The Leslie Model with Harvesting

by

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1.0 Introduction.

One of the simplest population growth models assumes that a populations **P** is closed (i.e., no immigration or emigration is allowed) and that each individual in **P** is identical with respect to survival rates and reproductive rates. This model provides a good approximation when growth is gauged over a small interval of time and P is made up of single cell organisms that reproduce by dividing [11]. The model provides a poor approximation, however, to a population's growth in general since populations consist of individuals with varying survival and reproduction rates. One model which was constructed to remedy this problem is the Leslie matrix model.

With the Leslie model, a population **P** is divided into age groups of equal time length called cohorts, where the reproduction and survival rates are allowed to vary between cohorts but not within a cohort. Furthermore, only the female portion of **P** is considered, although the same mathematical arguments would apply if both males and females were present and the ration of males to females remained constant within each cohort [11]. This model, introduced by Lewis [10] and Leslie [9], is a discrete time model with a discrete age scale. The Leslie model has been applied to many different populations, one of which is the hooded seal of the North Atlantic Ocean. By using the Leslie model, Filpse and Veling were able to conclude that hunting pressure in the years 1975 to 1979 was equal to or slightly greater than the hooded seal populations could tolerate [5].

This paper covers serval topics on the maintenance of a closed populations subject to harvesting. Section 2.0 introduces the Leslie model, states the Perron-Frobenius Theorem as it apples to the Leslie matrix, exposes some basic properties of the Leslie matrix, and then describes the long-ranges behavior of a population when its corresponding Leslie matrix is Primitive. Section 3.0 develops the Leslie model with harvesting, and demonstrates some basic connections between the dynamics of a population whose growth is governed by a Leslie model without harvesting, and the dynamics of the same population with harvesting. These first two sections are subordinate to section 4.0 where all reachable and holdable populations states are determined for a given Leslie matrix L and initial population. The climax of the paper occurs ins section 5.0 where the idea of an optimal harvesting scheme is presented, and it is shown how an optimal harvesting scheme can be found with the methods of linear programming.

2.0 Mathematical Formulation and Basic Results

We partition a population **P** into m age classes $\mathbf{P}_1, \mathbf{P}_2, \ldots, \mathbf{P}_m$ where $\mathbf{P}_i$, i=1,2,…,m consists of individuals in **P** of age i-1 to i time units. Each individual in $\mathbf{P}_i$ has a birthrate of b_i and probability s_i of reaching $\mathbf{P}_{i+1}$ after 1 time unit. Now let $x_i(t)$, $t = 0, 1, 2, \ldots$ represent the number of individuals in $\mathbf{P}_i$ at time t. Peilou has demonstrated that the dynamics of **P** can be captured by considering the first n age classes where $\mathbf{P}_n$ is the oldest age class with a nonzero birthrate [11]. There we will assume that $m = n$. Growth is then governed by the following difference equations:

$$x_1(t+1) = \sum_{k=1}^{n} x_k(t) b_k,$$

$$x_i(t) = x_{i-1}(t) s_{i-1}, \; i = 2, 3, \ldots, n.$$

These difference equations may be written as:

$$x(t+1) = Lx(t) \qquad t = 0, 1, 2, \ldots$$

where $x(t) = \left[x_1(t), x_2(t), \ldots, x_n(t)\right]^T \in M_{n,1}(\Re)$ and

$$L = \begin{bmatrix} b_1 & b_2 & \ldots & b_{n-1} & b_n \\ s_1 & 0 & \ldots & 0 & 0 \\ 0 & s_2 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & \ldots \\ 0 & 0 & \ldots & s_{n-1} & 0 \end{bmatrix}.$$

We call $L \in M_n(\Re)$ a Leslie matrix, and $x(t)$ the populations vector at time t. L is nonnegative with the following restrictions:

(i) $b_i \geq 0$, $\quad i = 1, 2, \ldots, n-1 \quad b_n > 0$

(ii) $s_i > 0$, $\quad i = 1, 2, \ldots, n-1$.

We now present a list of some basic properties enjoyed by the Leslie Matrix L [6].

2.1.a **Property.** *Irreducibility*. The Leslie matrix is irreducible.

2.1.b **Property.** *Characteristic polynomial.* The characteristic polynomial of the Leslie matrix is given by

$$f(\lambda) = \lambda^n - b_1\lambda^{n-1} - s_1 b_2 \lambda^{n-2} - \ldots - s_1 s_2 \ldots s_{n-2} b_{n-1} \lambda - s_1 s_2 \ldots s_{n-1} b_n.$$

2.1.c **Property.** *Nonsingularity*. The Leslie matrix is nonsingular.

2.1.d **Property.** Let $x, y \in M_{n,1}(\Re)$ with $x \geq 0$, $y \geq 0$ and $x \geq y$. Then $Lx \geq Ly$.

Proof: Let x, y be as given. Then $x = y + y'$ for some $y' \in M_{n,1}(\Re)$ with $y' \geq 0$. Thus $Lx = L(y + y') = Ly + Ly' \geq Ly$ since $Ly' > 0$. ■

The most important result pertaining to the Leslie matrix is an application of the Perron-Frobenius theorem. The theorem applies to any nonnegative irreducible matrix and this applies to the Leslie matrix [6], [7].

2.2 **Theorem.** Let $L \in M_n(\Re)$ be an irreducible Leslie matrix. Then

(i) $\rho(L)$ is a simple eigenvalue of L.

(ii) The eigenvector associated with $\rho(L)$ can be chosen to have positive components only.

The eigenvalue $\rho(L)$ is referred to as the Perron root of L, and $\omega \in M_{n,1}(\Re)$, $\omega > 0$ such that $L\omega = \rho(L)\omega$ is called a Perron eigenvector of L.

We can determine the behavior of $x(t)$ as t tends to infinity. This long-range behavior will depend on characteristics of the matrix L. If L is a primitive matrix (i.e., L is irreducible and $\rho(L)$ is a strictly dominant eigenvalue of L), then the following theorem applies [7].

2.3 **Theorem.** If $L \in M_n(\Re)$ be a primitive Leslie matrix, then

$\lim_{t \to \infty} x(t) / \rho(L)^t = \omega z^T x(0)$, where $L\omega = \rho(L)\omega$, $L^T z = \rho(L)z$ and $\omega^T z = 1$.

Since the long-range behavior of $x(t)$ is easy to determine when L is primitive, it would be advantageous to have a theorem which characterizes primitive Leslie matrices. Theorem 2.4 provides such a characterization [11].

2.4 **Theorem.** Let $L \in M_n(\Re)$ be a leslie matrix. Then L is primitive if and only if

$\gcd(N) = 1$ where $N = \{k | b_k \neq 0, k = 1, 2, \ldots, n\}$.

