Simple density-dependent matrix model for population projection

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Abstract

A matrix model based on a discrete time form of the logistic equation and the Leslie matrix model was developed for density-dependent population growth; the model is simpler and more easily applied than the model developed by Liu and Cohen in 1987 using a different discrete time form of the logistic equation. The new model requires no additional parameters, matrices, or mathematical functions, and it links life tables, the exponential growth equation, the logistic growth equation, and Leslie's matrix. The new model possesses the same qualitative dynamical behavior as both the model developed by Liu and Cohen and the discrete time logistic equation; it exhibits stable points, cycles, and chaos. It easily can be modified to include features developed for the logistic equation such as time lags. The model was applied to describe the growth of a white-tailed deer population introduced into a fenced reserve.

1. Introduction

Leslie (1945, 1948) and Lewis (1942) developed a matrix model, to describe change in population age structure over time, that is analogous to the exponential equation. Leslie's (1945) model is

$$N_{t+1} = MN_t, \qquad (1)$$

where N_t is the vector of age structure at time t and M is the population projection matrix

$$M = \begin{vmatrix} F_0 & F_1 & F_2 & \dots & F_v \\ P_0 & 0 & 0 & & \\ 0 & P_1 & 0 & & \\ \multicolumn{5}{c}{\dotfill} \\ 0 & & & P_{v-1} & 0 \end{vmatrix}, \qquad (2)$$

where F_i is the fecundity of age group i (the number of young produced per female of age i during time period t that live to the next time

period), and P_i is survival from age $i - 1$ at time t to age i at time $t + 1$ with continuous mortality. The population projection matrix is simpler if reproduction occurs during one short season, as it does for most wild animals, and if mortality is modeled as a discrete time process (e.g., Starfield and Bleloch, 1986). The number of young at time $t + 1$ produced by individuals of age $x - 1$ at time t is $N(x - 1,t)s_{x-1}m_x$, and thus the population projection matrix can be written in terms of life table components as

$$M = \begin{vmatrix} m_1 s_0 & m_2 s_1 & M_3 s_2 & \dots & m_k s_{k-1} & 0 \\ s_0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & 0 & \dots & 0 & 0 \\ \multicolumn{6}{c}{\dotfill} \\ 0 & 0 & 0 & \dots & s_{k-1} & 0 \end{vmatrix}, \qquad (3)$$

where m_i is the number of young produced by a female of age i, s_i is survival from age $i - 1$ to i, and $N(x - 1, t)$ is the number of individuals of age $x - 1$ at time t. The Leslie matrix model has been of limited use in ecology because it models exponential population growth.

Several density-dependent matrix models have been developed. Leslie (1959) modified his matrix model to describe population growth in a limited environment by dividing each element in column i with the term

$$q_{it} = 1 + aN_{t-i-1} + bN_t, \qquad (4)$$

where N_{t-i-1} is population size at time $t - i - 1$ and N_t is population size at time t, to give the matrix model

$$N_{t+1} = MQ_t^{-1}N_t, \qquad (5)$$

where

$$Q_t = \begin{vmatrix} q_{0t} & 0 & 0 & \dots & 0 \\ 0 & q_{1t} & 0 & & \\ 0 & 0 & q_{2t} & & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & & & q_{vt} \end{vmatrix}. \qquad (6)$$

Abundance approaches a carrying capacity $K = (L - 1)/(a + b)$, where L is the dominant latent root of M, but the model contains new parameters and is not based on the logistic equation.

Liu and Cohen (1987) applied a discrete time form of the logistic equation to develop a density-dependent matrix model. They began with a discrete time solution of the logistic equation (May, 1974)

$$N_{t+1} = N_t L \exp[-rN_t/K], \qquad (7)$$

where N is abundance, r is the intrinsic rate of natural increase, K is the environmental carrying capacity, and $L = e^r$. Liu and Cohen (1987) then proposed the following matrix model as a natural extension of the above discrete time solution:

$$N_{t+1} = M[N(t)]N_t, \qquad (8)$$

where N_t is the age structure vector at time t and the projection matrix $M[N(t)]$ is

