

**APPLICATION OF LESLIE MATRIX MODELS  
TO WILD TURKEY POPULATIONS**

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Raleigh  
1994

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# ABSTRACT

The Leslie matrix model is a popular and useful method for population projection based on age specific survival and fecundity rates. The first part of this project will describe the theorems, properties, application, and development of the Leslie matrix model in detail. In the second part, specific Leslie models are developed for wild turkeys in Iowa.

The Leslie matrix model has become very popular because of its easy understanding by biologists and because many theoretical properties can be easily studied using matrix algebra.

In the example for Iowa wild turkey populations, a simple, linear, deterministic model based on the Leslie model is built. The model's simplicity makes it easy to understand and analyze. However, its simplicity also means that it is far from biological reality. There are too few parameters to adequately describe the complexity of a real turkey population. However, it is a good model on which to build more complex and realistic models which may allow stochasticity and density dependence of survival and fecundity rates.

# THE LESLIE MATRIX MODEL

## Introduction

Births and deaths are age-dependent in most species except very simple organisms. It is usually necessary to take account of a population's age structure to get a reliable description of its dynamics. The English biologist P.H.Leslie (1945) introduced a model which uses the age-specific rates of fertility and mortality of a population. He developed the model based on the use of matrices. The matrix form makes the model flexible and mathematically easy to study. This basic model is an increasingly popular tool for describing population dynamics of plants (Usher 1969) and animals (Yu 1990, Crouse 1987). The Leslie matrix model is widely used to project the present state of a population into the future, either as an attempt to forecast the age distribution, or as a way to evaluate life history hypotheses by considering different sets of survival and fecundity parameters.

## Model structure

In the simplest Leslie matrix model (Leslie 1945), only females are considered. The female population can be divided into several categories by age or by size. The classification styles and their differences will be discussed later in this section. If it's grouped by age, the group intervals are supposed to have equal length of time. For example, it may be 5 years for human and 2 years for large whales (Cullen 1985). We assume that the survival and fecundity rates

of each category are constant over time and therefore not dependent on population density.

Define

$n_i(t)$  = the number of females alive in the group  $i$  at time  $t$ ,

$P_i$  = the probability that a female of group  $i$  at time  $t$  will be alive in group  $i+1$  at time  $t+1$ ,

( $t+1$  means  $t$ +one unit of time),  $P_i$  lies between 0 and 1,

$F_i$  = the number of daughters born per female in group  $i$  from time  $t$  to time  $t+1$ ,

let  $i=1,2,\dots,x$ , then

$$n_1(t+1) = F_1 * n_1(t) + F_2 * n_2(t) + \dots + F_x * n_x(t)$$

$$n_2(t+1) = P_1 * n_1(t)$$

$$n_2(t+1) = P_2 * n_2(t) \tag{1.1}$$

...

$$n_x(t+1) = P_{x-1} * n_{x-1}(t)$$

These equations can be represented in matrix form as

$$\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t) \tag{1.2}$$

where  $\mathbf{n}(t)$  is a column vector with components of the number of individuals in each recognized category at time  $t$ .  $\mathbf{A}$  is a nonnegative, square matrix of order  $x$  with all the elements zero except those in the first row and in the subdiagonal immediately below the principal diagonal.

$$A = \begin{bmatrix} F_1 & F_2 & F_3 & \dots & F_{x-1} & F_x \\ P_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & P_2 & 0 & \dots & 0 & 0 \\ 0 & 0 & P_3 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & \dots & P_{x-1} & 0 \end{bmatrix} \quad (1.3)$$

$$0 < P_i < 1 \quad ; \quad F_i \geq 0$$

A is known as the "Leslie matrix" based on age classifications or the "population projection matrix" modeled on stage classifications (Lefkovich 1965, Groenendaeo et al. 1988, Crouse et al. 1987). The projection matrix was introduced by Lefkovich (1965). The stages in the projection matrix model are not necessarily related to age. Its main assumption is that all individuals in a given stage are subject to identical mortality, growth, and fecundity schedules. These matrices are more complicated in appearance than the Leslie matrices, but have almost the same analytical method. Fig. 1.1 shows the life cycle graph depending on different decomposition of the life cycle.

The arrows in the graph indicate the transitions which are possible for an individual from one time to the next. The Leslie matrix corresponding with the life cycle graph (A) in Fig 1.1 is just the same as (1.3) and much simpler than the projection matrix for the stage-classified population, (B) of Fig 1.1, obtained as follows:

$$A = \begin{bmatrix} F_{11} & F_{12} & F_{13} & F_{14} & \cdot & \cdot & \cdot & \cdot & F_{1x} \\ P_{21} & P_{22} & P_{23} & 0 & \cdot & \cdot & \cdot & \cdot & 0 \\ 0 & P_{32} & P_{33} & P_{34} & \cdot & \cdot & \cdot & \cdot & 0 \\ 0 & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & 0 \\ 0 & \cdot & \cdot & \cdot & \cdot & \cdot & P_{x-1 \ x-2} & P_{x-1 \ x-1} & P_{x-1 \ x} \\ 0 & \cdot & \cdot & \cdot & \cdot & \cdot & 0 & P_{x \ x-1} & P_{x \ x} \end{bmatrix} \quad (1.4)$$

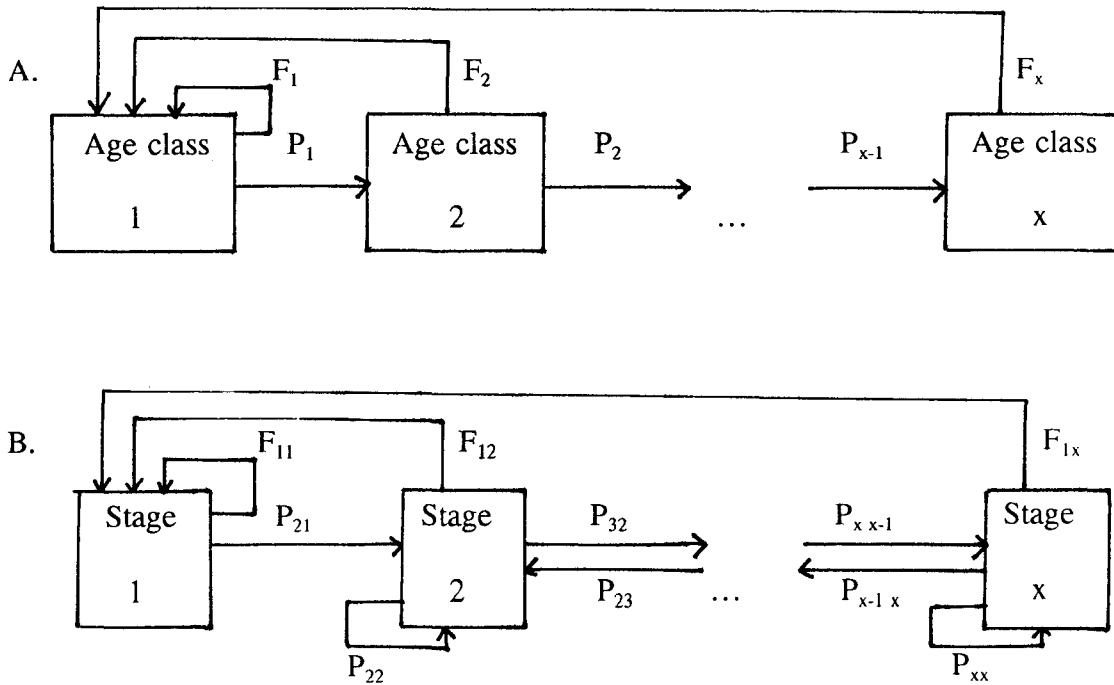


Fig 1.1 Life cycle graphs for two choices of categories. (A) Age-classified population. (B)

One example of stage-classified population.

In the stage-classified model, the possibility of an individual of group  $i$  moving backwards to the previous group, moving forwards to the next group, or staying the same group at next time period is considered.

The choice of categories is a very important step in establishing a population matrix model (Groenendael et al. 1988). Since sometimes it is hard to determine age-specific parameters of the model for some organisms with variable development, stage categories may be more appropriate than age categories (e.g. for turtles, Crouse 1987). For other organisms like mammals and birds, their development is more dependent on age than size and therefore age categories are used frequently.

