$$F_n = P_n m[(n + 1)\Delta]. \tag{1.5}$$

These formulas are based on the assumption that the population breeds only at times $t = n\Delta$, where n is integer-valued.

An issue that may be of importance under some circumstances is the use of a Leslie matrix with relatively few elements (i.e., large Δ) to model a continuously breeding population. This is particularly important in the construction of large-scale spatiotemporal models of age-structured populations since in these models it is desirable to keep the number of age classes to a minimum. The present paper describes formulas that may be used to compute the F_n and P_n of the Leslie matrix and that have the property that the behavior of the solution of the resulting Leslie matrix model is not strongly dependent on the time increment Δ.

The formulas given in the present paper are intended for use primarily in the simulation of insect populations. It is often the case in insect populations that the intrinsic death rate $\mu(x)$ depends on the life stage, but is independent of age within a particular life stage. We shall assume that this is the case in the population under consideration. It would be a straightforward matter to generalize the formulas we present to the case in which $\mu(x)$ is some arbitrary function of x. We shall not, however, pursue this generalization. In the next section we give a derivation of the formulas for F_n and P_n. In Section 3 we give a numerical example of the application of the formulas.

2. Derivation of the Formulas

Assume that the life history data of the population is specified in terms of the age-specific birth rate $m(x)$ and the intrinsic death rate $\mu(x)$. Assume further that $m(x)$ is continuous and that $\mu(x)$ is piecewise constant. Subdivide the population into N age classes, each of duration Δ, such that $\mu(x)$ is independent of x within a given age class. Let $\mu(x) = \mu_n$ for $n\Delta \leq x < (n + 1)\Delta$ and define

$$\phi_n = e^{-\mu_n\Delta}. \tag{2.1}$$

ϕ_n denotes the conditional survivorship of age class n—that is, of a cohort of females entering age class n, a fraction $\phi_n > 0$ survive to enter age class $n + 1$. If $m(x)$ were not continuous but rather all individuals in the age class were born at time $n\Delta$, then P_n would

equal ϕ_n. The formulas for the F_n and P_n are given in terms of the function $m(x)$ and the ϕ_n.

The method of deriving the F_n and P_n is to subdivide an age class n into K subclasses of increment $\delta = \Delta/K$ and study the dynamics of each of the subclasses. One then lets K tend to infinity and δ tend to zero. We begin by establishing the age structure within an age class. Assume that the population of age class n is $u_n(t)$, and that within an age class at any fixed time the population in subclass k is a geometrically decreasing function of k so that if at time t the population of subclass 0 is y then there is a $q_n < 1$ such that the population of subclass k is yq_n^k. By summing over the age subclasses and using the formula for geometric sums, we have

$$y = \left(\frac{1 - q_n}{1 - q_n^K}\right)u_n(t). \tag{2.2}$$

We now derive the formula for P_n. Between time t and $t + \delta$ the cohort in subclass k moves to subclass $k + 1$ and its population declines from $q_n^k yu_n(t)$ to $p_n q_n^k yu_n(t)$, where $p_n = \phi_n^{1/K}$. The cohort in subclass $K - 1$ moves to subclass 0 of age class $n + 1$. After K time steps of increment δ the time value has changed from t to $t + \Delta$, and the cohort that was originally in subclass k of age class n with a population of $q_n^k yu_n(t)$ is now in subclass k of age class $n + 1$ with a population of $p_n^{K-k}p_{n+1}^k q_n^k yu_n(t)$. Summing over all subclasses, substituting from equation (2.2) for y, rearranging terms, and using the identity for geometric sums yields

$$u_{n+1}(t + \Delta) = p_n^K\left(\frac{1 - q_n}{1 - q_n^K}\right)\left(\frac{1 - q_{n+1}^K}{1 - q_{n+1}}\right)u_n(t). \tag{2.3}$$

As yet we have made no assumptions about the value of q_n. A reasonable assumption, and the one that we shall use, is that within an age class the population is at a stable age distribution. To achieve this, let λ be the solution of the Euler equation

$$1 = \int_0^\infty e^{-\lambda x}m(x)l(x)\ dx. \tag{2.4}$$

Let $\alpha = \lambda^\Delta$ and let $q_n = (\phi_n/\alpha)^{1/K}$. Then within a given age class the populations of the subclasses will be approximately in a stable age distribution. Substituting $\phi_n = p_n^K$, letting K tend to infinity, and using l'Hôpital's rule leads to

$$P_n = \phi_n\frac{\ln \phi_n}{\ln \phi_{n+1}}\left(\frac{\alpha - \phi_{n+1}}{\alpha - \phi_n}\right). \tag{2.5}$$