$M[N(t)]$

$$= \begin{vmatrix} f_1 F_1[N(t)] & f_2 F_2[N(t)] & \dots & f_v F_v[N(t)] \\ p_1 E_1[N(t)] & 0 & & \\ 0 & p_2 E_2[N(t)] & & \\ \cdots & \cdots & \cdots & \cdots \\ 0 & & p_{v-1}E_{v-1}[N(t)] & 0 \end{vmatrix}, \qquad (9)$$

where:

$$F_i[N(t)] = \exp\left[-\sum_{j=1}^{v} a_{ij}N_j(t)\right], \qquad (10)$$

$$E_i[N(t)] = \exp\left[-\sum_{j=1}^{v} b_{ij}N_j(t)\right], \qquad (11)$$

and f_i is a density-independent fertility coefficient, p_i is a density-independent survivorship coefficient, $F_i[N(t)]$ and $E_i[N(t)]$ are density-dependent functions for fertility and survivorship, a_{ij} measures the sensitivity of fertility of an individual of age i to the density of individuals of age j, and b_{ij} measures the sensitivity of survivorship of individuals of age i to the density of individuals of age j.

The Liu and Cohen (1987) matrix model was based on the logistic equation, but it has many parameters in addition to those found in a combined life and fertility table or Leslie's matrix, its relation to Leslie's matrix is unclear, and in an application of the model to a laboratory population of *Tribolium* many simplifying assumptions were necessary (Desharnais and Liu, 1987).

In this study a simple density-dependent matrix model based on a different discrete time form of the logistic equation is developed and applied; it requires no additional parameters, matrices, or mathematical functions, and it is easy to apply to either laboratory or field populations when a combined life and fecundity table and estimate of the carrying capacity are available. The simple model provides a link between life table parameters, the logistic growth equation, and Leslie's original projection matrix. To illustrate the ease with which the new model can be applied to field populations, it was applied to model growth of a white-tailed deer population.

2. Model development

The Leslie matrix model gives the new age structure directly from the old age structure, but the Leslie matrix equation can be written as

$$N_t = N_{t-1} + (M - I)N_{t-1}, \qquad (12)$$

where N_t is the vector of age structure at time t, M is the Leslie matrix, I is the identity matrix, and $M - I$ is a transition matrix. The above form of Leslie's matrix equation is analogous to the discrete time form of the exponential equation, i.e.,

$$N_t = N_{t-1} + rN_{t-1}, \qquad (13)$$

and the matrix $M - I$ is analogous to the intrinsic rate of increase r.

A second, and more frequently used discrete time form of the logistic equation is (May, 1974)

$$N_{t+1} = N_t + [(K - N_t)/K]rN_t, \qquad (14)$$

and a matrix model analogous to this equation is

$$N_{t+1} = N_t + D(N)(M - I)N_t, \qquad (15)$$

where $D(N)$ is a density-dependent function. In the system of equations described by the above matrix model the number of individuals of age x at time t for ages greater than zero equals the number of age x at time $t - 1$ plus a transition. The transition is the density-dependent function multiplied by the difference between the number of individuals of age x at time $t - 1$ and the projected number of individuals of age x at time t.

The simplest form of the density-dependent function is $D(N) = (K - N)/K$, used in the logistic equation, where K is the environmental carrying capacity and N is the sum of the elements in the age structure vector at time $t - 1$. This function is only useful for simulation of population growth when the initial population size is far less than the carrying capacity, for if the initial abundance is small compared to the carrying capacity, the age structure at the carrying capacity is near the stable age distribution given by the Leslie matrix. If the initial population size is relatively large, a more general density-dependent function is necessary, with a den-

sity-dependent term for each age; it could be a diagonal matrix with terms of the form $[c_x K - N(x,t)]/c_x K$, where c_x is the proportion of age x in the stable age distribution, which can be determined from either a life table or the Leslie matrix. The density-dependent matrix model derived here contains no new functions, no new matrices, and no new parameters; the model can be applied using an estimate of the carrying capacity and information available in a combined life and fecundity table.