If age and size are both important and significant interactions exist between them, a two-dimensional model using both stages and age classes simultaneously can be developed (Yu 1990).

In Yu's study, developmental stages are as meaningful as chronological age classes in the corn earworm (CEW) management. He divided the CEW population into five stages and split the first stage into four age groups, the remaining stages into six age groups, except taking the last stage as a single age group. Thus, his projection matrix is a  $23 \times 23$  matrix taking both stage and age into account.

In this project, I will mainly discuss the properties of an age-classified matrix model based on form (1.3). The model has linear, time invariant functions which project the current state of the population into the next state. The female population alone will be considered.



## Parameter estimation

### Survival probability $P_i$

The values of  $P_i$  can be obtained from a life table or experimental data. It is usually assumed that (Leslie 1945, Poole 1974)

$$P_i = \frac{L_{i+1}}{L_i} \quad (1.5)$$

where  $L_i$  = the number alive in the age group  $i$  to  $i+1$  in the stationary or life table age distribution.  $P_i$  is assumed to be constant over a unit of time and not dependent on the total number in the population. Actually, seasonal differences and density dependence of the survival rate do exist, but we assume that they are not significant enough to count.

### Fecundity rates $F_i$

$F_i$  is determined not only by the average number of female births per mother per time period,  $m_i$  in the life table, but also by infant survival rates (Leslie 1945, Groenendael et al. 1988). Populations can be divided into two cases of breeding systems, 'birth-flow' population with continuous reproduction and 'birth-pulse' populations with discrete reproduction (Caughley 1977).

Populations, e.g. human, of the first case produce offspring at a rate almost constant throughout the year and those of the second case produce offspring over a restricted season, e.g.

blue whale. In birth-flow populations, the estimation of  $F_i$  involves integration of continuous fertility and infant mortality functions over the time interval (Leslie 1945).

For birth pulse populations reproduction is during a short period of time per year. It is important to know the exact breeding period with respect to the time step in birth-pulse populations. Two different ways of counting the population, census just before or after reproduction, will influence the estimation of  $F_i$  (Cullen 1985). Some studies count the population just before reproduction and we illustrate that here. Define

$M_i$  = average number of female offspring per female in category  $i$  born between  $t$  and  $t+1$ ,

$S_0$  = the offspring survival rate between birth and the time when they are counted as part of the population,

$$\text{then } F_i = S_0 * M_i \quad i = 1,2,\dots,x \quad (1,6)$$

$F_i$ , the age specific fecundity rate, is assumed to be constant and not dependent on density just as the age specific survival rate,  $P_i$ , is.

## Eigensystem

One advantage of using Leslie matrices is the flexibility of their mathematical formulation. By applying linear algebra techniques to the model, several biological phenomena can be interpreted.

Consider the homogeneous discrete-time system (1.2),  $\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t)$ , where  $\mathbf{A}$  is a square matrix (1.3). If  $\mathbf{A}$  has the formula,

$$\mathbf{A} \mathbf{e}_i = \lambda_i \mathbf{e}_i \quad (1.7)$$

then  $\lambda_1, \dots, \lambda_x$  are called the eigenvalues of  $\mathbf{A}$  with  $|\lambda_1| > |\lambda_2| \geq |\lambda_3| \geq \dots \geq |\lambda_x|$  and  $\mathbf{e}_1, \dots, \mathbf{e}_x$  are the corresponding linearly independent eigenvectors. The eigenvalue  $\lambda_1$  of greatest magnitude is the dominant eigenvalue. Then the solutions to  $\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t)$  have the form (Doucet and Sloep 1992),

$$\begin{aligned} n_1(t) &= a_{11} \lambda_1^t + a_{12} \lambda_2^t + \dots + a_{1x} \lambda_x^t \\ n_2(t) &= a_{21} \lambda_1^t + a_{22} \lambda_2^t + \dots + a_{2x} \lambda_x^t \\ &\dots \\ n_x(t) &= a_{x1} \lambda_1^t + a_{x2} \lambda_2^t + \dots + a_{xx} \lambda_x^t \end{aligned} \quad (1.8)$$

For large  $t$ , although the influence of  $\lambda_{2,3,\dots,x}$  does not necessarily disappear except that their absolute values are smaller than 1, the first term with the dominant eigenvalue will grow faster than the others. Therefore,  $n_i(t)$  will become similar to the single term  $a_{i1} \lambda_1^t$ . Each age class eventually will grow exponentially at the rate of the dominant eigenvalue,  $\lambda_1$ , per time period.

The system (1.2) is asymptotically stable if and only if the eigenvalues of  $\mathbf{A}$  all have

magnitude less than one (Luenberger 1979), that is,  $|\lambda_i| < 1$  for every  $i$ . The state vector  $\mathbf{n}(t)$  will tend to an equilibrium point (the origin) for any initial condition if the system is asymptotically stable. Once the system state vector is equal to an equilibrium point, it will remain equal to that for all future time.

The system is called marginally stable if no eigenvalues have magnitude greater than one but one or more is exactly equal to 1. If unity is an eigenvalue of  $A$ , then the corresponding eigenvector is an equilibrium point. If unity is not an eigenvalue of  $A$ , the origin is the only equilibrium point of the system (Luenberger 1979). Therefore, if unity is the dominant eigenvalue, the state vector eventually will be a specific multiple of the associated eigenvector and won't change in future. It means that population size will remain the same for each age class after it accomplishes that point. When the dominant eigenvalue  $\lambda_1=1$ , we say the population is stationary.

Each eigenvalue defines not only a characteristic growth rate but also a characteristic frequency of oscillation (Luenberger 1979). For a discrete-time system, no oscillations are derived from a positive eigenvalue, in other words, oscillations are due to a negative or complex eigenvalue with period 2 or with a larger period respectively (Doucet et al. 1992).

Some eigenvalue-eigenvector theorems for Leslie matrices are useful in determining the development of a population (Cullen 1985).

- (1) A Leslie matrix has at least one positive real eigenvalue.
- (2) If there are at least two consecutive age classes that are fertile, a positive real dominant eigenvalue always exists.

## Stable age distribution

According to the outstanding properties of the dominant eigenvalue, a population growing based on the Leslie matrix will have an age composition which is entirely determined by its Leslie matrix and does not depend on the initial composition after a period of time. Then from some year on, next year's population will be a multiple of this year's. This age composition is called a stable age distribution.

$$\mathbf{n}(t+1) = \lambda_1 \mathbf{n}(t) \quad (1.9)$$

The multiple  $\lambda_1$  is the dominant eigenvalue of the Leslie matrix  $A$  (1.3) and if  $\mathbf{e}_1$  is the associated eigenvector, the stable age distribution can be obtained from  $\mathbf{e}_1$ . Let

$$\mathbf{e}_1 = \begin{bmatrix} v_1 \\ v_2 \\ \cdot \\ \cdot \\ \cdot \\ v_x \end{bmatrix} \quad (1.10)$$

and  $v = v_1 + v_2 + \dots + v_x$ , then the vector  $\mathbf{S}$  is called the stable age distribution of the population (Cullen 1985).

$$\mathbf{S} = \begin{bmatrix} \frac{v_1}{v} \\ \frac{v_2}{v} \\ \cdot \\ \cdot \\ \cdot \\ \frac{v_x}{v} \end{bmatrix} \quad (1.11)$$

Two different Leslie matrices may have the same  $\lambda_1$  and the same stable age composition, that is, given a value of  $\lambda_1$  and a stable age vector, more than one Leslie matrix can be determined (Pielou 1977). For example,

$$X = \begin{bmatrix} 0.3 & 1.6 & 6.0 \\ 0.5 & 0 & 0 \\ 0 & 0.5 & 0 \end{bmatrix}$$

and

$$Y = \begin{bmatrix} 0.7 & 1.9 & 1.5 \\ 0.5 & 0 & 0 \\ 0 & 0.5 & 0 \end{bmatrix}$$

X and Y both have the same dominant eigenvalue,  $\lambda_1 = 1.5$ , and the same stable vector  $S = [0.69 \ 0.23 \ 0.08]^T$ . Since they are actually unlike, they differ in other eigenvalues.