Thus in order check the primitivity of L, one need only calculate the greatest common divisor of the subscripts corresponding to nonzero birthrates. It has been observed that populations whose growth is governed by nonprimitive Leslie matrices are rare [11].

3.0 The Leslie Model with Harvesting

In this section we investigate the population dynamics of a populations **P** subject to harvesting, where the harvesting is carried out in the manner described by Beddington and Taylor [1]. We assume that in the absence of harvesting, the growth of **P** is governed by a Leslie matrix $L \in M_n(\Re)$. Let $x(0)$ be the initial population vector. A certain fraction of each age group in the initial population is to be harvested. Let $h_i(0)$ be the fraction of $x_i(0)$ harvested. Then the vector representing the remaining population is given by

$$(I - D_{h(o)})x(0)\text{, where}$$

$h(0) = \left[h_1(0), h_2(0), \ldots, h_n(0)\right]^T$ and $D_{h(0)} = \operatorname{diag}(h_1(0), h_2(0), \ldots, h_n(0))$.

The growth of this remaining population is governed by the Leslie model, so that

$$x(1) = L(I - D_{h(0)})x(0).$$

We continue this harvesting procedure to obtain population vectors $x(2), x(3), \ldots$ where

$$x(t+1) = L(I - D_{h(t)})x(t) \quad t = 0, 1, 2, \ldots,$$

$h(t) \in M_{n,1}(\Re)$ is the age-specific harvesting vector at time t, and $D_{h(t)}$ is the diagonal matrix with the components of $h(t)$ down its main diagonal. Naturally, there is the restriction

$$0 \le h_i(t) \le 1 \quad i = 1, 2, \ldots, n,$$

which ensures that no more is harvested than is available.

Following are some important results that compare L to $L(I - D_h)$ where $h \in M_{n,1}(\Re)$ and $0 \le h \le 1$. These results will be used extensively throughout the remainder of this paper.

3.1 **Result.** $0 \le L(I - D_h) \le L$.

Proof: $0 \le L(I - D_h) = L - LD_h \le L$, since $LD_h \ge 0$. ■

3.2 **Result.** Let $A, B \in M_n(\Re)$, $A \ge 0$ and $B \ge 0$ with $A \ge B$, then $\rho(A) \ge \rho(B)$.

A proof of Result 3.2 can be found in Horn and Johnson [7].

3.3 **Result.** $\rho(L) \ge \rho(L(I - D_h))$, with equality if and only if $D_h = 0$.

Proof: By Results 3.1 and 3.2, $\rho(L) > \rho(L(I - D_h))$, and clearly if $D_h = 0$, equality holds. Now assume that $\rho(L) = \rho(L(I - D_h))$. We wish to show that if follows that the harvest vector is zero. By property 2.1.b, the characteristic polynomials of L and $L(I - D_h)$ are

$f(\lambda) = \lambda^n - b_1\lambda^{n-1} - s_1 b_2 \lambda^{n-2} - \ldots - s_1 s_2 \ldots s_{n-1} b_n$ and

$g(\lambda) = \lambda^n - (1 - h_1) b_1 \lambda^{n-1} - (1 - h_1)(1 - h_2) s_1 b_2 \lambda^{n-2} - \ldots$

$$-(1-h_1)(1-h_2)\ldots(1-h_n)s_1s_2\ldots s_{n-1}b_n,$$

respectively. For convenience, define $\alpha = \rho(L) = \rho(L(I-D_h))$. Then $f(\alpha) = g(\alpha)$, so that $\alpha^n - f(\alpha) = \alpha^n - g(\alpha)$. We proceed using proof by contradiction. Suppose that $h_1 > 0$. Then comparing the terms of $\alpha^n - f(\alpha)$ and $\alpha^n - g(\alpha)$, we find that
$b_1\alpha^{n-1} \geq (1-h_1)b_1\alpha^{n-1}$, … ,
$s_1s_2\ldots s_{n-2}b_{n-1}\alpha \geq (1-h_1)(1-h_2)\ldots(1-h_{n-1})s_1s_2\ldots s_{n-2}b_{n-1}\alpha$ and
$s_1s_2\ldots s_{n-1}b_n\alpha \geq (1-h_1)(1-h_2)\ldots(1-h_n)s_1s_2\ldots s_{n-1}b_n$. However, these inequalities imply that $\alpha^n - f(\alpha) > \alpha^n - g(\alpha)$, contradicting our hypothesis that the Perron root of L and $L(I-D_h)$ were equal. Therefore, $h_1 \neq 0$. Similar contradictions arise when we assume $h_i > 0$ for $i = 2, \ldots, n$. Hence $h = 0$. ■

This result verifies what our common sense would tell us about harvesting a population: any amount of harvesting is certain to decrease the natural growth rate of a population (measured by the Perron root). For a population that is struggling to persist, any amount of sustained harvesting of the populations could drive it to extinction. This, we will find, occurs when $\rho(L(I-D_h)) < 1$.

3.4 **Result.** $x(t) \leq L^t x(0)$ for all $t \in \aleph$.

Proof: The proof is by induction on t. Let $B = \{t \;\varepsilon\; \aleph \mid x(t) \leq L^t x(0)\}$. If $t = 0$, then $x(0) = L^0 x(0)$, so that $0 \in B$. Now suppose that $0 \in B$. Then

$$x(k+1) = L(I-D_{h(k)})x(k)$$

$$\leq L(I-D_{h(k)})L^k x(0) \qquad \text{(since } x(k) \leq L^k x(0)\text{)}$$

$= L^{k+1}x(0) - LD_{h(k)}L^k x(0)$ (by the distributive property)

$\leq L^{k+1}x(0)$ (since $LD_{h(k)}L^k x(0) \geq 0$).

Therefore $k + 1 \in B$, and by the principle of mathematical induction, $x(t) \leq L^t x(0)$ for all $t \in \aleph$. ■

Simply stated, Result 3.4 says that at all times, each cohort of a harvested population will have the same or fewer numbers than it would if it were not previously harvested. This makes sense based on the model chosen. This may not hold in reality, however, since it is possible for cohort interaction. For example, heavy harvest of one cohort during one year, might allow another to flourish in the face of more food or space resources per animal. Modeling this phenomenon would require a nonlinear model rather than the linear model we have chosen.

Adding harvest makes the long-range behavior of a population whose growth is governed by the Leslie model more difficult to determine. The transition matrix is now a variable which depends on the harvesting vectors through time, and is no longer constant with a constant Perron eigenvalue. The flexibility in the choice of harvest vectors $h(0), h(1), h(2), \ldots$ provides many possibilities. However, in the case where $\rho(L) < 1$, the asymptotic behavior is easily determined.

3.5 **Theorem.** Let $A \in M_n(\Re)$, with $A \geq 0$. Then $\lim_{t \to \infty} A^t = 0$ if and only if $\rho(A) < 1$.

