

Modeling Population Dynamics

Gary C. White

INTRODUCTION

Population modeling is a tool used by wildlife managers. At its simplest, population modeling is a book keeping system to keep track of the four components of population change: births, deaths, immigration, and emigration. In mathematical symbolism, a population model can be expressed as

$$N_{t+1} = N_t + B_t - D_t + I_t - E_t .$$

Population size (N) at time $t+1$ is equal to the population size at time t plus births (B) minus deaths (D) plus immigrants (I) minus emigrants (E). The simplicity of the relationship belies its usefulness. If you were managing a business, you would be interested in knowing how much money was being paid out of the business, relative to how much money was coming in. The net difference represents your “profit”. The same is true for managing a wildlife population. By knowing the net change in the size of the wildlife population from one year to the next, you as a wildlife manager know whether the population is “profitable” (i.e., gaining in size), or headed towards bankruptcy (i.e., becoming smaller).

Two examples will demonstrate typical uses of population models in big game management. In November 1995, voters in Colorado passed an amendment to the state’s constitution that outlawed hunting black bears during spring. Wildlife managers were asked if the bear population would increase because of no spring harvest. A population model can be used to answer this question. The second example of the use of a model is to determine which of two management schemes (e.g., no antlerless harvest versus significant antlerless harvest) will result in

the largest buck harvest in a mule deer population. Both of these examples require specific information to answer the questions posed. The models in both cases are important in conceptualizing the problem, and in defining exactly what information is needed to answer the question.

The main use of the model in the previous examples is to predict the result of some management action; such as stopping spring bear hunting, or implementing an antlerless harvest. Another use of population models is to conceptualize the dynamics of a population in a rigorous mathematical notation. Such a conceptual model allows biologists to think more clearly about the dynamics of a population. A third use of models is to test hypotheses about population dynamics from observed data. For example, biologists might entertain competing models, one based on density independence, the other with density dependence. Which of these models best explains our observations of a mule deer population?

Computational tools are needed to build population models on a computer. Spreadsheets are a natural vehicle to build population models. They were developed for modeling the functioning of a business (i.e., keeping track of income and outflow) and hence are particularly suited for modeling population dynamics. Modern spreadsheets include a natural language to specify a population model, graphics to display the results, random number functions to model stochasticity, and optimization functions useful in optimizing some attribute of the model's output (e.g., annual harvest), or in estimating parameter values from data. Complex models can be built (Lubow et al. 1997) and then made available via the WWW (see <http://www.cnr.colostate.edu/~bruce/software.htm> for these spreadsheet models of linked-sex harvest strategies.

A major advantage of using spreadsheets to develop the model is that you fully understand the mechanics of the model you've developed. You know what relations are assumed in the model because you put them in the model. As a user of another's model, spreadsheet models allow you to dissect the model to see what relations were programmed. Most of the earlier models of population dynamics were built with pre-defined models, such as ONEPOP (Gross et al. 1973) and later POP-II (Bartholow 1992). I describe these models as black box models, because as both a model developer and a model user, you are not quite sure what is in the model. You can not peer into the black box of a model to see the inner workings. Even if you can study the computer code, the coding is arcane enough to make interpretation challenging. Further, the limitations of the original model framework limit what you could do with your model. Thus, spreadsheets provide openness and flexibility not provided by black box models.

The goal of this chapter is to show how to develop and use population models with spreadsheet software such as Quattro©, Lottus©, or Excel©. At an elementary level, density-independent versus density-dependent population growth models will be compared. Still at an elementary level, I will describe models that incorporate density dependence into an age-structured model. At a more advanced level, sources of stochasticity in population dynamics will be acknowledged, and I will develop stochastic models to mimic this observed variation in the data. Finally, spreadsheets will be used to fit models and estimate parameters from observed data on populations. To fully understand the last two topics, deeper training in mathematics and statistics will be required. After all, population modeling is a quantitative subject.