The approach to S depends on how much larger  $|\lambda_1|$  is than  $|\lambda_2|, \dots, |\lambda_x|$ . The larger the difference between them, the faster the population moves toward stability. Therefore, X and Y have various approaching rates to the stable age composition.

The convergence towards the stable age composition occurs only if  $\lambda_1$  is "strictly" larger than the other eigenvalues. Beginning with an unstable or stable age distribution, a population in an unlimited environment will reach a stable age distribution in time, whether increasing, decreasing, or staying at the same density (Poole 1974). Unfortunately, there is an exception to this rule (Poole 1974, Doucet and Sloep 1992). When there exists one of the negative or complex eigenvalues has the same absolute value as  $\lambda_1$ , the contribution of  $\lambda_1^t$  will never

dominate the other contributions and the population will oscillate forever. This happens when the entries of the first row of Leslie matrix are all zero except the rightmost one. For example (Poole 1974),

$$A = \begin{bmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{bmatrix}$$

The eigenvalues of A are

$$\lambda_1 = 1 \quad \lambda_{2,3} = -\frac{1}{2} \pm \frac{\sqrt{3}}{2} i$$

and

$$|\lambda_1| = |\lambda_2| = |\lambda_3|$$

The dominant eigenvalue is 1, so the population will neither increase or decrease as a trend.

Note that

$$A^2 = \begin{bmatrix} 0 & 3 & 0 \\ 0 & 0 & 2 \\ \frac{1}{6} & 0 & 0 \end{bmatrix} \quad A^3 = I$$

$$A^4 = A \quad A^5 = A^2 \quad A^6 = I$$

and so forth. The population will oscillate with period 3 time units and never approach stability unless it begins with a stable age distribution.

## Application and Generalization

In the original Leslie matrix model, the last age class is assumed to be removed from the population after a time unit. So the entry with row  $x$  and column  $x$  is 0 in the matrix (1.3). Actually, individuals in the last age class may not die after one time unit and their survival probability and fecundity rate will just stay the same until they die. It indicates that we allow members of the last group to live and reproduce for some years. Besides, older individuals are assumed to be essentially the same as those of the last age group. Let

$P_x$  = the probability that an individual of group  $x$  at time  $t$  will alive and stay in the group  $x$  at time  $t+1$ .

Then the Leslie matrix can be written as

$$A = \begin{bmatrix} F_1 & F_2 & F_3 & \cdot & \cdot & \cdot & F_{x-1} & F_x \\ P_1 & 0 & 0 & \cdot & \cdot & \cdot & 0 & 0 \\ 0 & P_2 & 0 & \cdot & \cdot & \cdot & 0 & 0 \\ 0 & 0 & P_3 & \cdot & \cdot & \cdot & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \cdot & \cdot & \cdot & P_{x-1} & P_x \end{bmatrix} \quad (1.12)$$

and the last equation of (1.1),  $n_x(t+1) = P_{x-1} n_{x-1}(t)$ , is replaced by

$$n_x(t+1) = P_{x-1} n_{x-1}(t) + P_x n_x(t)$$

which is an aggregation of all remaining age classes.



The basic Leslie matrix model is a deterministic model. The parameters, survival and reproductive rates, are constant over time. In real population, those parameters may change with many factors. In the cases of human population, the survival rates, especially among the elderly, will change with new medical advances or better feeding habits, and the fecundity rates will be affected by changing social attitudes toward marriage and family. The effect of harvest and seasonal differences on survival probabilities should be considered for animal or plant populations. If the parameter values for years are randomly generated from a specific probability distribution, the model will be stochastic.

Only females are considered in Leslie's model (1945). In bisexual populations, the basic model can be modified to keep track of both sexes (Pielou 1977, Cullen 1985). The Leslie matrix in its classical form makes no allowance for density dependent population growth and it is fundamentally linear. Considering the effect of density dependence on fertility and survival rates will turn the model into a nonlinear one (Pielou 1977). The size of the current population will play an important role in determining those parameters and the initial size has a lasting effect on the population's future chances of reproducing and surviving.

# APPLICATION

## TO EASTERN WILD TURKEY IN IOWA

### Introduction

The eastern wild turkey (*Meleagris gallopavo silvestris*), one of five subspecies, inhabits roughly the eastern half of the United States. Turkey hunting has a substantial economic effect in many rural communities. It not only brings in revenue because of the actual turkey hunting, but it also enhances the development of the related industries of turkey-hunting clothes and equipment. Improvement of the knowledge of turkey population dynamics is important to formulate hunting regulations and other turkey management practices.

Much research about the rates of reproduction, mortality, and survival, and the movement of wild turkeys has been done (Dickson 1992). However, there were few models established for evaluating turkey populations. For a specific combination of survival and reproductive rates, a model may tell us whether a wild turkey population will grow, decline, or remain stable. The survival rates will obviously also depend on the level of harvest. By changing the harvest level we can see the effect on the population size and consider changes to the hunting regulations and enhance the management of wild turkeys.

A Leslie matrix model is developed for the population dynamics of eastern wild turkeys in Iowa. The parameters used in the model are based on Iowa wild turkey studies (Suchy et al.

1983, Dickson 1992), and the population characteristics will be interpreted by the model analysis.

## Objectives

1. To build a model in order to predict the population size and age structure of Iowa wild turkeys in the future.
2. To see the effect of harvest level (percent of total population) on the population age structure and growth.
3. To find the most appropriate wild turkey hunting seasons.

## Model structure

An age-classified model is built here. There could be several stages in the age structure of the wild turkey population. A three-stage model is chosen in order to simplify the modeling procedure. The first category is "poults", aged from 0 to 1, the second category is "yearlings", aged from 1 to 2, and the last category is "adults", aged 2 and older. Reproduction occurs from yearlings onwards. The time unit is one year. Only females are considered in this model.

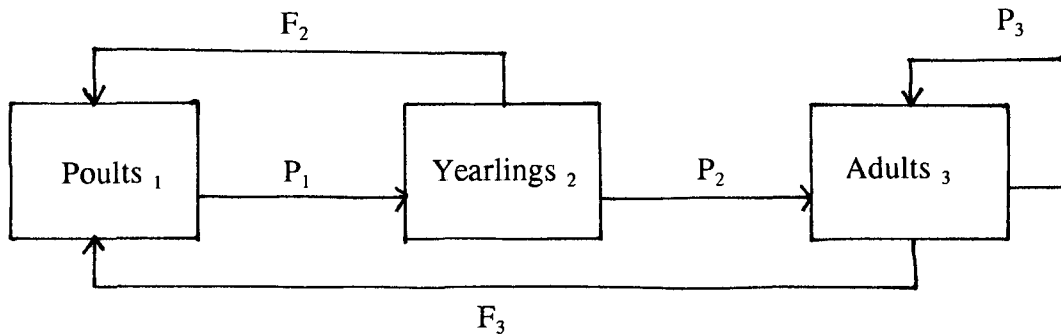
Let

$P_i$  = the probability that a female of group  $i$  at time  $t$  will be alive in group  $i+1$  for  $i=1,2$  or will stay in group  $i$  for  $i=3$  at time  $t+1$ .

$F_i$  = the number of daughters born per female in group  $i$  from time  $t$  to time  $t+1$ .

$i = 1, 2, \text{ or } 3.$

The life cycle graph is as follows,



The state variables are the numbers of poults, yearlings, and adults, denoted as  $n_1$ ,  $n_2$ , and  $n_3$  respectively. Then,

$$\begin{aligned}
 n_1(t+1) &= F_2 n_2(t) + F_3 n_3(t) \\
 n_2(t+1) &= P_1 n_1(t) \\
 n_3(t+1) &= P_2 n_2(t) + P_3 n_3(t)
 \end{aligned}
 \tag{2.1}$$

A matrix form can be derived from those equations.

$$\mathbf{n}(t+1) = A \mathbf{n}(t)
 \tag{2.2}$$

i.e.