The same density-dependent function was applied to both birth and death, as it is in the logistic equation, but the Leslie matrix and thus the transition matrix $M - I$ can be separated into a matrix for births and a matrix for deaths (e.g., Usher, 1969; Goodman, 1969; Jensen, 1974) and separate density-dependent functions could be applied to each process. Although more realistic, this would increase the difficulty of parameter estimation.

3. Application and discussion

The dynamics of the white-tailed deer (*Odocoileus virginianus borealis* Miller) population on the George Reserve in southeastern Michigan provides a classic example of the growth potential of white-tailed deer populations in favorable habitat (McCullough, 1979). The George Reserve is a 464-ha area given to the University of Michigan in 1930 with the stipulation that the property be allowed to follow its natural course without interference by humans. Deer had been extirpated from the area, and there is some question as to whether or not deer were present in any of southern Michigan at that time (McCullough, 1979). A 2.9-m-high fence around the reserve was completed in 1927, and the following year 2 male and 4 female deer from Grand Island on Lake Superior were released on the property. In 1933, only 5 years later, the first annual deer drive was held and 160 deer were counted, which far exceeded the maximum thought possible (McCullough, 1979). Later studies indicated that the carrying capacity of the reserve was about 220 deer (McCullough, 1979), and these studies also

Table 1
Life table and fecundity schedule for white-tailed deer in the George Reserve (adapted from McCullough, 1979)

x	N_x	l_x	$(1-q_x)$	m_x
0	75	1.000	0.713	0
1	57	0.713	0.645	2
2	35	0.460	0.648	2
3	22	0.298	0.560	2
4	11	0.167	0.563	2
5	4	0.094	0.777	2
6	4	0.073	0.753	2
7	1	0.055	0.436	2

provided data for construction of a current life table and a fecundity table for deer at low population densities (Table 1). Estimation of the transition matrix $M - I$ parameters using the life table and fecundity table statistics gives

$M - I$

$$
= \begin{vmatrix}
0.426 & 1.290 & 1.296 & 1.120 & 1.126 & 1.554 & 0 \\
0.713 & -1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.645 & -1 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.648 & -1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.560 & -1 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.563 & -1 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.777 & -1
\end{vmatrix}.
$$

(16)

The transition matrix was applied to calculate the age structure of the female deer population beginning with a population of 4 aged 1 female deer at time zero. The deer population had considerable capacity to increase and attained the carrying capacity after only 6 years (Fig. 1). The number of female deer calculated for 1933 is 81,
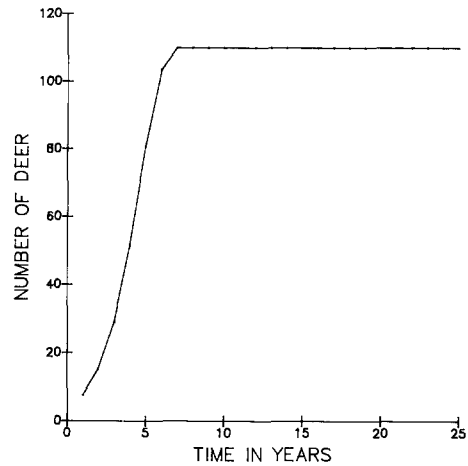

Fig. 1. White-tailed deer population density of the George Reserve calculated with the density-dependent matrix model.

which would give 162 deer of both sexes and this was near the number observed in the first deer drive in 1933. The age structure of the population quickly approached the stable age distribution (Table 2).

Modification of the simple density-dependent matrix is as simple as modification of the logistic equation itself; for example, a time lag can be introduced into the density-dependent matrix model just as it was introduced into the logistic equation by Hutchinson (1948); the result is

$$N_{t+1} = N_t + D(N_{t-g})(M - I)N_t,$$ (17)

Table 2
Age structure of simulated white-tailed deer population (females) on George Reserve with and without a one-year time lag