DENSITY-INDEPENDENT POPULATION GROWTH

Density-independent population growth is based on the concept that the population grows at the same rate, no matter how large or small it has become. With the big game populations considered here, population growth generally is not continuous as in bacteria or protozoans. Rather, a birth pulse takes place at a defined time of year. Thus, I will build models based on difference equations, as opposed to differential equations that assume continuous population growth (See Box 1). To define density-independent population growth with a difference equation, assume that the population always increases by $1 + R$ times each year. That is,

$$N_{t+1} = N_t + N_t \times R = N_t \times (1 + R) ,$$

so that

$$N_t = N_0 (1 + R)^t.$$

Finite rate of growth (R) is composed of all the processes that change the population size(i.e.,

$$R = \text{finite birth rate} - \text{finite death rate} + \text{finite immigration rate} - \text{finite emigration rate}.$$

Box 1. The differential equation for density-independent population growth is given by

$$\frac{dN}{dt} = rN .$$

With integration, $N_t = N_0 e^{rt}$ where $e^r = \lambda = N_{t+1}/N_t$. Which do you use: differential or difference equation? Biological reasons suggest using difference equations: North American big game populations have discrete birth pulses, not continuous births as is assumed by differential equations. Mathematical reasons also suggest using difference equations: they are easier to construct and solve in a computer spreadsheet.

The above population model can be thought of as a uni-sex, uni-age population(i.e., all the animals in the population are the same age and sex). The annual rate of change of the population is λ , with

$$N_{t+1}/N_t = 1 + R = \lambda.$$

For increasing populations, $\lambda > 1$, whereas for decreasing populations, $\lambda < 1$. The concept of the annual rate of change of a population is larger than just density-independent population growth, and is generally used to describe the observed annual changes in population size.

The key point about density-independent population growth is that R , and hence λ , do not change with the size of the population. For density-independent population growth, the values of R and λ are fixed, so that the population grows the same relative amount each year. This is hardly a realistic model for biological populations, except maybe for the observed human population expansion! The consequences of density-independent, or exponential population growth, is that the population expands exponentially (Figure 1).

The following example shows how spreadsheet equations are iterative on the previous value, i.e., iterative equations are created by copying a formula. Time is in column A, and population size is in column B. Row 1 initializes time to 0 and the population to 100. Row 2 represents the population at time 1, row 3 at time 2, etc.

Row/Col	A (= time)	B (= N)
1	0	100 (= N_0)
2	+A1+1	+B1*(1+ R)
3	+A2+1	+B2*(1+ R)
4	+A3+1	+B3*(1+ R)
5	+A4+1	+B4*(1+ R)
6	+A5+1	+B5*(1+ R)
7	+A6+1	+B6*(1+ R)

Each entry in column A is 1 added to the previous value of t . Each entry in column B is just the previous row's value multiplied by $(1 + R)$, or λ . If you are unfamiliar with spreadsheets, you are advised to purchase one of the beginner's guides to the particular flavor of spreadsheet you will be using. Most are very good at explaining the basics of entering formulas, and copying the formulas to new cells to create an iterative model. Particularly important is the concept of relative versus absolute addressing of cell values.

Problem 1. Develop a spreadsheet model of density-independent population growth. Use an initial population of $N_0 = 2$, so that your results can be compared to the graph in Figure 1. To implement the model in a spreadsheet, define a row in the upper portion of the sheet as the parameter R , followed by the values of R that you want to model. The next row provides the headings of your model. The first column should be time. Initialize each column to the initial population size, i.e., 2. Then, enter the formulas to compute the population size based on the value of R for the column in the $t = 1$ row. Each formula will refer to the value of R in the first row with absolute addressing and the cell immediately above it with relative addressing; i.e., $+B3*(1+B\$1)$. Once you have the formula correct, and are generating the correct value, you can copy it down each of the 3 population columns. The result should look something like this:

	A	B	C	D
1	R	0.01	0.02	0.03
2	Time	Population 1	Population 2	Population 3
3	0	2	2	2
4	1	2.02	2.04	2.06
5	2	2.0402	2.0808	2.1218
6	3	2.060602	2.122416	2.185454
7	4	2.081208	2.164864	2.251018
8	5	2.102020	2.208162	2.318548

With the graphics capabilities of the spreadsheet package you are using, develop the following plots.