For a proof of this theorem see Horn and Johnson [7].

3.6 **Result.** If $\rho(L) < 1$, then $\lim_{t \to \infty} x(t) = 0$.

Proof: By Result 3.4, $x(t) \le L^t x(0)$ for all $t \in \aleph$, and by Theorem 3.5, $\lim_{t \to \infty} L^t x(0) = 0$. Therefore, $\lim_{t \to \infty} x(t) = 0$. ■

This result demonstrates that a population whose Perron eigenvalue is less than one is doomed. Most likely, a wildlife manager, detecting such a condition, would avoid any harvesting and would initiate a recovery plan to increase birth or survival rates.

4.0 Reachability and Holdability

Sometimes wildlife managers (and very often those responsible for pest control) are faced with the problem of managing a population to a desirable level. If a population is so large that it depletes the resources of its habitat, then some action must be take to bring its size to a less taxing level. Suppose that $L \in M_n(\Re)$ is know to be a desirable age distribution vector for a population **P**. We seek a harvesting scheme such that $x(k) = m$ for some positive integer k, where $x(0)$, the initial population vector, is specified. If such a harvesting strategy exists, we say that the population vector m is *reachable.* A manager may further insist that $x(k+1) = m$ so that the population reaches age distribution m and can be held thereafter at m. If such a harvesting scheme exists, we say that m is *holdable*. In other words, m can be made a stable equilibrium of the difference equations.

The aim of this section is to determine the set of reachable vectors and the set of holdable vectors for a given Leslie matrix L and initial population vector $x(0)$. In the upcoming definitions and results, L is assumed to be an irreducible Leslie matrix, $x(t)$ is the population vector at time t, $h(t)$ is the vector of age-specific harvest rates at time t, $D_{h(t)} = \operatorname{diag}(h_1(t), h_2(t), \ldots, h_n(t))$, $\rho(L)$ is the Perron eigenvalue of L and ω is a

Perron eigenvector of L. Furthermore, assume that $x(0) \neq 0$, so that in the absence of harvesting, the population is guaranteed to be nonzero (i.e., $L^t x(0) \neq 0$ for $t = 0, 1, 2, \ldots$).

4.1 **Definition.** A nonnegative vector $m \in M_{n,1}(\Re)$ is said to be *reachable in k steps* if there exists a finite sequence of vectors

$$S = \{h(0), h(1), \ldots, h(k-1)\},\ h(t)\ \varepsilon\ M_{n,1}(\Re),\ 0 \leq h(t) \leq 1$$

$$t = 0, 1, \ldots, k-1$$

such that $x(t+1) = L(I - D_{h(t)})x(t)$ and $x(k) = m$.

4.2 **Definition.** If $m \in M_{n,1}(\Re)$ is reachable in k steps for some positive integer k, then m is called *reachable.*

4.3 **Definition.** A nonnegative vector $m \in M_{n,1}(\Re)$ is said to be *holdable in k steps* if it is reachable in k steps and there is a harvesting vector $h(k) \in M_{n,1}(\Re)$ with $0 \leq h(t) \leq 1$ such that $x(k+1) = L(I - D_{h(k)})x(k) = x(k)$, and $x(k) = m$.

4.4 **Definition.** If $m \in M_{n,1}(\Re)$ is holdable in k steps fro some positive integer k, then m is called *holdable.*

Armed with these definitions and the elementary results presented earlier, we are prepared to describe holdable sets and reachable sets for a given Leslie matrix L and initial population vector $x(0)$. In the case where L is primitive, Theorem (see below) gives a straightforward characterization of all reachable vectors when $\rho(L) > 1$ and Theorem gives a characterization of all holdable vectors when $\rho(L) > 1$. For a manager interested in maintaining a population at viable levels, these two theorems are the most relevant, for the other theorems proceed under the assumption that $\rho(L) \leq 1$, in which case harvesting would deplete the population.

4.5 **Lemma.** If $m \in M_{n,1}(\Re)$ is reachable in k steps, then $\Sigma \leq m_1 \leq \Sigma + b_n e_n^T L^{k-1} x(0)$, where $\Sigma = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1}$.

Proof: Assume that m is reachable in k steps, and let $x(k-1) = x$, $h = h(k-1)$. Then $m = LD_h x$ so that

$$m_1 = b_1(1-h_1)x_1 + b_2(1-h_2)x_2 + \ldots + b_n(1-h_n)x_n$$

$$m_2 = s_1(1-h_1)x_1$$

$$m_3 = s_2(1-h_2)x_1$$

$$\ldots$$

$$m_n = s_{n-1}(1-h_{n-1})x_{n-1}.$$

Substituting the last $n-1$ of these equations into the first equation, we obtain

$$m_1 = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1} + b_n(1-h_n)x_n.$$

The term $b_n(1-h_n)x_n$ achieves its minimum value of zero when $h_n = 1$, and its maximum value of $b_n x_n$ when $h_n = 0$. By Result 3.4, $b_n x_n \leq b_n e_n^T L_{k-1} x(0)$, and the result follows. ■

The above Lemma gives us a simple condition on the size of the youngest cohort, m_1, of a reachable population vector. The lower bound Σ represents the number of individuals born to all but the oldest cohort of the population during the previous time step given that the current population vector is m. If the youngest cohort of m is less than the least allowable number of offspring born during the previous time step, Σ, then m is not reachable. If the oldest cohort is completely harvested (i.e., $h_n = 1$) during the previous time step and if $x(k+1) = m$, then $m_1 = b^T x(k-1) = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1} = \Sigma$, which demonstrates that the lower bound cannot be made any larger.

The upper bound in Lemma 4.5 represents maximum allowable number of births during the previous time step ($t = k-1$) given the present population vector is m. It is achieved when the population has no prior harvest history, therefore the upper bound can be made no smaller.

4.6 **Lemma.** Let $m \in M_{n,1}(\Re)$ $m \geq 0$, and let L be a primitive Leslie matrix. If $\rho(L) > 1$, the there exists a positive integer j' such that $L^j x(0) \geq m$ for all positive integers j such that $j \geq j'$.

Proof: By Theorem 2.3, $\lim_{t \to \infty} x(t) / \rho(L)^t = \omega z^T x(0)$ where $\omega, z \in M_{n,1}(\Re)$ $\omega > 0$, $z > 0$, $L\omega = \rho(L)\omega$ and $L^T z = \rho(L) z$. Assume that $\rho(L)$, then $\lim_{t \to \infty} x(t) = \lim_{t \to \infty} \rho(L)^T \omega z^T x(0) = \infty$. Hence for any $m \in M_{n,1}(\Re)$ there exists a positive integer j' such that $L^j x(0) \geq m$ for all positive integers j such that $j \geq j'$. ■

Lemma 4.6 demonstrates that given any particular population vector that a wildlife deems desirable, the population will eventually meet or exceed it. This is due to the exponential growth inherent in the Leslie matrix model. When the Perron eigenvalue exceeds one, the population is guaranteed to explode in the absence of harvesting.