We now turn to the derivation of the F_n. This derivation follows the same outline as that of the P_n. We subdivide the age class n into K subclasses and follow the births of daughters to members of these subclasses as time evolves from t to $t + \Delta$. In the interval of time between t and $t + \delta$ the $q_n^k yu_n(t)$ females in subclass k give birth to a total of $q_n^k ym(n\Delta + k\delta)\delta u_n(t)$ daughters. At time $t + \delta$ the populations in the subclasses (including the newly born females in subclass 0 of age class 0) each advance one subclass and undergo mortality. In the interval $t + j\delta$ to $t + (j + 1)\delta$ the total number of females born to the population by females who were in age class n at time t is

$$b_j = \sum_{k=0}^{K-j-1} yq_n^k p_n^j m[n\Delta + (j + k)\delta]\ \delta u_n(t)$$

$$+ \sum_{k=K-j}^{K-1} yq_n^k p_n^{K-k} p_{n+1}^{j+k-K}m[n\Delta + (j + k)\delta]\ \delta u_n(t). \tag{2.6}$$

The fecundity F_n represents the total number of females born to a member of age class n during the interval t to $t + \Delta$ that survive to time $t + \Delta$. An approximate formula for F_n is obtained by summing the b_j from $j = 0$ to $K - 1$, taking into account mortality in age class 0, and dividing out the common factor $u_n(t)$. Performing this operation yields

$$F_n \approx \delta \left(\frac{1 - q_n}{1 - q_n^K} \right) \sum_{j=0}^{K-1} p_0^{K-j-1} \left\{ \sum_{k=0}^{K-j-1} q_n^k p_n^j m[n\Delta + (j + k)\delta] \right.$$

$$\left. + \sum_{k=N-j}^{K-1} q_n^k p_n^{K-k} p_{n+1}^{i+j-K} m[n\Delta + (j + k)\delta] \right\}. \tag{2.7}$$

Letting K tend to infinity leads to a closed-form expression for F_n that may be written

$$F_n = - \frac{\ln \nu_n}{\Delta(1 - \nu_n)} \int_0^\Delta \phi_0^{1-x/\Delta} \left[\int_0^{\Delta-x} \nu_n^{\xi/\Delta} \phi_n^{x/\Delta} m(n\Delta + x + \xi) \, d\xi \right.$$

$$\left. + \int_{\Delta-x}^\Delta \nu_n^{\xi/\Delta} \phi_n^{1-\xi/\Delta} m(n\Delta + x + \xi) \, d\xi \right], \tag{2.8}$$

where $\nu_n = \phi_n/\alpha$. In principle, for functions $m(x)$ of a simple form such as $m(x) = axe^{cx}$, the integral in equation (2.8) may be evaluated explicitly. In practice this expression is rather lengthy and it is more convenient to evaluate the integral numerically. Indeed, computational experience indicates that good results can be obtained using the sum of equation (2.7) with a reasonably large value of K (say, $K = 10$).

Equations (2.3) and (2.7) or (2.8) provide the desired formulas for P_n and F_n. While the formula for F_n is rather complicated, it needs to be evaluated only once if the life-table data are independent of time. In the next section we give an example of the application of these formulas in which we compare the results obtained with them to those obtained using two alternative approximations.

3. A Numerical Example

In this section we apply the method described in the previous section, together with two alternative methods, to life tables for an infestation of Mediterranean fruit fly (*Ceratitis capitata* Wied.), or medfly, in California. A detailed description of the arguments involved in developing these life tables is given by Plant (1986) and will not be repeated here.

The time unit is 1 day, with the maximum age taken to be 80 days. The birthrate function $m(x)$ is given by

$$m(x) = \begin{cases} 0, & x \leqslant 32 \\ 3.05(x - 32)e^{-.12(x-32)}, & x > 32 \end{cases}. \tag{3.1}$$

The intrinsic death rate is

$$\mu(x) = \begin{cases} .12, & 0 \leqslant x < 10 \\ .05, & 10 \leqslant x < 20 \\ .02, & 20 \leqslant x < 80 \end{cases}. \tag{3.2}$$

Leslie matrix elements were generated using three methods. The formulas used for these methods are as follows:

Method 1 (e.g., Emlen, 1984):

$$P_n = \phi_j^{\Delta/10}, \tag{3.3}$$

where j is the appropriate life stage for age class n.

$$F_n = P_n m[(n + 1)\Delta]. \tag{3.4}$$

Method 2 (similar to the method of Leslie, 1945). P_n is computed as in Method 1.

$$F_n = P_0^{3/4} \int_{(n+1/2)\Delta}^{(n+1)\Delta} m(x)\,dx + P_n P_0^{1/4} \int_{(n+1)\Delta}^{(n+3/2)\Delta} m(x)\,dx. \tag{3.5}$$

Method 3 P_n is computed according to equation (2.3) and F_n is computed according to equation (2.9).

These methods were tested using age class durations Δ of 1, 2, 5, and 10 days. The first test was to compute the dominant eigenvalues λ_Δ and compare them with the solution λ of the Euler equation (2.4). This value is 1.0734. Since this represents the finite rate of growth per day, the appropriate comparison is between this value and that of $\lambda_\Delta^{1/\Delta}$. Table 1 shows the results of this test. The per-day growth rate of each of the methods converges to λ as expected. For $\Delta = 10$, the per-day growth rates of the three methods differ from λ by .9%, 1.1%, and .07%, respectively. Therefore, although Method 3 is an order of magnitude more accurate than the other two methods, all three of the methods are fairly accurate in their approximation of λ. This observation has also been made by Pollard (1973).