A. Graph population size versus time, just as in Figure 1.

B. Graph change in population size versus population size, where change in population size is N_{t+1} / N_t . What sort of simple graph results?

Solutions to this problem, and other problems in this chapter are available as Quattro Pro spreadsheets at <http://www.cnr.colostate.edu/~gwhite/bgmodel>.

To achieve density-dependent population growth, we must let R be a function of population size, N_t [and hence time, $R(t)$]. The simplest possibility is a linear relationship,

$$R(N_t) = R(t) = R_0 \left(1 - \frac{N_t}{K} \right),$$

which is generally known as logistic population growth because of the linear relationship between growth rate and population size (Figure 2). Note that the population growth rate equals zero when N_t carrying capacity (K), the threshold at which population growth goes to zero. The population growth rate is negative for population sizes above K .

With this function, $R(t) = f(N_t, K)$. Then, substituting the new $R(t)$ function into the equation for population growth, $N_{t+1} = N_t [1 + R(t)]$, the population growth curve in Figure 3 results.

The difference equation for the logistic equation is then

$$N_{t+1} = N_t \left[1 + R_0 \left(1 - \frac{N_t}{K} \right) \right]$$

where the parameters R_0 is the maximum rate of population growth for an infinitesimally small population size and K is the size of the population that results in zero population growth. See Box 2 for a discussion of the differential form of the logistic equation. The plot of N_t versus t is shown in Figure 4, where the population stabilizes in time at a level of K .

Box 2. The differential equation version of the logistic growth curve is in all basic ecology text books:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) .$$

The solution of this differential equation is

$$N = \frac{K}{1 + \left(\frac{K}{N_0} - 1 \right) e^{-rt}} .$$

North American large mammal populations do not have continuous population growth, but rather discrete birth pulses, so the differential equation form of the logistic equation will not be considered further in this chapter.

The per capita finite rate of increase for the logistic equation is

$$\frac{N_{t+1} - N_t}{N_t} = R_0 - \frac{R_0 N_t}{K} .$$

The concept of maximum sustained yield (MSY) can be derived from the logistic function (see Chapter 10 for more on harvest and MSY). The population size that results in the maximum increase in the population is the population size that generates the maximum sustained yield.

Sustainable yield is defined as the harvest that can be taken each year (i.e., a sustained harvest).

This harvest is maximized when the increase in the population is maximized (i.e., the maximum value of $N_{t+1} - N_t$). This maximum is achieved for $N_t = K/2$ (Figure 4). However, this relation

only holds for the logistic model. Other models, with different relations between the finite

population rate of growth and population size result in different population sizes that produce MSY.

To solve for the population size that maximizes yield, you must use calculus to differentiate the equation for yield with respect to N_t ; i.e.,

$$N_{t+1} - N_t = N_t \left[1 + R_0 \left(1 - \frac{N_t}{K} \right) \right] - N_t,$$

which produces the solution that

$$N_t = K / 2.$$

Substituting the value $K/2$ into the equation for yield produces the result that the annual yield is

$$\frac{KR_0}{4}.$$

Once more, these results only apply to the logistic population growth model. Other models result in different population levels that produce MSY (See Box 3).

Problem 2. Develop a spreadsheet model of the density-dependent population growth as a difference equation model. You can assume that the rate of change of the finite growth rate is linear in terms of population size, i.e., logistic population growth. Reasonable parameter values are $K = 300$ and $R_0 = 0.12$.