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \end{bmatrix} = \begin{bmatrix} 0 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} * \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \end{bmatrix}
 \tag{2.3}$$

The Leslie matrix A, a square matrix of order 3, is defined in this three-age-class model as

$$A = \begin{bmatrix} 0 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} \quad 0 < P_1, P_2, P_3 < 1 \quad F_2, F_3 > 0 \quad (2.4)$$

Estimating parameters annually we overlook some complications, for example, different mortality rates in different seasons. A number of studies on estimating the survival and reproductive processes were well done for wild turkeys. It is not too hard to estimate the parameters,  $P_i$  and  $F_i$ , to use in the model. This is the reason why an age-classified model is chosen rather than a stage (size)-classified model in this project.

### Assumptions

The basic assumptions are as follows:

1. The survival and reproductive rates are constant over time within each age-class and are therefore not dependent on population density.
2. The individuals in each group always go to next group from one time to the next except those in the last age-class which may stay for some years before they die.
3. The conditions of each individual in the same stage are similar, that is, all individuals in that stage have the same survival and reproductive rates.

In practice survival and fecundity do vary from year to year due to environmental factors. If the Leslie model is still applied using averages there is a degree of approximation involved. In practice survival and fecundity may also be density dependent.

## Parameter estimation

### Survival probability $P_i$

The survival rates are derived from a study on Iowa wild turkey populations (Suchy's et al. 1983).

$$\begin{aligned}P_1 &= 0.445 \\P_2 &= 0.616 \\P_3 &= 0.610\end{aligned}$$

They are the average estimates of the data from 1977 to 1981.

### Fecundity rates $F_i$

From Dickson (1992), some information about Iowa turkey populations is important for estimating the reproductive rates. Estimates of nesting and renesting rates (Table 2.1) indicates that a higher proportion of adult hens attempt to nest. Clutch size (Table 2.2) is also larger for adult hens than for yearlings. Since reproduction starts from yearling-stage, the value of  $F_1$  is zero.

Recall that  $F_i$  should be determined not only by the number of daughters born per female per time period but also by infant survival probabilities (hatching success).

$$\text{Hatching success} = \frac{\text{number eggs hatching}}{\text{clutch size}} = 0.85$$

*for successful nests.*

Table 2.1 Nesting rates and nest success for Iowa wild turkey hens. (Dickson 1992)

	First nest		Renest	
	nesting rate	nest success	re nesting rate	nest success
yearling	0.42	0.56	0.12	0.00
adults	0.97	0.38	0.32	0.52

Table 2.2 Clutch size for Iowa wild turkey hens. (Dickson 1992)

	clutch size	
	First nest	Renest
yearlings	8.8	7.0
adults	9.4	9.1

Using the values in Table 2.1, Table 2.2, and the hatching success,  $F_2$  and  $F_3$  can be estimated as follows,

### F<sub>2</sub> estimation

$$\begin{aligned} F_2 &= \frac{\text{number of female poults}}{\text{number of females}} \\ &= \frac{\text{number of female eggs}}{\text{number of females}} * \frac{\text{number of female poults}}{\text{number of female eggs}} \\ &= \frac{\text{female eggs of first nesting} + \text{female eggs of renesting}}{\text{number of females}} \\ &\quad * \frac{\text{number of female poults}}{\text{number of female eggs}} \\ &= \frac{(0.42) (0.56) (1) \left(\frac{8.8}{2}\right) + 0}{1} * 0.85 \\ &= 0.880 \end{aligned}$$

### F<sub>3</sub> estimation

Use the similar way as above.

$$\begin{aligned} F_3 &= \frac{(0.97) (0.38) (1) \left(\frac{9.4}{2}\right) + (0.97) (0.62) (0.32) (0.52) (1) \left(\frac{9.1}{2}\right)}{1} * 0.85 \\ &= 1.860 \end{aligned}$$

Therefore, the original Leslie matrix of Iowa wild turkey population in this project is obtained.

$$A = \begin{bmatrix} 0 & 0.880 & 1.860 \\ 0.445 & 0 & 0 \\ 0 & 0.616 & 0.610 \end{bmatrix} \quad (2.5)$$



# Result and discussion

## 1. Stability

I used a FORTRAN program to find eigenvalues and eigenvectors of the Leslie matrix  $A$ . The initial values of state variables are

$n_1(0)$  = the initial number of female poults in the population = 580.00

$n_2(0)$  = the initial number of female yearlings in the population = 122.70

$n_3(0)$  = the initial number of female adults in the population = 156.10

which are the 1977-78 data derived from Suchy et al. (1983). For the original matrix (2.5), eigenvalues are  $\lambda_1=1.15$ ,  $\lambda_{2,3}=-0.27\pm 0.40i$  and  $|\lambda_1|=1.15>1$  which show that the population is unstable. Actually, some parameters will fluctuate at random in the real situation. For example, nest success fluctuates widely from year to year in weather conditions or rainfall (Dickson 1992). To study the sensitivity of the model to individual parameter values and to manage the turkey populations, I will change the parameter values one by one until I get the stable situation. I emphasize that this is done to investigate model properties but sometimes the results may not be biologically reasonable. Let  $\lambda_1$  be the dominant eigenvalue.

Case1 The adult reproductive rate,  $F_3$ , is decreased from 1.86 to 0.80. The Leslie matrix changed to be

$$A = \begin{bmatrix} 0 & 0.880 & \mathbf{0.800} \\ 0.445 & 0 & 0 \\ 0 & 0.616 & 0.610 \end{bmatrix}$$

Then eigenvalues are  $\lambda_1=0.999$ ,  $\lambda_2=0.05$ ,  $\lambda_3=-0.42$ ,  $|\lambda_i| < 1$ . It is asymptotically stable.

In this case, a big change in  $F_3$  is required to obtain the stable situation.

Case2 The poult survival rate,  $P_1$ , is decreased from 0.445 to 0.260. Other parameters remain the same values as in the original matrix. That is

$$A = \begin{bmatrix} 0 & 0.880 & 1.860 \\ \mathbf{0.260} & 0 & 0 \\ 0 & 0.616 & 0.610 \end{bmatrix}$$

The eigenvalues of this model are  $\lambda_1=0.998$ ,  $\lambda_{2,3}=-0.19 \pm 0.35i$  and  $|\lambda_i| < 1$ . It is a stable system.

Case3 The yearling survival rate,  $P_2$ , is decreased from 0.616 to 0.28. Other parameters remain the same values as in the original matrix. Then  $\lambda_1=0.996$ ,  $\lambda_2=0.02$ ,  $\lambda_3=-0.40$ .

Case4 The adult survival rate,  $P_3$ , is decreased from 0.61 to 0.15. Other parameters remain the same values as in the original matrix. Then  $\lambda_1=0.997$ ,  $\lambda_{2,3}=-0.42 \pm 0.52i$ .

Case5 It's hard to get a stable state if only  $F_2$  is decreased.  $|\lambda_1|$  is still bigger than 1 when  $F_2$  had been decreased to 0.01 which is too small for the yearlings fertility.

Case6 I tried to change both  $F_2$  and  $F_3$  simultaneously. Then when  $F_2$  is reduced from 0.88 to 0.40 and  $F_3$  is changed from 1.86 to 1.13,  $\lambda_1=0.999$ ,  $\lambda_{2,3}=0.19 \pm 0.41i$ . This is more biologically reasonable than case 1. There are several ways to change the values of  $F_2$  and  $F_3$  in this case.

In case1,2,3,4, and 6, the absolute values of  $\lambda_i$  are less than one. Those systems are asymptotically stable and because unity is not an eigenvalue of  $A$ , the origin is the only equilibrium point of system. The population is going to be extinct after a long run.

If unity is the dominant eigenvalue of A, instead of going to be extinct, the population will eventually achieve a stable age distribution, which is proportional to the corresponding eigenvector of unity. This situation is called the marginal stability. In order to get the marginal stability, I change the parameter values one by one again from the original matrix (Table 2.3).