Table 2 shows a comparison of the stable age distributions of the three methods. To achieve a proper comparison the table shows the lumped age distributions in which the number of individuals in the stable age distribution between the ages of 0 to 10 days, 10 to 20 days, and so on, is given. Only data for $\Delta = 1$ and $\Delta = 10$ are shown; the values for $\Delta = 2$ and $\Delta = 5$ are intermediate, as expected. Once again Method 3 is most accurate, but this time Method 2 is second most accurate.

The third test deals only with survivorship. At time $t = 0$ individuals are distributed uniformly across all age classes. Equations (1.1), the equations describing survivorship, are then iterated for 10 days (i.e., the population goes through 10 days of survivorship with no births). After 10 days, the fraction of survivors from the original age groups 0–10 days, 10–20 days, and so forth, are tabulated. This test gives a representation of the accuracy of

Table 1
Values of growth rate per day $\lambda_\Delta^{1/\Delta}$ for each of the three methods tested, for age class duration
$\Delta = 1, 2, 5,$ *and* 10 *days*

	Δ			
Method	1	2	5	10
1	1.0733	1.0746	1.0787	1.0832
2	1.0722	1.0710	1.0676	1.0614
3	1.0733	1.0732	1.0728	1.0727

Table 2
Proportion of population in each age group at stable age distributions for age class durations
$\Delta = 1$ *and* 10 *days*

	Method 1		Method 2		Method 3	
Age	$\Delta = 1$	$\Delta = 10$	$\Delta = 1$	$\Delta = 10$	$\Delta = 1$	$\Delta = 10$
0–10	.778	.839	.775	.791	.770	.769
10–20	.144	.113	.145	.131	.148	.148
20–30	.049	.030	.048	.044	.049	.050
30–40	.019	.011	.019	.018	.019	.020
40–50	.007	.009	.008	.008	.007	.008
50–60	.003	.002	.003	.004	.003	.003
60–70	.001	.001	.002	.002	.002	.002
70–80	.001	.000	.001	.001	.001	.001

the approximation for P_n. Table 3 shows the results of this test. As in Table 2, only the results for $\Delta = 1$ and $\Delta = 10$ are shown. Survivorships are computed using the same formula in Methods 1 and 2. Survivorship in the adult age classes is not changed in either method by the change in Δ since it is independent of age in these age classes. In the immature life stages, however, survivorship is strongly affected by the value of Δ.

The fourth test is concerned with the transient dynamics of the model. The model was iterated for 100 simulated days. The initial condition was a uniform distribution of individuals in the egg/larval life stage and no individuals in any other life stage. Let f_{el} denote the fraction of the total population in the egg/larval life stage. Table 4 shows the difference $f_{el,1} - f_{el,10}$, where the second subscript denotes the value of Δ, for values of t ranging from $t = 0$ to $t = 100$. Method 1 does very poorly. Both Methods 2 and 3 perform fairly well although Method 2 appears slightly better.

Table 3
Proportion of the population of each age group surviving 10 *days for each method,*
$\Delta = 1$ *and* 10 *days*

Age	Methods 1 and 2		Method 3	
	$\Delta = 1$	$\Delta = 10$	$\Delta = 1$	$\Delta = 10$
0–10	.418	.300	.432	.389
10–20	.685	.600	.695	.676
20–70	.800	.800	.800	.800

Table 4
Differences between solutions using $\Delta = 1$ *and* $\Delta = 10$ *in fraction of the population in egg/larval stage at successive values of* t, $0 \leq t \leq 100$ *days*

t	Model 1	Model 2	Model 3
0	.00	.00	.00
10	.00	.00	.00
20	.00	.00	.00
30	−.02	−.05	−.06
40	−.01	.08	.05
50	.00	.10	.07
60	.49	.08	.13
70	−.09	−.07	−.07
80	−.06	.05	.01
90	.12	.04	.06
100	.28	.05	.06

4. Conclusion

The method for computing the elements of the Leslie matrix presented in this paper is based on the assumption that within each age class the population declines geometrically. This permits a continuous time intra-age class formulation while retaining the discrete time inter-age class formulation. This method gives an accurate representation of the overall growth rate, stable age distribution, and relative dynamics of the life stages.

RÉSUMÉ

On donne des formules pour calculer les fécondités par classe d'âge F_n, et les probabilités de survie P_n de la matrice de Leslie. Ces formules sont principalement destinées à être utilisées pour des populations comme celles d'insectes, où la mortalité dépend de la phase, mais ne dépend pas de l'âge dans une phase. Les éléments de la matrice de Leslie sont calculés en subdivisant chaque classe d'âge en sous-classes, et en faisant tendre le nombre de sous-classes vers l'infini. Les éléments de la matrice, calculés de cette façon, fournissent une représentation relativement précise de la dynamique de la population, même quand peu de classes sont utilisées pour subdiviser la population.

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