- A. Graph population size versus time
- B. Graph change in population size versus population size.
- C. Graph per capita change in population size versus population size

Box 3. The mathematical expression of density dependence can take many forms. W. E. Ricker (1954) invented a discrete population model for fishery stocks (also see Ricker 1975:282):

$$N_{t+1} = N_t \exp \left[R_0 \left(1 - \frac{N_t}{K} \right) \right] .$$

Note that the density dependence in this model becomes stronger at higher densities, due to the exponential function relating density to carrying capacity.

Another example is provided by assuming a linear relationship between N_t/N_{t+1} and N_t (instead of between $(N_{t+1} - N_t)/N_t$ and N_t as in the logistic equation), so that the following model can be defined:

$$\frac{N_t}{N_{t+1}} = \beta + \frac{1 - \beta}{K} N_t ,$$

with intercept β and slope $\frac{1 - \beta}{K}$. The resulting population growth model is

$$N_{t+1} = \frac{KN_t}{K\beta + (1 - \beta)N_t} .$$

By taking the limit of the per capita rate of population growth as N_t approaches zero, we find that R_0 can be specified as a function of the parameter β as

$$R_0 = \frac{1 - \beta}{\beta} ,$$

giving the following parameterization of the model:

$$N_{t+1} = \frac{KN_t(R_0 + 1)}{K + N_t R_0} .$$

This model is generalized by Hassell (1975), Hassell et al. (1976) and May (1976) as

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^b} .$$

These three models predict MSY at values other than $K/2$. As an exercise, you might graph these functions with the logistic model in a spreadsheet to compare the differences.

AGE-STRUCTURED POPULATION MODELS

Age-structured models add complexity to a population model, but make the model more realistic in that essential features of the population growth process are captured by the model. I will continue to use difference equations to define the population model because discrete age classes require difference equations for simple solutions. Let $N_{i,t}$ be the number of individuals of age class i at time t . I define time t as the start of the biological year, or the instance in time immediately following the birth pulse or reproduction. The finite rate of change parameter (R) of the density-independent model is now broken into component parts: survival (1 - mortality), reproduction, immigration, and emigration. As an example, consider a mule deer population with four age classes: fawns (F), yearlings (Y), 2-year-old adults (A_2), and adults older than 2 years ($A_{>2}$). Only females are considered in the following example. I need to define the following parameters to develop the model. Estimates of these parameters to use in the model would be obtained with the methods described in Chapter 4.

- (1) Fawn survival rate (S_F) is 0.35 (i.e., only 35% of the fawns that are born live to their first birthday).
- (2) Yearling survival rate (S_Y) is 0.8 (i.e., 80% of the yearlings [fawns that celebrate their first birthday] live to celebrate their second birthday).
- (3) Adult survival rate (S_A) is 0.85 (i.e., 85% of the adults [both 2 years old and older] survive to celebrate their next birthday).
- (4) Each adult >2 years old gives birth to 1.6 fawns (birth rate of adults > 2 years old, $B_{A>2}$), of which half are female and half are male (sex ratio defined as the proportion of births that are female, $SR = 0.5$).

- (5) Each adult exactly 2 years old has 0.8 fawns (birth rate of yearlings, B_{A_2}), of which half are female and half are male.
- (6) Fawns on their first birthday (i.e., having just become yearlings) are assumed to not reproduce.
- (7) Immigration and emigration are assumed to be zero for all age classes.
- (8) Start with 10 adult females >2 years old, so that $N_{F,0} = 0$ (number of fawns at time 0), $N_{Y,0} = 0$ (number of yearlings at time 0), $N_{A_2,0} = 0$, and $N_{A>2,0} = 10$.

With these specifications, the number of adults that survive to time 1 is $N_{A>2,1} = N_{A>2,0} \times S_A$, giving $N_{A>2,1} = 10 \times 0.85$. The number of fawns born at time 1 is $N_{F,1} = N_{A>2,0} \times S_A \times B_A \times SR$, giving $N_{F,1} = 10 \times 0.85 \times 1.6 \times 0.5 = 6.8$. Because we assumed only 10 adults >2 years old at time 0, our population at time 1 consists of only fawns and adults >2.