Table 2.3 The eigenvalues of marginally stable populations obtained by adjusting parameters separately

	original value	modified value	$\lambda_1$	$\lambda_2$	$\lambda_3$
P <sub>1</sub>	0.445	0.261928	1	-0.195 + 0.3485i	-0.195 - 0.3485i
P <sub>2</sub>	0.616	0.286669	1	-0.394	0.004
P <sub>3</sub>	0.610	0.16196	1	-0.419 + 0.52i	-0.419 - 0.52i
F <sub>3</sub>	1.860	0.86559	1	-0.394	0.004

## 2. Sensitivity Analysis

I used the change of the total population size based on the change of the parameter as an indication of parameter sensitivity. If  $Q(p)$  means the total population size ( $Q$ ) is a function of the parameter ( $p$ ), then for example,

$$5\% \text{ sensitivity of } Q \text{ to } p = \frac{Q(p+5\%p) - Q(p-5\%p)}{2 \cdot 5\% \cdot Q(p)}$$

Table 2.4 shows that  $P_1$ , the poult survival rate, is the most sensitive parameter. In Suchy et al. (1983), they reasoned that the most sensitive parameters would be those that produced a stationary population with the smallest change in parameter value. Recall the data in Table 2.3.

Table 2.4 The 5%, 10%, and 15% sensitivities of the total population size to each parameter

Parameters	Sensitivities		
	5 %	10 %	15 %
$P_1$	1.4359	1.4361	1.4364
$P_2$	0.9627	0.9627	0.9627
$P_3$	1.0219	1.0240	1.0275
$F_2$	0.4873	0.4873	0.4875
$F_3$	1.0930	1.0930	1.0930

A decrease of 41% in poult survival rate ( $P_1$ ) is the smallest reduction of all parameters to produce stationary populations. So  $P_1$  should be the most sensitive parameter which is shown in Table 2.4. Changes in survival rates of female poults have a great effect on the population's net rate of change. The fecundity rate of adults is the second most sensitive parameter.

### 3. Stable age distribution

Recall that any population beginning with an unstable or stable age distribution will reach a stable age composition in time, the exception being a matrix with the first row which only has one nonzero entry at the rightmost position. Fortunately, the turkey model is not that kind of matrix and it will come to a stable age distribution sooner or later depending on the differences between the dominant eigenvalue and the other ones.

For the unstable, original matrix, the dominant eigenvalue is 1.1533 and the corresponding eigenvector is  $[1.26 \ 0.486 \ 0.551]^T$ . Then the stable age distribution is  $S=[0.55 \ 0.21 \ 0.24]^T$ . Fig 2.1 shows the simulation of 15 years. Although the population keeps growing, the age composition reaches a constant ratio after nine years and won't change in the future.

One asymptotically stable system is chosen (case 2) to do the simulation of forecasting the population size.

$$A = \begin{bmatrix} 0 & 0.880 & 1.860 \\ \mathbf{0.250} & 0 & 0 \\ 0 & 0.616 & 0.610 \end{bmatrix}$$

Fig 2.2 shows the result of fifteen-year simulation. After a short period (within five years) of oscillation, the age distribution reaches stability although the population is decreasing.

We are interested in the stationary situation. When the dominant eigenvalue becomes one, not only the age composition approaches a stable state but also the population size won't change eventually. Then the population will never overgrow or die out. Pick the stationary cases I have run before and do the simulation for each one. Fig 2.3, 2.4, 2.5, 2.6 show the result of those marginally stable systems gotten by adjusting  $P_1$ ,  $P_2$ ,  $P_3$ ,  $F_3$  respectively. There are oscillations in all of them but it does not take a long time.