4.7 **Theorem.** $m \in M_{n,1}(\Re)$ is reachable in $j+1$ steps if and only if the following two conditions hold:

(i) $\Sigma \le m_1 \le \Sigma + b_n x_n$, where $x = L^j x(0)$ and $\Sigma = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1}$.

(ii) $m \le L^{j+1} x(0)$.

Proof: Suppose that $m \in M_{n,1}(\Re)$ is reachable in $j+1$ steps. by Lemma 4.5 condition (i) must hold. To show condition (ii) must hold, we use a proof by contradiction. If (ii) does not hold, the there exists a positive integer i, $1 \le i \le n$, such that $m_i > e_i^T L^{j+1} x(0)$. However, by Result 3.4, $x(j+1) \le L^{j+1} x(0)$ which implies that $e_i^T x(j+1) \le e_i^T L^{j+1} x(0) < m_i$ so that m is not reachable in $j+1$ steps. This completes the argument that the two conditions are necessary. To show that they are also sufficient, we construct a sequence of harvesting vectors that yields the desired vector m.

Now suppose that the conditions (i) and (ii) hold and specify a harvesting sequence $S = \{h(0), h(1), \ldots, h(j)\}$ where $h(0) = h(1) = \ldots = h(j-1) = 0$ and $h = h(j)$ is defined by

$$
\begin{aligned}
h_i &= 0 && \text{if } x_i = 0,\ 1 \le i \le n \\
h_i &= 1 - m_{i+1} / s_i x_i && \text{if } x_i > 0,\ 1 \le i \le n-1 \\
h_n &= 1 - (m_1 - \Sigma) / b_n x_n && \text{if } x_n > 0
\end{aligned}
$$

where $x = \begin{bmatrix} x_1 & x_2 & \ldots & x_n \end{bmatrix}^T = x(j)$, and $\Sigma = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1}$. It is easily verified that this choice for $h(j)$ gives $m = L(I - D_{h(j)}) x(j) = x(j+1)$.

We next demonstrate that the above choice for $h(j)$ satisfies the required constraint, $0 \le h(j) \le 1$. Since the parameters m_i, s_i, b_i, and x_i are all nonnegative, it is clear that our constructed harvest vector, $h(j)$, is less than or equal to one in its first $n-1$

components. Its last component, h_n, is also less than or equal to 1 by condition (ii). Therefore, the harvest vector satisfies $h(j) \le 1$. We next show that the harvest vector is nonnegative using a proof by contradiction. We know that, by definition of h, if $x_i(j) = 0$ then $h_i = 0$ and therefore when any x component is zero, the corresponding harvest vector component is nonnegative as required. Suppose that there exists a $x_i(j)$ such that $x_i(j) > 0$, $1 \le i \le n-1$ and that its corresponding harvest is negative (i.e., $e_i^T h < 0$). Then

$$m_{i+1} = e_{i+1}^T(L - LD_{h(j)})x(j) = e_{i+1}^T Lx(j) - (1-h_i)s_i x_i(j)$$
$$> e_{i+1} Lx(j) = e_{i+1}^T L^{j+1} x(0),$$

which contradicts condition (ii). Finally, if the nth component of the harvest vector, h_n, is less than zero and $x_n(j) > 0$, then our constructed harvest vector h gives $m_1 - \Sigma > b_n x_n$, which contradicts condition (i). Hence m is reachable in $j+1$ steps. ■

Theorem 4.7 gives conditions that are sufficient and necessary for a vector m to be reachable in k steps and its proof demonstrates a harvesting strategy that controls the population vector to m. This harvesting strategy, in general, is only one of many such strategies that culminate in m after k steps. It consists for no harvest until time step $k-1$, at which time a harvest $h(k-1)$ is applied that produces the vector m in the next time step.

4.8 **Theorem.** Assume that L is primitive. If $\rho(L) > 1$, then $m \in M_{n,1}(\Re)$ is reachable if and only if

$$\Sigma = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1} \le m_1 .$$

Proof: Assume that $\rho(L) > 1$ and let $\Sigma \le m_1$. By Lemma 4.6 there exists a positive integer j' such that $L^j x(0) \ge m$ for all positive integers j such that $j \ge j'$. By the same Lemma there exists a positive integer j'' such that $L^j x(0) \ge \left[0, 0, \ldots, 0, (m_1 - \Sigma)/b_n\right]^T$ for all positive integers j such that $j \ge j''$. Let $j \ge max\{j', j''\}$, then $m \le L^{j+1}x(0)$ and $e_n^T L^j x(0) \ge e_n^T \left[0, 0, \ldots, 0, (m_1 - \Sigma)/b_n\right]^T$. These are the conditions for reachability guaranteed by Theorem 4.7. Now suppose that m is reachable, them by condition (i) of Theorem 4.7, $\Sigma \le m_1$. ■

4.9 **Lemma.** If $m \in M_{n,1}(\Re)$ is reachable, then m is holdable if and only if

(i) $\Sigma \le m_1 \le \Sigma + b_n m_n$, where $\Sigma = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1}$.

(ii) $m \le Lm$.

Proof: Assume that m is reachable. We need only demonstrate that m is reachable (from starting vector m) in one step. The proof then follows by induction. Assuming that the initial population vector is m, by Theorem 4.7, m is reachable in one step if and only if $\Sigma \le m_1 \le \Sigma + b_n m_n$ and $m \le Lm$. These are precisely the two conditions needed. ■

4.10 **Theorem.** Assume that L is primitive and that $\rho(L) > 1$. Then $m \in M_{n,1}(\Re)$, $m > 0$ is holdable if and only if the two conditions of Lemma 4.9 hold.

Proof: If m is holdable, then by Lemma 4.9, conditions (i) and (ii) must hold. Assume now that the two conditions hold and $\rho(L) > 1$. Then by Theorem4.8, m is reachable, and thus by Lemma 4.9, m is holdable. ■

We next turn our attention to the case where $\rho(L) < 1$, in which case a population is doomed unless the birthrates or survival rates can be sufficiently increased.

4.11 **Theorem.** If $\rho(L) < 1$, then the zero vector is the only holdable population vector.