At time 2, our population consists of 3 different age classes. The number of yearlings will be $N_{Y,2} = N_{F,1} \times S_F$, the number of adults >2 years old will be $N_{A>2,2} = N_{A>2,1} \times S_A$, and the number of fawns born at time 2 is $N_{F,2} = N_{A>2,1} \times S_A \times B_{A>2} \times SR$. The resulting population sizes are $N_{F,2} = 5.78$, $N_{Y,2} = 2.38$, $N_{A_2,2} = 0$, and $N_{A>2,2} = 7.225$.

By time 3, our population consists of all four age classes. The number of yearlings will be $N_{Y,3} = N_{F,2} \times S_F$, the number of 2-year-old adults will be $N_{A_2,3} = N_{Y,2} \times S_Y$, the number of adults >2 years old will be $N_{A>2,3} = N_{A>2,2} \times S_A$, and the number of fawns born at time 3 is $N_{F,3} = N_{A>2,2} \times S_A \times B_{A>2} \times SR + N_{Y,2} \times S_Y \times B_{A_2} \times SR$. The resulting population sizes are $N_{F,3} = 5.5746$, $N_{Y,3} = 2.023$, $N_{A_2,3} = 1.904$, and $N_{A>2,3} = 6.14125$.

From this beginning, I can write out the general set of iterative difference equations that defines the population model:

$$N_{A>2,t+1} = N_{A>2,t}S_A + N_{A2,t}S_A,$$

$$N_{A2,t+1} = N_{Y,t}S_Y,$$

$$N_{Y,t+1} = N_{F,t}S_F, \text{ and}$$

$$N_{F,t+1} = (N_{A>2,t} + N_{A2,t})S_A B_{A>2}SR + N_{Y,t}S_Y B_{A2}SR, \text{ or equivalently}$$

$$N_{F,t+1} = N_{A>2,t+1}B_{A>2}SR + N_{A2,t+1}B_{A2}SR.$$

Because of the different reproductive rate of adults exactly 2 years old, and those older, I have to keep track of the number of animals in both of these age classes, even though they have the same survival rate. Yearlings and fawns have a different survival rate than the 2 adult age classes, so they also have to be followed separately.

After you have solved problem 3, you will get a graph like Figure 5. After the initial fluctuations because only adults >2 years old were in the population, we see a curve identical to density-independent population growth (Figure 1). This result should not surprise you – nowhere in the model did we include a density-dependent relation. As a result, the population stabilizes and grows at a constant rate (i.e., $\lambda = 1.044492$). To obtain this value, you compute the ratio of $N_{Total, t+1}/N_{Total, t}$ for each time period, until the effects of the initial population size have worn off and the growth rate stabilizes.

- Problem 3.** Develop a spreadsheet model of the example mule deer population.
- A. Graph population size for each age class, plus the total population, versus time.
 - B. Graph change in population size versus population size -- what kind of population growth is being modeled?
 - C. Estimate λ .
 - D. Estimate the stable age distribution (i.e., the proportion of the population that will be fawns, yearlings, adults 2-years old, and adults >2-years old).

Another feature of this model is that the ratios of the various age classes stabilize. That is, the ratios of the numbers of animals in each age class are constant, regardless of the population size. This property of age-structured models was first formalized by Leslie (1945) in his development of the use of matrices in population modeling (See Box 4). Caughley (1974) cautioned against the use of age ratios to infer population change for this reason.