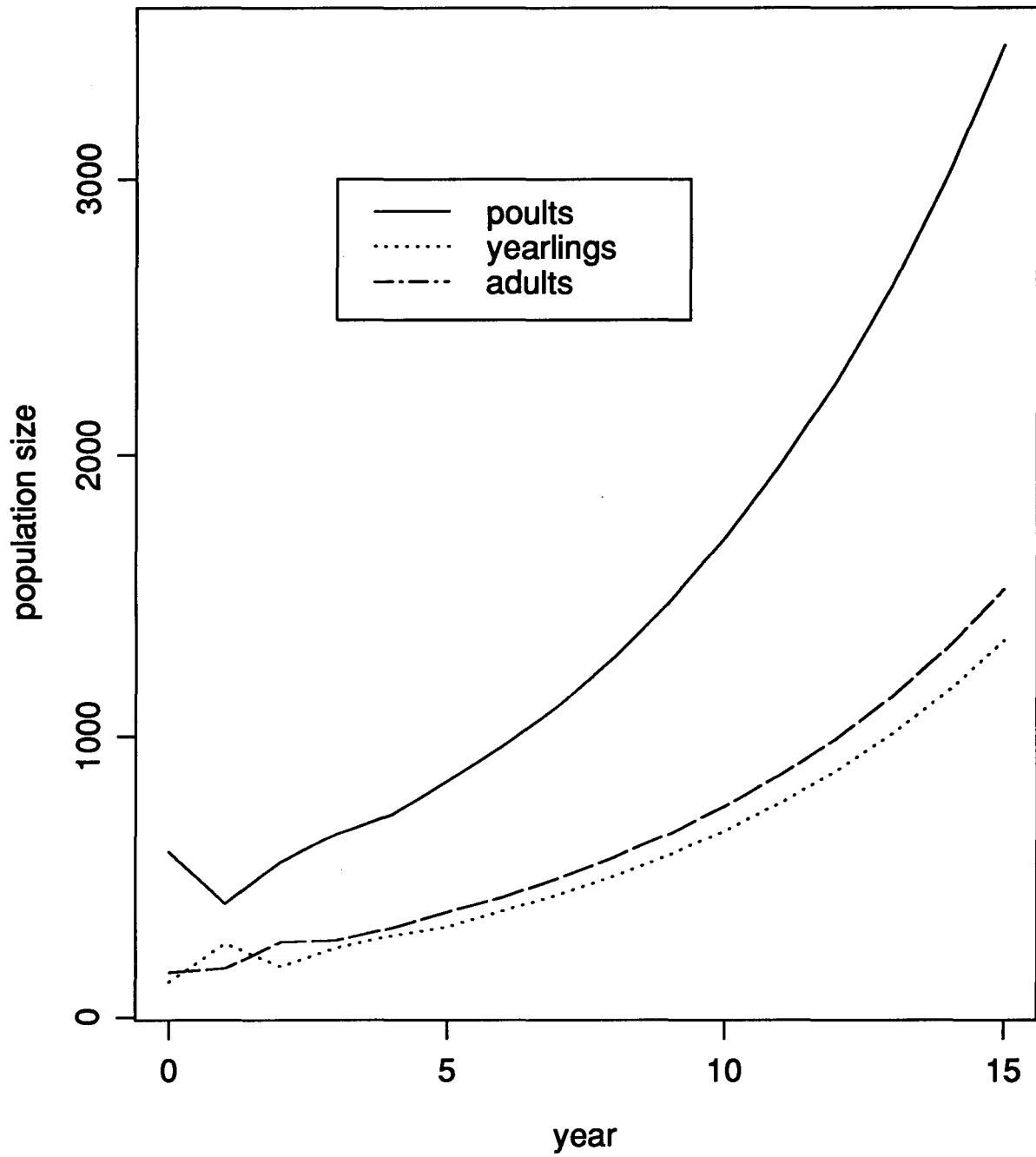


Fig 2.1 Simulation of original population model

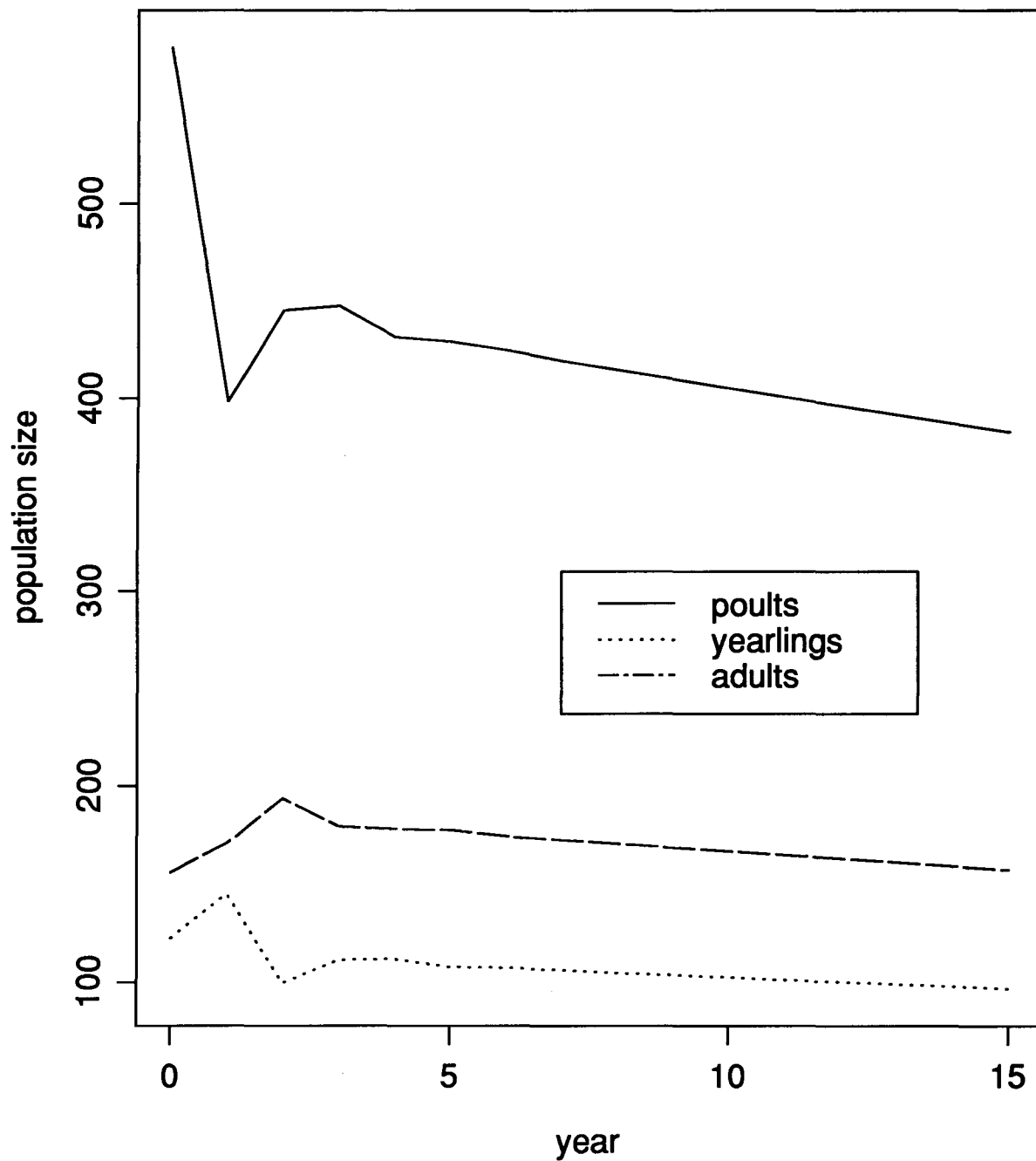


Fig 2.2 Simulation of the asymptotically stable population model obtained by adjusting P1