Proof: Let $\rho(L) < 1$ and assume that is a holdable vector. Then there exists a harvest vector $h \in M_{n,1}(\Re)$, $0 \le h \le 1$ such that $m = L(I - D_h)m$. This implies that either $m = 0$, or m is an eigenvector of $L(I - D_h)$ with corresponding eigenvalue of 1. However by Result 3.3, $\rho(L(I - D_h)) \le \rho(L)$, which makes an eigenvalue of 1 impossible for $L(I - D_h)$, since $\rho(L) < 1$. Hence $m = 0$ is the only holdable population vector. If we let $h(0) = 1$, it is clear that $m = 0$ is reachable in 1 step. ■

4.12 **Theorem.** If $\rho(L) = 1$ and m is holdable, then $m = c\omega$, where c is a nonnegative real constant.

Proof: Suppose that $\rho(L) = 1$ and that m is holdable. Then there exists a harvest vector $h \in M_{n,1}(\Re)$, $0 \le h \le 1$ such that $m = L(I - D_h)m$. This implies that either $m = 0$ or m is an eigenvector of $L(I - D_h)$ with corresponding eigenvalue 1. If $m = 0$, then $m = 0 \cdot \omega$. If $m \ne 0$, then by Result 3.3, $1 = \rho(L(I - D_h)) \le \rho(L) = 1$, which implies that $D_h = 0$. Hence m is a Perron eigenvector of L so that $m = c\omega$ for some real, nonnegative constant c. ■

An age distribution (population vector) is said to be *stable* if the percentage of the population in each cohort is constant over time. In the case that its growth is governed by a Leslie model without harvesting and the age distribution is not zero, the population is stable if and only if the population vector is an eigenvector of the matrix L. Notice that for a stable population vector, x, the equation holds $Lx = \rho(L)x$, and the population growth is completely determined by $\rho(L)$, the Perron eigenvalue. When the population vector is stable, and the Perron eigenvalue is greater than 1, the population increases over time in each of its cohorts; when the Perron eigenvalue is less 1, the population decreases in each of its cohorts. To generalize the idea of a population increasing or decreasing in all of its cohorts, we characterize all vectors $x \geq 0$ such that $Lx \geq x$, and all vectors $y > 0$ such that $Ly \leq y$.

4.13 **Definition.** For $x \in M_{n,1}(\Re)$, $x \geq 0$ and $x \neq 0$, define $D(L) = \{x \mid Lx \leq x\}$ and $I(L) = \{x \mid Lx \geq x\}$. $D(L)$ consists of all nonzero population vectors that decrease when multiplied by L and $I(L)$, those that decrease when multiplied by L.

4.14 **Result.** Let L have Perron root $\rho(L)$ and Perron eigenvector ω. If $\rho(L) \leq 1$, then $\omega \in D(L)$. If $\rho(L) \geq 1$, then $\omega \in I(L)$.

The next theorem exploits the multiplying behavior of the Leslie matrix to determine bounds for the Perron eigenvalue. When L multiplies its Perron eigenvector, then the Perron eigenvalue is simply $\|L\omega\| / \|\omega\|$. When L multiplies other nonnegative vectors, we may not be able to identify the Perron eigenvalue, but we can bracket it. This is equivalent to observing a population growing over one time step to make assessments of its intrinsic natural rate of increase.

4.15 **Theorem.** Let $x \in M_{n,1}(\Re)$, $x \geq 0$. (i) If $Lx > \alpha x$ for some real scalar $\alpha > 0$, then $\rho(L) > \alpha$. (ii) If $Lx < \alpha x$, then $\rho(L) < \alpha$.

Proof: Assume that $x \in M_{n,1}(\Re)$, $x \geq 0$ and $Lx > \alpha x$ for some real scalar $\alpha > 0$. Then there exists $z \in M_{n,1}(\Re)$, with $z > 1$, such that $Lx = D_z \alpha Lx$. This implies that $\alpha = \rho(D_z^{-1}L)$. By similarity, $\rho(D_z^{-1}L) = \rho(D_z D_z^{-1} L D_z^{-1}) = \rho(L D_z^{-1})$. Since $L D_z^{-1} \leq L$, by Result 3.3, $\alpha = \rho(LD_z^{-1}) < \rho(L)$, which proves (i). To prove (ii) we use a similar argument. ■

4.16 **Corollary.** (i) If $\rho(L) > 1$, then $D(L) = \phi$. (ii) If $\rho(L) < 1$, then $I(L) = \phi$. (iii) If $\rho(L) = 1$, then $D(L) = I(L) = \{x \in M_{n,1}(\Re) \mid x = c\omega, c \in \Re, c > 0\}$.

Proof: Assume that $x \in M_{n,1}(\Re)$, $x \geq 0$. If $x \in D(L)$ and $Lx < x$, then by part (i) of Theorem 4.15 $\rho(L) < 1$. If $x \in D(L)$ and $Lx = x$, then $\rho(L) = 1$. Thus by the contrapositive, (i) holds. Similarly, (ii) follows form part (ii) of Theorem 2.15 and the observation that $\rho(L) = 1$ when $Lx = x$.

Finally, if $\rho(L) = 1$ and $Lx = x$, then by the Perron - Frobenius theorem, there exists $\omega > 0$ such that $x = c\omega$ and therefore $c\omega \in D(L)$ and $c\omega \in I(L)$ for some positive real scalar c. Theorem 4.15 forbids the possibility that $\rho(L) = 1$ with $Lx > x$ and the possibility that $\rho(L) = 1$ with $Lx < x$. Therefore all the elements of $D(L)$ and $I(L)$ are of the form $x = c\omega$ for some positive real scalar c. ■

We have shown that if a population is observed to increase in each of its cohorts over a time step, then the Perron eigenvalue of its Leslie matrix is greater than one, and the population will eventually explode. If the population is observed to decrease in each of its cohorts, then the Perron eigenvalue is less than one, and the population will eventually go extinct. If the cohorts remain the same size, then the population has reached a stable age distribution (population vector), and will remain constant over time with a Perron eigenvalue equal to 1.

4.17 **Theorem.** Let $x \in M_{n,1}(\Re)$, $x \geq 0$, $x \neq 0$. Then $x \in I(L)$ if and only if there exists $\beta \in M_{n,1}(\Re)$, $0 < \beta \leq 1$ such that $D_\beta L x = x$, and we may specify $\beta_i = 1$ whenever $x_i = 0$.

Proof: First assume that $x \in I(L)$ so that $Lx \geq x$. This gives rise to the following inequalities:

$$\sum_{i=1}^{n} b_i x_i \geq x_1 \quad \text{and} \quad s_i x_i \geq x_{i+1}, \quad i = 1, 2, \ldots, n-1.$$

Therefore, there exists $c \in M_{n,1}(\Re)$, $c \geq 1$ such that

$$\sum_{i=1}^{n} b_i x_i = c x_1 \quad \text{and} \quad s_i x_i = c_{i+1} x_{i+1}, \quad i = 1, 2, \ldots, n-1.$$

Let $c_i = 1$ whenever $x_i = 0$. these equations can be written as $Lx = D_c x$. Let $D_\beta = D_c^{-1}$ so that $D_\beta L x = x$, $0 < \beta \leq 1$ and $\beta_i = 1$ whenever $x_i = 0$.