Age	Year												
	0	1	2	3	4	5	6	7	8	9	10	11	12
With no time lag													
0	0	5	10	19	34	54	69	73	73	73	73	73	73
1	4	0	3	7	12	19	24	25	25	25	25	25	25
2	0	2	0	2	4	6	7	8	8	8	8	8	8
3	0	0	1	0	1	2	2	2	2	2	2	2	2
4	0	0	0	1	0	0	0	1	1	1	1	1	1
With one-year time lag													
0	0	5	10	20	40	70	103	109	62	29	34	56	87
1	4	0	3	7	13	24	36	38	21	10	12	19	30
2	0	2	0	2	4	7	11	12	7	3	4	6	9
3	0	0	2	0	1	2	3	4	2	1	1	1	3
4	0	0	0	1	0	1	1	1	2	1	1	1	3

where $D(N_{t-g}) = (K - N_{t-g})/K, N_{t-g}$ is the total population size at time $t - g$, and g is the duration of the time lag. Calculation of deer numbers was done with a one-year time lag (Fig. 2 and Table 2). The population size projected with a time lag is similar to that obtained with the logistic equation with a one-year time lag; there is considerable variation in abundance. With a time lag the age structure undergoes continual change after 1933 (Table 2), as abundance repeatedly overshoots the carrying capacity and then collapses. The George Reserve deer population began to be harvested as it approached the carrying capacity in 1933, and it is not known if the population would have overshot the carrying capacity and then collapsed. Harvesting resulted in a gradual decline in numbers (McCullough, 1979).

The density-dependent matrix model developed here exhibits stability characteristics comparable to those of both the matrix model explored in detail by Liu and Cohen (1987) and the discrete time logistic equation explored by May (1974). McCullough (1979) showed that mortality rates were not dependent on density, but that fecundity rates were, so to examine conditions necessary for population cycles or chaotic behavior the fecundity rates of individuals of age one and older were increased. For simplicity, these simulations were done with integer population abundances; the initial age structure was 4 individuals of age 1. If $m_x < 2.89$ the population is
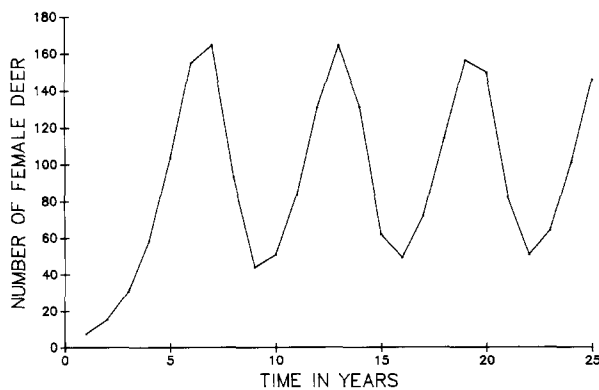
Table 3
Dynamical behavior of the George Reserve white tailed deer population described by the density-dependent matrix model with increased fecundities for age > 0. To maintain non-negative abundances for all age groups, it is necessary for $m_x < 4.19$

Dynamical behavior	Fecundity, m_x
stable	$m_x < 2.89$
2-point cycles	$3.89 \geqslant m_x > 2.89$
4-point cycles	$4.05 \geqslant m_x \geqslant 3.90$
Chaos	$m_x \geqslant 4.10$

stable (Table 3). For larger values of m_x, the population exhibits cycles, and then finally as m_x increases further the population exhibits chaotic behavior in that the trajectory is sensitive to minor changes in the initial age structure. The intrinsic rates of natural increase necessary to obtain cyclic or chaotic behavior with the logistic equation were very high (May, 1974), and the fecundity rates necessary to obtain cycles or chaotic behavior with the density-dependent matrix model also were very high. For the George Reserve, McCullough (1979) reported the relation between recruitment rate y of fawns and the number of yearling and adult females x as $y = 3.077 - 0.048x$, with $R^2 = 0.62$. The number of fawns recruited might approach 3 under the most favorable conditions, but this is only beginning to approach the value of m_x necessary to create cycles or chaotic behavior in the deer population.

The logistic equation and density-dependent matrix models assume that population growth is a function of population size, but they do not describe the factors that limit population growth. Based on additional data McCullough (1979) concluded that growth of the deer population was food limited, and that production of young was severely affected by high densities.

Fig. 2. White-tailed deer population density of the George Reserve calculated with density-dependent matrix model with a time lag of 1 year.

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