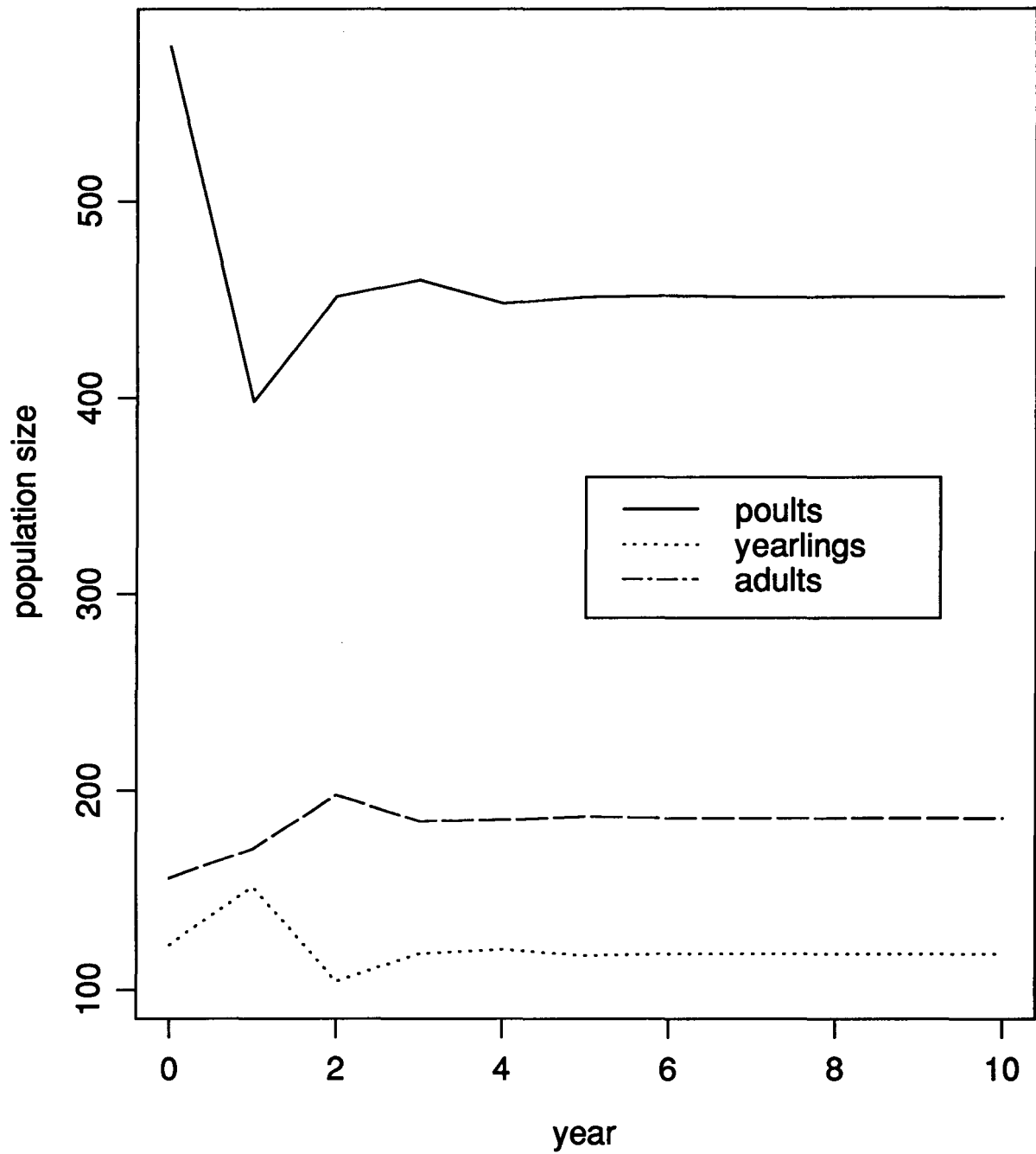


Fig 2.3 Simulation of the stable population model obtained by adjusting P1



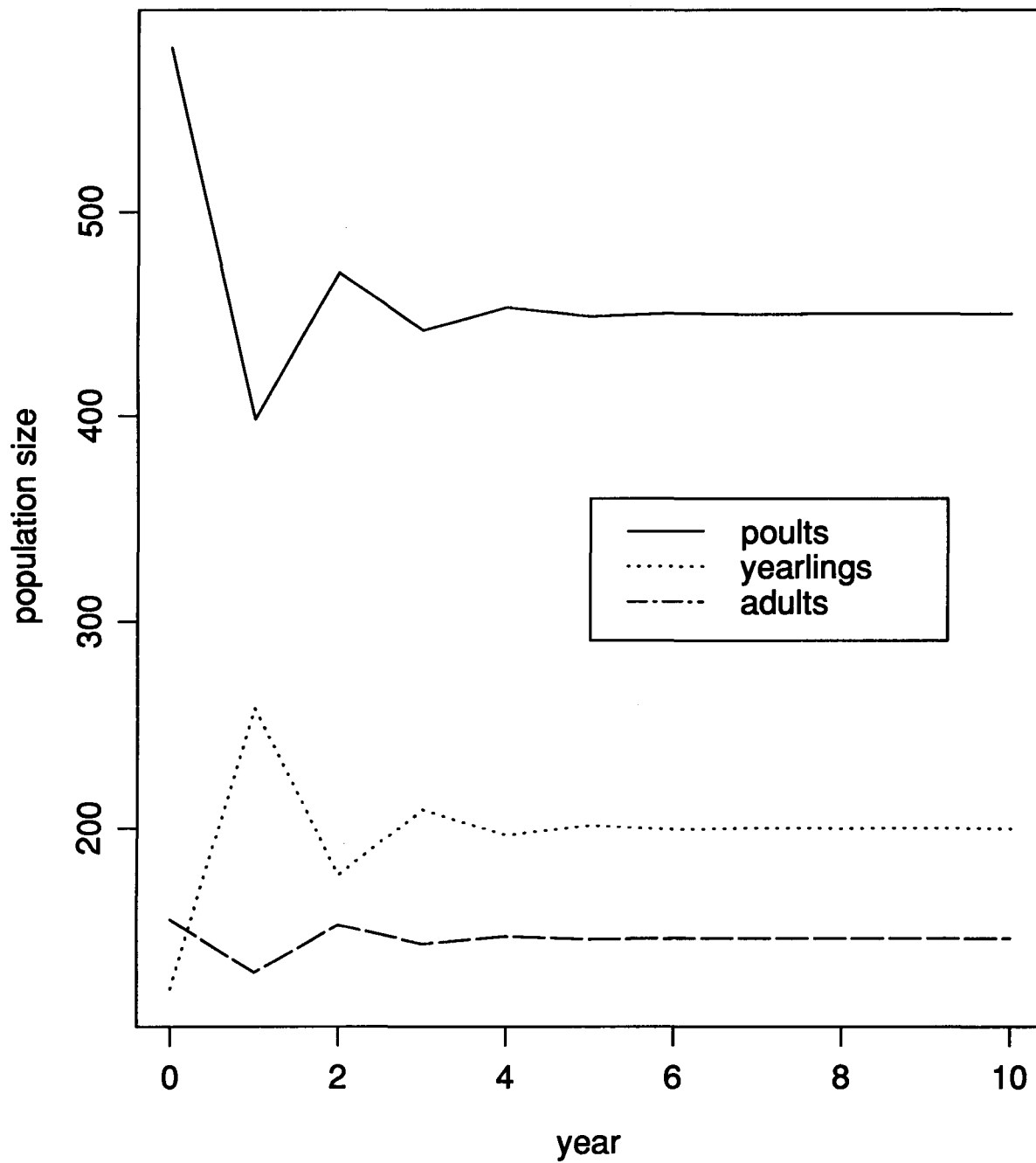


Fig 2.4 Simulation of the stable population model obtained by adjusting P2

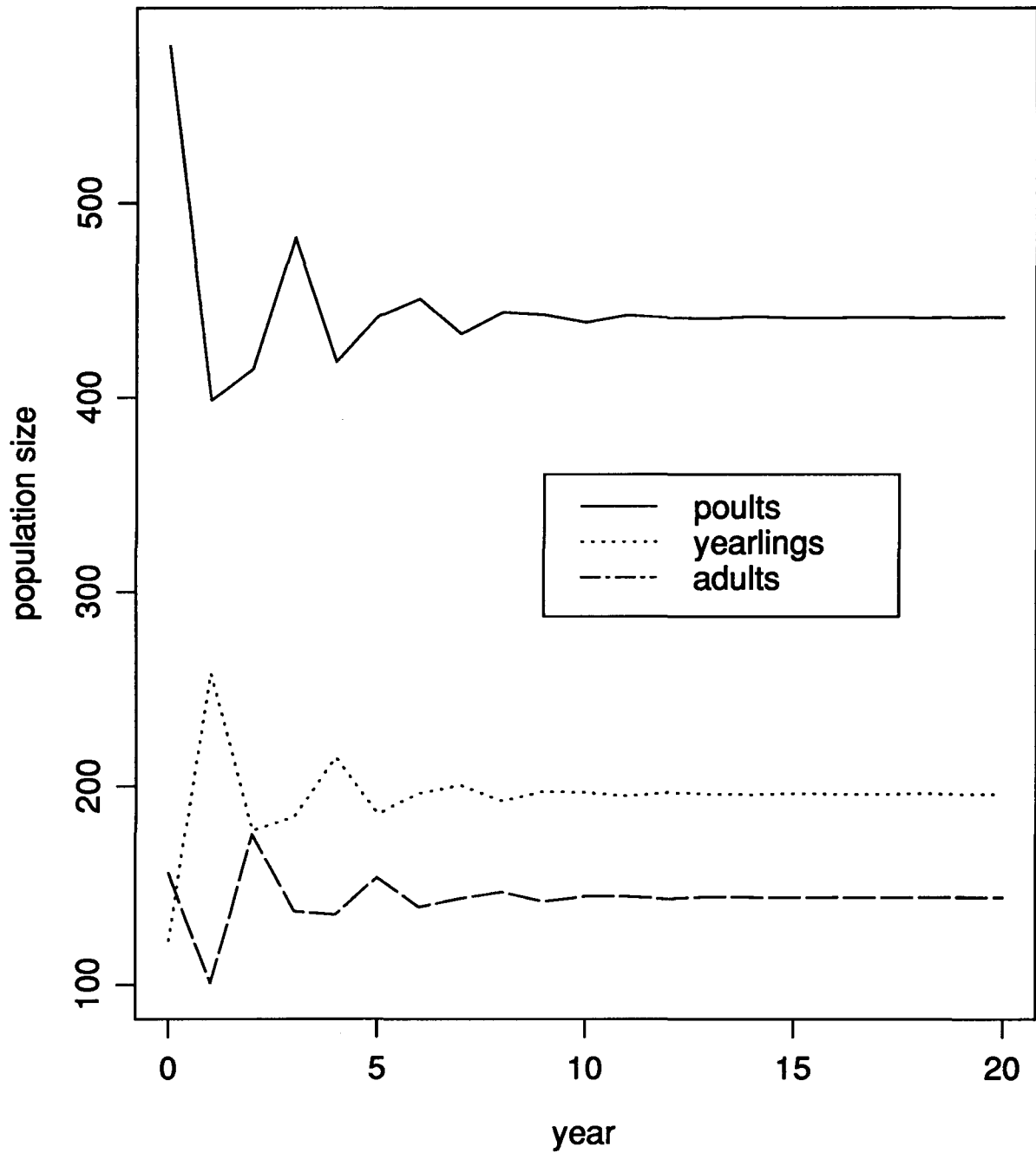


Fig 2.5 Simulation of the stable population model obtained by adjusting P3

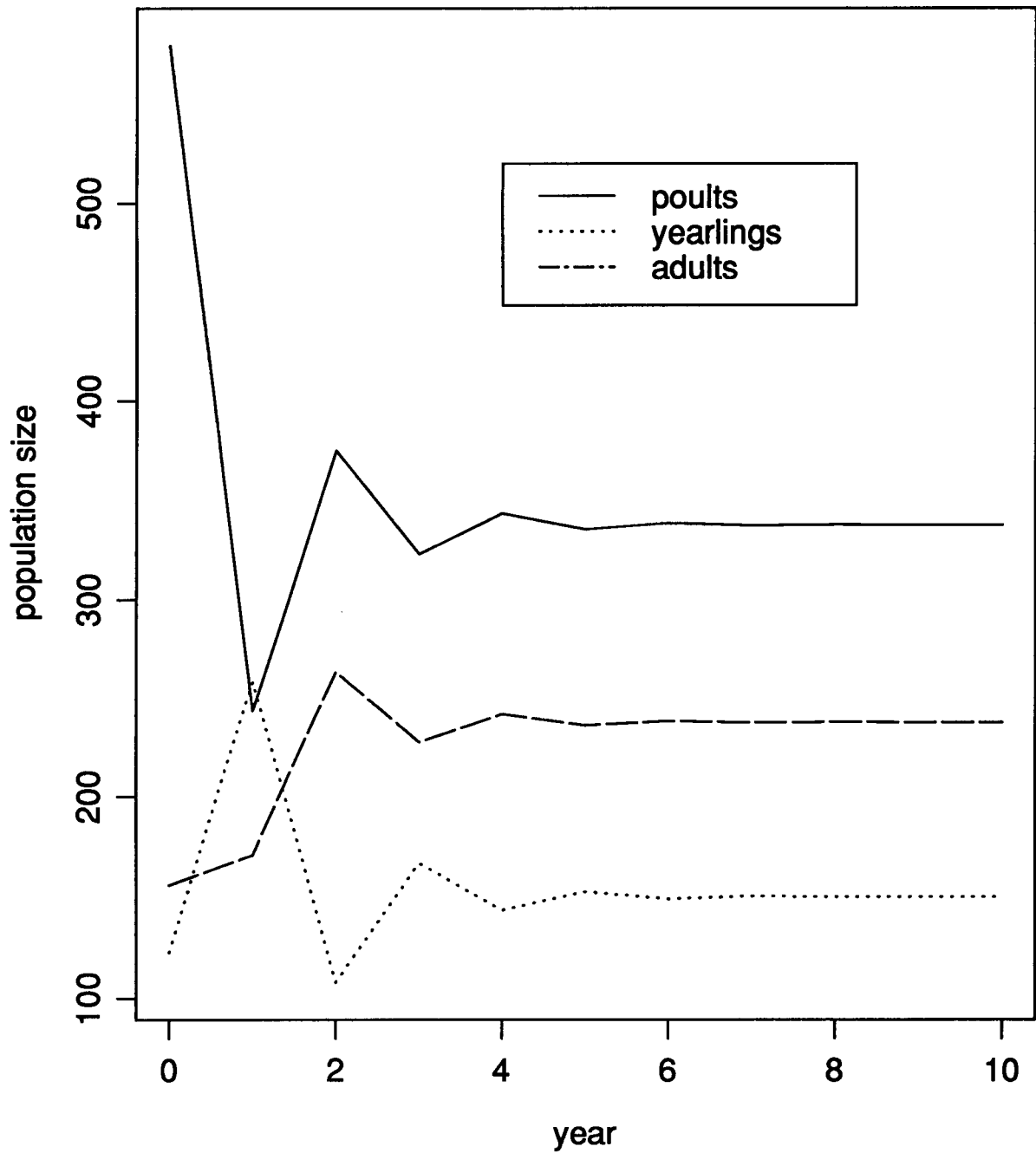


Fig 2.6 Simulation of the stable population model obtained by adjusting F3

#### 4. The effect of harvest

Harvest will influence the parameters in yearlings and adults stages directly and in poults stage indirectly. We assume that only the survival probabilities of yearlings and adults are affected by the harvest level which is defined as the percentage of the total population. Only fall hunting seasons are considered because the model is for female populations and it's usually only males can be hunted in the spring seasons. Data from the book named "The Wild Turkey" (Dickson 1992) suggests possible reductions in  $P_2$  and  $P_3$  due to harvest (Table 2.5).

Table 2.5 The survival rates of adult hens and yearling hens for different fall harvest level

Fall harvest level ( % of Total population)	Survival rates	
	female adults ( $P_3$ )	female yearlings ( $P_2$ )
5	0.610	0.596
10	0.579	0.550
15	0.551	0.508
20	0.523	0.466

I changed the parameters of the original matrix based on this possible effect of harvest and tried to figure out the trend. According to the different harvest level,  $P_2$  and  $P_3$  are replaced by the values in the table. Then the dominant eigenvalue is decreasing with the increase of harvest level (Table 2.6).

Table 2.6 The eigenvalues of different turkey systems based on the original Leslie matrix according to different harvest levels

Harvest level	$\lambda_1$	$\lambda_{2,3}$
5	1.146	$-0.268 \pm 0.388i$
10	1.114	$-0.268 \pm 0.365i$
15	1.085	$-0.267 \pm 0.342i$
20	1.056	$-0.267 \pm 0.317i$

These results are surprising and suggest some inadequacy of our model because when the 20 percent of total population is removed by hunting one might expect the population size should be smaller and smaller, that is, the dominant eigenvalue should be smaller than 1. The result didn't tell us that. Maybe it is because the model is too simple or there is something wrong with our parameter estimation. As it has been mentioned before, the survival and fecundity rates will vary from time to time depending on many factors, like weather condition. Among those parameters, the survival rate of poults,  $P_1$ , will change much widely than the others. So  $P_1$  is chosen to be adjusted to do some more analysis. If  $P_1$  changed from 0.445 to 0.330, the result of simulation will be as follows (Table 2.7).

Table 2.7 The eigenvalues of turkey populations based on the modified matrix by changing  $P_1$  according to different levels of harvest

Harvest level	$\lambda_1$	$\lambda_{2,3}$
5	1.0549	$-0.2224 \pm 0.3597i$
10	1.0241	$-0.2226 \pm 0.3405i$
15	0.9957	$-0.2223 \pm 0.3209i$
20	0.9669	$-0.2219 \pm 0.2992i$

This result perhaps looks more plausible than the previous one. The dominant eigenvalue starts to be below than 1 when the harvest level is 15, 15 percent turkeys of the whole population have been hunted.