Now suppose that $\beta \in M_{n,1}(\Re)$, $0 < \beta \leq 1$ such that $D_\beta L x = x$. Then $Lx = D_\beta^{-1} x$, where $D_\beta^{-1} \geq I$ so that $D_\beta^{-1} x > x$ which implies that $Lx \geq x$. ■

The next theorem is analogous to Theorem 4.17, but it is for vectors that do not increase any component when multiplied by L. It is stated here without proof, but its proof is similar to that of Theorem 4.17. What both of these theorems say is that, if a vector's components do not increase (decrease) when it is multiplied by L, then L may be scaled by a diagonal matrix so that the vector is a Perron-eigenvector of the resulting scaled version of L.

4.18 **Theorem.** Let $x \in M_{n,1}(\Re)$, $x \geq 0$, $x \neq 0$. Then $x \in D(L)$ if and only if there exists $\beta \in M_{n,1}(\Re)$, $\beta \geq 1$ such that $D_\beta L x = x$, and we may specify $\beta_i = 1$ whenever

$x_i = 0$.

4.19 **Lemma.** Let $x \in M_{n,1}(\Re)$, $x \geq 0$, $x \neq 0$ with $x \in I(L)$, then $L^t x \in I(L)$ for all nonnegative integers t.

Proof: The argument is made by induction. Let $V = \{t \in \aleph \mid L^t x \in I(L), x \in I(L)\}$. $0 \in V$ since it is assumed that $x \in I(L)$. Suppose now that $k \in V$, so that $L^k x \in I(L)$. By Theorem 4.17, there exists $\beta \in M_{n,1}(\Re)$, $0 < \beta \leq 1$ such that $D_\beta L L^k x = L^k x$. Therefore,

$$L(L^{k+1}x) = L(D_\beta^{-1} L^k x) = L((D_\beta^{-1} - I + I)L^k x) =$$

$$L((D_\beta^{-1} - I)L^k x + L^k x) = L(D_\beta^{-1} - I)L^k x + L^{k+1} x \geq L^{k+1} x.$$

This last inequality holds because $L(D_\beta^{-1} - I)L^k x \geq 0$. Hence $k+1$ and by induction, $L^t x \in I(L)$ for all nonnegative integers t. ■

4.20 **Lemma.** Let $x \in M_{n,1}(\Re)$, $x \geq 0$, $x \neq 0$ with $x \in D(L)$, then $L^t x \in D(L)$ for all nonnegative integers t.

The proof of Lemma 4.20 is analogous to the proof of Lemma 4.19 and is therefore omitted. The two results tell us that in the absence of harvesting, once a population begins to increase (decrease) over time in each cohort, it continues to do so.

It may be important to know the minimum time that it takes for a population subject to harvesting to be controlled to a reachable population vector m. This is especially true when the cost of having the population away from a desirable age distribution vector is high.

4.21 **Definition.** Let $m \in M_{n,1}(\Re)$ be reachable. $\chi(m)$ is defined as the minimum number of steps necessary to reach m. Notice that $\chi(m)$ depends on L and $x(0)$, but for brevity, these arguments are suppressed.

4.22 **Theorem.** Assume that $x(0) \in I(L)$, $x(0) > 0$ and $m \in M_{n,1}(\Re)$ is reachable. Then, m is reachable in k steps for any positive integer k with $k \geq \chi(m)$.

Proof: Let $m \in M_{n,1}(\Re)$ be reachable. Then by Theorem 4.7,

$$\Sigma \leq m_1 \leq \Sigma + b_n e_n^T L^{\chi-1} x(0), \text{ where } \Sigma = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1} \text{ and } \chi = \chi(m).$$

Since $x(0) \in I(L)$, Lemma 4.19 implies that $L^t x(0) \in I(L)$ for all nonnegative integers t. Therefore $m \leq L^{\chi} x(0) \leq L^{\chi+1} x(0) \leq L^{\chi+2} x(0) \leq \ldots$, and

$m_1 \leq \Sigma + b_n e_n^T L^{\chi-1} x(0) \leq \Sigma + b_n e_n^T L^{\chi} x(0) \leq \ldots$. Thus by Theorem 4.7, m is reachable in k steps for each positive integer k such that $k \geq \chi$. ■

4.23 **Theorem.** Assume that $x(0) \in D(L)$, $x(0) > 0$ and $m \in M_{n,1}(\Re)$ is reachable in k steps. Then, m is reachable in $j + 1$ steps for any positive integer j such that $0 \leq j \leq k - 2$.

Proof: Since m is assumed to be reachable in k steps, by Theorem 4.7,

(i) $\Sigma \leq m_1 \leq \Sigma + b_n e_n^T L^{k-1} x(0)$, where $\Sigma = \sum_{i=1}^{n-1} \frac{b_i}{s_i} m_{i+1}$. and

(ii) $m \leq L^k x(0)$.

Furthermore, by Lemma 4.20, $m \leq L^k x(0) \leq L^{k-1} x(0) \leq \ldots \leq Lx(0) \leq x(0)$, and

$m_1 \leq b_n e_n^T L^{k-1} x(0) + \Sigma \leq b_n e_n^T L^{k-2(1)} x(0) + \Sigma \leq \ldots \leq b_n e_n^T L^0 x(0) + \Sigma$. Therefore conditions (i) and (ii) of Theorem 4.7 are satisfied for $0 \leq j \leq k - 2$, so that m is reachable in $j + 1$ steps, with $0 \leq j \leq k - 2$. ■

It follows from Theorem 4.23 that if m is reachable and $x(0) \in D(L)$, then $\chi(m) = 1$. In general, when $x(0)$ is not guaranteed to belong to $D(L)$ or $I(L)$, $\chi(m)$ is more difficult to determine. One way to do this, however, is to use Theorem 4.7, which demonstrates that if m is reachable, then $\chi(m)$ is the minimum positive integer k such that (i) $\Sigma \le m_1 \le \Sigma + b_n e_n^T L^{k-1} x(0)$ and (ii) $L^k x(0) \ge m$. This means that χ can be found by raising L to powers until $L^k x(0) \ge m$, and then checking to see if condition (i) holds. It would be nice if their were a method for determining $\chi(m)$ without raising L to various powers. The following result is for such a special case.

4.24 **Result.** Assume that m is reachable. If $x(0) = \omega$, and $m = c\omega$ for some nonnegative, real scalar c, then $\chi(m)$ is the minimum positive integer k such that $\rho(L)^k \ge c$ and $(m_1 - \Sigma)/b_n \le \rho(L)^{k-1}\omega_n$.