Box 4. The Leslie (1945, 1948) matrix (also known as a projection matrix or transition matrix), is often used to model mathematically age-structured populations. The Leslie matrix for the mule deer example presented in the text would be

$$\underline{L} = \begin{bmatrix} 0 & 0 & S_A B_{A2} & S_A B_{A>2} \\ S_F & 0 & 0 & 0 \\ 0 & S_Y & 0 & 0 \\ 0 & 0 & S_A & S_A \end{bmatrix},$$

where the underline under L indicates a matrix. Then, the vector of population sizes at time $t+1$ is defined recursively as

$$\underline{N}_{t+1} = \underline{L} \times \underline{N}_t.$$

Other references pertinent to matrix projections are Lefkovich (1965), Usher (1966, 1969), Caswell (1989), and Manly (1990).

The omission of density dependence in our model is a serious violation of biological logic – nobody expects a deer population to grow indefinitely. Thus, we need to consider how to incorporate density dependence into our model. As discussed in Chapter 8, various mechanisms regulate big game populations. One of the most important is increased mortality of the young in response to increased population density. For example, Bartmann et al. (1992) demonstrated that overwinter fawn survival of mule deer in northwest Colorado declined with increasing density in a pasture experiment. The logistic regression function they fit to their observed survival was

$$S_F = \frac{\exp(1.1906 - 0.0195 \times \text{Dec. Density})}{1 + \exp(1.1906 - 0.0195 \times \text{Dec. Density})},$$

which results in a decline in fawn survival with increasing December density of deer.

Implementing this function into our age-structured model results in population growth shown in Figure 6. Now, the population stops growing when it reaches its carrying capacity, K , because λ approaches 1 and population growth ceases.

Problem 4. Insert the density-dependent function of Bartmann et al. (1992) for S_F in your spreadsheet model created in problem 3.

A. How does λ change with time? What is the final value of λ ?

B. Does your graph of population size resemble Figure 6.?

C. Start with your spreadsheet from problem 3 and incorporate density dependence into B_{A_2} and $B_{A>2}$. Reasonable functions might be $B_{A>2} = 2.3 - 0.01 N_{Total}$ and $B_{A_2} = 1.5 - 0.01 N_{Total}$. Do the resulting curves of population growth resemble Figure 6 also? Why is K not the same for this function as for density dependence in S_F ?

Several important points are made with this example. First, density dependence was only incorporated into one parameter of the model (i.e., S_F). Even though all the other parameters are still density-independent, the population size converges to a constant value, K . Thus, our

model assumes that the birth rate in the population is constant across density, even though biologically this might not be the most reasonable assumption.

Second, incorporation of density dependence into any single parameter will result in the population converging to a constant size if the population would go extinct by making this parameter zero. That is, the effect of density must be great enough to force the value of λ to equal one. If making the parameter zero is not enough to make $\lambda = 1$, the effect of density via this parameter will not result in the population approaching K . An example of a parameter that would not result in a constant population if it were made a function of density is the birth rate of 2-year-old females in our age-structured model. Changing B_{A2} to 0 results in $\lambda = 1.0296$, which is not adequate to limit population growth. Thus, making B_{A2} a function of population density would not, by itself, be enough to regulate population growth. Other parameters in the model also would have to be made a function of density to achieve regulation. However, biologically, B_{A2} is very likely a function of density.

Third, the relationship between S_F and density was not linear, in contrast to the logistic population growth model discussed earlier. Evidence has accumulated that the effects of density in ungulates are strongest near K , and are not constant. That is, the relationship between survival and/or birth rates and density is not linear (Fowler 1981).

Finally, a caution about developing age-structured models. Modelers have to be extremely careful to define the time of year when they census the model population. In the example presented here, the census occurred just after the birth pulse. Fawns in this model were just born. An alternative model would be to census the population just prior to the birth pulse. Then, the fawn age class would consist of animals almost 1-year old. The structure of the model would

look quite different, but the results, such as the estimate of λ , would be identical (assuming you have structured the model correctly). Noon and Sauer (1992) discuss how to structure models with different census times. Constantly be aware of how you have defined the population measured by N , and structure your equations appropriately.