## Future work

This turkey model is very simple. The turkey population is a complicated system. There are too few parameters in the model to properly describe the complexity of a real turkey population. The matrix is extensible and more parameters can be added to the model. Interactions between those parameters could be considered or the whole population may be divided into more stages. For example, if the time unit is six months, each stage can be divided into two groups. Then the new model will have twice as many as stages the old model has and the parameter estimates will be more reliable because of less environmental variation. The Leslie matrix  $A$  would be extended to be  $6 \times 6$ .

In a real turkey population, the number of each group will affect the survival and fecundity rates of the population. The influence of density may not be ignored. If a model takes account of the effect of density dependence on the survival and fecundity rates, then the model will be a nonlinear model.

Another way to make the model powerful is to allow stochasticity. The Missouri Model in the book (Dickson 1992) used a stochastic model. In that model, if the data of those parameters which can be estimated from a radio-marked sample of wild turkeys for specific years is inputted, then the parameters are randomly generated from a uniform distribution within the 95 percent confidence interval around the mean of each parameter value for the data years. This makes the model stochastic.

Another type of future work would be to consider survival as different functions of harvest rate. The functions could be constructed to reflect additivity of hunting and natural mortality as some degree of compensation (i.e. as hunting mortality increases perhaps natural mortality decreases to some extent). This is a very complex topic beyond the scope of this project.

# LITERATURE

- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons Ltd, New York, N.Y. 234pp.
- Crouse, D.T., L.B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* 68:1412-1423.
- Cullen, M.R. 1985. Linear models in biology. Ellis Horwood Ltd, England. 213pp.
- Dickson, J.G. 1992. The wild turkey: biology and management. Stackpole Books. Harrisburg, PA. 463pp.
- Doucet, P., and P.B. Sloep. 1992. Mathematical modeling in the life sciences. Ellis Horwood Ltd, England. 490pp.
- Groenendael, J.van, H. de Kroon, and H. Caswell. 1988. Projection matrices in population biology. *Trends in Ecology and Evolution* 3, 264-269.
- Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. *Biometrics* 21, 1-18.
- Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33: 183-212.
- Luenberger, D.G. 1979. Introduction to dynamic systems: theory, models and applications. John Wiley & Sons, New York, N.Y. 446pp.
- Pielou, E.C. 1977. Mathematical ecology. John Wiley & Sons, Inc., New York, N.Y. 385pp.
- Poole, R.W. 1974. An introduction to quantitative ecology. McGraw-Hill, Inc., New York, N.Y. 532pp.



Suchy, W.J., W.R. Clark, and T.W. Little. 1983. Influence of simulated harvest on Iowa wild turkey populations. *Proc. Iowa Acad. Sci.* 90:98-102.

Usher, M.B. 1969. A matrix model for forest management. *Biometrics* 25, 309-315.

Yu, Y. 1990. A Leslie model, threshold function and uncertainty for chemical control of corn earworm. Ph.D. Thesis. North Carolina State University. Raleigh, N.C. 148pp.