The proof of Result 4.24 follows easily from Theorem 4.7 and the fact that ω is the Perron eigenvalue associated with $\rho(L)$, therefore, it is omitted. The Result can be generalized to provide an upper bound from $\chi(m)$. The following Theorem provides such a generalization.

4.25 **Theorem.** Assume that $m \in M_{n,1}(\Re)$ is reachable and let $c = max\{r \in \Re \mid r\omega \le x(0)\}$. then $\chi(L) \le min\{k \in P \mid c\rho(L)^k\omega \ge m$ and $(m_1 - \Sigma)/b_n \le c\rho(L)^{k-1}\omega_n\}$.

Proof: Since $c\omega \le x(0)$, by Property 2.1.d, $L^k x(0) \ge L^k c\omega = c\rho(L)^k\omega$. Therefore, if $c\rho(L)^k\omega \ge m$, then $L^k x(0) \ge m$, and if $(m_1 - \Sigma)/b_n \le c\rho(L)^{k-1}\omega$, then $(m_1 - \Sigma)/b_n \le L^{k-1}x(0)$. therefore $V_1 = \{k \in P \mid L^k x(0) \ge m$ and

$(m_1 - \Sigma)/b_n \le e_n^T L^{k-1} x(0)\}$ $\subseteq$ $V_2 = \{k \in P \mid c\rho(L)^k \omega \ge m$ and

$(m_1 - \Sigma)/b_n \le c\rho(L)^{k-1}\omega_n\}$. Hence $\chi(m) = min V_2 \le min V_1$. ■

5.0 Optimal Harvesting Strategies

In section 4.0 we characterized the set of population vectors that are reachable for a given Leslie matrix L and initial population vector $x(0)$. If m is reachable in k steps, then there exists a nonempty set $A_k(m)$ which is defined as the set of all finite harvest sequences S, where $S = \{h(0), h(1), \ldots, h(k-1)\}$ such that m is reachable through S. Since m is assumed to be reachable, $A_k(m)$ is guaranteed to be nonempty. Assume that each individual in the ith age class of the harvested population has a value of v_i when harvested. We then define the vector $v \in M_{n,1}(\Re)$ by $v = \begin{bmatrix} v_1 & v_2, & \ldots & v_n \end{bmatrix}^T$, which is know as the *value vector* and is assumed to be constant over time. The harvest of the initial population has a value of $v^T D_{h(0)} x(0)$ and the harvest of the population at time j has a value of $v^T D_{h(j)} x(j)$, where j is a positive integer. Form time 0 to $k-1$, there is a total value of

$$\sum_{i=0}^{k-1} v^T D_{h(i)} x(i),$$

which we intend to maximize over the set $A_k(m)$; this quantity is known as the k*-step yield.*

5.1 **Definition.** For a given finite sequence of harvest vectors $S = \{h(s), h(s+1), \ldots,$ $h(k-1)\}$,

$$y(s, k-1) = \sum_{i=s}^{k-1} v^T D_{h(i)} x(i)$$

is called the yield over the time interval $[s, k-1]$.

The problem we have described above is know as an optimal control problem with fixed endpoints [2]. The fixed endpoints are $x(0)$ and $m = x(k)$, where m is assumed to be reachable in k steps. In the language of control theory, $\{x(0), x(1), \ldots\}$ is known as the trajectory, the set $A_k(m)$ is the set of allowable controls, and $y(0, k-1)$ is the objective which we intend to maximize [2]. the problem stated is the language of optimal control is as follows: For a given Leslie matrix L, initial population vector $x(0)$, and a reachable vector m, find controls $h(0)$, $h(1)$, …, $h(k)$ such that $x(k) = m$ and $y(0, k-1)$ is as large as possible.

Many investigators have analyzed the problem of maximizing the *sustainable yield* of a population when $\rho(L) \geq 1$ {1], [4], [8], [12], [13]. In the sustainable yield problem, the population is harvested in such a way that the population distribution and size remain constant. The problem consists of maximizing $v^T x$ over all vector $x \in M_{n,1}(\Re)$ such that x is holdable in 1 step, starting with initial vector $x(0) = x$, with $1^T x = 1$.

This so-called maximum sustainable yield problem can easily be posed as a linear program [1]. The optimal control problem with fixed endpoints described above can also be solved using linear programming. The following theorem is used to construct the constraints of this linear program.

5.2 **Theorem.** Let $m \in M_{n,1}(\Re)$ be reachable in k steps, and let $S = \{h(0), h(1), \ldots, h(k-1)\}$ with $h(t) \in M_{n,1}(\Re)$, $x(t+1) = L(I - D_{h(t)})x(t)$,

$t = 0, 1, \ldots, k-1$, where $h_i(t) = 0$ when $x_i(t) = 0$. Then $S \in A_k(m)$ if and only if

(i) $x(k) = m$ and

(ii) $0 \le L^{-1}x(t) \le x(t-1) \quad t = 1, 2, \ldots, k$.

Proof: Assume that $S = \{h(0), h(1), \ldots, h(k-1)\}) \in A_k(m$. Then (i) $m = x(k)$ follows immediately. For $t = 0, 1, \ldots, k, L^{-1}x(t) = (I - D_{h(t-1)})x(t-1) =$ $x(t-1) - D_{h(t)}x(t-1) \le x(t-1)$ since $D_{h(t-1)}x(t-1) \ge 0$. Furthermore, since $D_{h(t-1)} \le 1$, $L^{-1}x(t) \ge 0$. Thus condition (ii) holds.

Now assume that conditions (i) and (ii) hold for S. We need only show that $0 \le h(t) \le 1$. By condition (i),

$$0 \le L^{-1}x(t) \le x(t-1)$$

$$\Rightarrow \quad 0 \le L^{-1}(L(I - D_{h(t-1)})x(t-1)) \le x(t-1)$$

$$\Rightarrow \quad 0 \le (I - D_{h(t-1)})x(t-1) \le x(t-1).$$

Therefore, $0 \le (1 - h_i(t-1))x_i(t-1) \le x_i(t-1)$ for $i = 1, 2, \ldots, n$. If $x_i(t-1) > 0$, then $0 \le (1 - h_i(t-1)) \le 1$ so that $0 \le h_i(t-1) \le 1$. If $x_i(t-1) = 0$, then by choice of S, $h_i(t-1) = 0$. Hence $(S = \{h(0), h(1), \ldots, h(k-1)\}) \in A_k(m)$. ■

One last result is needed to present the problem as a linear program. It is a result that allows us to write the yield as a function of the trajectory.

5.3 **Result.** Let $L, x(0), v^T$ bet given if $(S = \{h(0), h(1), \ldots, h(k-1)\})$ is a k-step harvesting policy with corresponding trajectory $T = \{x(0), x(1), \ldots, x(k)\}$, then

$$y(0, k-1) = v^T x(0) - v^T x(k) + \sum_{t=1}^{k-1} v^T (I - L^{-1}) x(t).$$

Proof: By definition, $y(0, k-1) = v^T(D_{h(0)}x(0) + D_{h(1)}x(1) + \ldots + D_{h(k-1)}x(k-1))$. Now $x(t+1) = L(I - D_{h(t)})x(t)$, so that $D_{h(t)}x(t) = x(t) - L^{-1}x(t+1)$ for $t = 0, 1, \ldots, k-1$. Substituting these equations into the above expression for $y(0, k-1)$, we have $y(0, k-1) = v^T(x(0) - L^{-1}x(1) + \ldots + x(k-1) - L^{-1}x(k))$

so that $y(0, k-1) = v^T x(0) - v^T x(k) + \sum_{t=1}^{k-1} v^T (I - L^{-1}) x(t)$. ■

We are now ready to develop the linear program. Let $x(0)$ and L be given, and let m be reachable in k steps. We are interested in maximizing $y(0, k-1)$ with respect to B, the set of all trajectories T, that are derived from an admissible k-step harvesting strategy. By Theorem 5.2, at trajectory T belongs to the set B if and only if (i) $x(k) = m$ and (ii) $0 \le L^{-1}x(t) \le x(t-1)$, $t = 1, 2, \ldots, k$. Since m is assumed to be reachable in k step, B is certainly nonempty. Also, since B is closed and bounded and $y(0, k-1)$ is continuous over B, $y(0, k-1)$ takes on its maximum value over a point in B [2]. Since the constraints on $T \in B$ are linear in T, and $y(0, k-1)$ is linear in T, the methods of linear programming me be applied to find an optimal trajectory, T^*. Once a trajectory $T^* = \{x^*(0), x^*(1), \ldots, x^*(k-1)\}$ is discovered, the equations

$$x^*(t+1) = L(I - D_{h^*(t)})x^*(t) \qquad t = 0, 1, \ldots, k-1$$

may be used to solve for $S^* = \{h^*(0), h^*(1), \ldots, h^*(k)\}$, letting $h_i^*(t) = 0$ whenever $x_i^*(t) = 0$, $i = 1, 2, \ldots, n$.

The following is a formal statement of the problem as a linear program [3].

5.4 **The Linear Program.**

$$\text{maximize: } \sum_{t=1}^{k-1} v^T(I - L^{-1})x(t) \text{ where } x(t+1) = L(I - D_{h(t)})x(t)$$

$$\text{subject to : (i) } x(k) = m \text{ and (ii) } 0 \le L^{-1}x(t) \le x(t-1) \text{ where } t = 1, 2, \ldots, k.$$

The example below will demonstrate how to use linear programming and Theorem 4.7 to solve an optimal yield problem.

5.5 **Example.**

Let $L = \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix}$, $v = \begin{bmatrix} 2 \\ 1 \end{bmatrix}$, $x(0) = \begin{bmatrix} 20 \\ 8 \end{bmatrix}$, and $m = \begin{bmatrix} 10 \\ 5 \end{bmatrix}$.

(a) Determine whether m is reachable in 2 steps. Is m also holdable in 2 steps?

(b) Determine the 2-step harvesting policy.

Solution: a) We show that conditions (i) and (ii) of Theorem 4.7 hold. Note that $\Sigma = b_1 m_2 / s_1 = 0$ and $e_2^T L x(0) = e_2^T \begin{bmatrix} 8 & 20 \end{bmatrix}^T$, so that $\Sigma \le m_2 = 5 \le \Sigma + e_2^T L x(0)$. Therefore condition (i) is satisfied. Also, $L^2 x(0) = \begin{bmatrix} 20 & 8 \end{bmatrix}^T \ge \begin{bmatrix} 10 & 5 \end{bmatrix}^T = m$, and therefore condition (ii) is satisfied. Hence m is reachable in 2 steps.

(b) We proceed by solving the linear program set down in 5.4 for an optimal trajectory. Let $x(1) = x = \begin{bmatrix} x_1 & x_2 \end{bmatrix}^T$.

$$\text{maximize: } v^T(I - L^{-1})x = \begin{bmatrix} 1 & -1 \end{bmatrix}^T x$$

$$\text{subject to : (i) } x(2) = m$$

and (ii) $0 \le \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \end{bmatrix} \le \begin{bmatrix} 20 \\ 8 \end{bmatrix}$ $0 \le \begin{bmatrix} 0 & 1 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} 10 \\ 5 \end{bmatrix} \le \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$.

These constraints reduce to $10 \le x_2 \le 20$ and $5 \le x_1 \le 8$. The feasible region is therefore a rectangle in the x_1-x_2 plane with vertices $(5, 10)$, $(5, 20)$, $(8, 10)$, and $(8, 20)$. It is well known that the solution is realized at one of these vertices [2]. The table below gives the value of the objective at each of these vertices.

Vertex	**Objective**
$(5, 10)$	-5
$(5, 20)$	-15
$(8, 10)$	-2
$(8, 20)$	-12

It is apparent that the objective function is maximized at $x(1) = \begin{bmatrix} 8 & 10 \end{bmatrix}^T$. the corresponding yield (using Result 5.3) is equal to 21. We now use the fact that $x(t+1) = L(I - D_{h(t)})x(t)$ for $t = 0, 1$ and the optimal trajectory to obtain the optimal harvesting policy—

$$S^* = \{h^*(0), h^*(1)\} = \left\{ \begin{bmatrix} 1/2 \\ 0 \end{bmatrix}, \begin{bmatrix} 3/8 \\ 0 \end{bmatrix} \right\}. \quad \square$$

6.0 Conclusion

This paper has examined the problem of optimally controlling a population **P**, which is subject to harvesting and whose growth is approximated by a Leslie matrix, to a given reachable size and distribution. The results exhibited will undoubtedly prove useful to a wildlife manager who makes use of the Leslie matrix model.

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Notation

$\Re$	the real numbers
P	the positive integers
$\aleph$	the natural numbers
$M_{m,n}(\Re)$	m-by-n matrices from $\Re$
$M_n(\Re)$	n-by-n matrices from $\Re$
$\rho(L)$	the spectral radius of $L \in M_n(\Re)$
I	the identity matrix in $M_n(\Re)$
e_i	ith standard basis vector in $M_{n,1}(\Re)$
A^T	transpose of $A \in M_{m,n}(\Re)$
A^{-1}	inverse of a nonsingular matrix $A \in M_n(\Re)$
$gcd(J)$	the greatest common divisor of the set $J \subseteq P$
x_i	the ith component of $x \in M_{n,1}(\Re)$ (usually)
□	end of example
■	end of proof

VITA

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