A “short-cut” often used to build age-structured models is to ignore a portion of the life cycle. A common example of this trick used in big game models is to measure recruitment to the population as the number of young alive at the start of the winter, when age ratio surveys are performed (see Chapter 4). For example, the Colorado Division of Wildlife estimates December fawn:doe ratios for mule deer via helicopter surveys. The values of B_{A2} and $B_{A>2}$ cannot be distinguished, because the age of adults cannot be distinguished from the air. In fact, yearlings cannot be reliably distinguished from adults, so the estimate of fawns:does reflects the number of fawns produced for the 3 age classes N_Y , N_{A2} , and $N_{A>2}$, even though N_Y animals do not produce fawns. The reason for making this biologically incorrect assumption is that estimation of the true recruitment for each of these age classes would require monitoring the fate of marked, known-aged animals, and is not economically feasible. Thus, by taking this short-cut, reasonable population models can be developed from field data.

Another short-cut used in the model presented here is that no senility is assumed (i.e., adults 3-years old have the same survival rate as adults >20 years old). This assumption is made because of the difficulty in obtaining year-specific and age-specific survival rates. The assumption is not really all that unrealistic, in that few animals live to the age where senility becomes a factor, even at high survival rates such as 0.85 used in our mule deer model. Senility is not difficult to model, just requiring different survival rates as a function of age. The problem is obtaining the

data to support senility effects, particularly given that survival likely varies by year. Incorporating age-specific and year-specific effects into a model requires a large amount of data to support the complexity. Similarly, age-specific reproductive rates can be extended to more than four age classes by increasing the number of age classes in the model. The limitation is data to support the assumptions.

Another extension to the basic model presented here is to include multiple areas, so that immigration and emigration can take place between areas. You can think of emigration as the death of an animal on the first area, and its immigration to a second area as a birth, albeit older than age 0. Models that incorporate multiple areas with immigration and emigration between areas approach the general concept of a metapopulation (McCullough 1996).

STOCHASTIC POPULATION MODELS

Real populations never exhibit deterministic population growth (i.e., population dynamics as modeled by a deterministic equation that has a constant rate of growth such as has been presented above). Rather, population levels fluctuate from year to year and from site to site. Being able to predict the amount of random variation that we would expect to see in a population is useful for making predictions about the future size of a population. Specifically, predictions about the persistence of a population are part of a specialized modeling field called population viability analysis (Boyce 1992).

Variation in population sizes can be classified into two general mechanisms. The true population may vary through time and space, even though a deterministic model predicts a constant population. Variation in the true population size is termed process variation, because of stochasticity in the population growth process. Several mechanisms can cause process variation.

Demographic variation is the randomness that exists as to whether an individual reproduces or survives. For example, the outcome of whether an individual with a specified survival probability survives is based on a Bernoulli distribution. I like to call this source of variation “penny flipping variation” because the variation about the expected number of survivors parallels the variation about the observed number of heads from flipping coins. To illustrate demographic variation, suppose the probability of survival of each individual in a population is 0.8. Then on average, 80% of the population will survive. However, random variation precludes exactly 80% surviving each time this survival rate is applied. From purely bad luck on the part of the population, a much lower proportion of the population may survive for a series of years, resulting in extinction. Because such bad luck is most likely to happen in small populations, this source of variation is particularly important for small populations, and hence the name demographic variation. The impact is small for large populations. As the population size becomes large, the relative variation decreases to zero. That is, the variance of N_{t+1}/N_t goes to zero as N_t goes to infinity. Thus, demographic variation is generally not an issue for persistence or modeling of larger populations.

To illustrate further how demographic variation operates, consider a small population with $N = 100$ and a second population with $N = 10,000$. Assume both populations have identical survival rates of 0.8. With a binomial model of the process, the probability that only 75% or less of the small population survives is 0.1314 for the small population, but 3.194E-34 (i.e., a very small probability) for the larger population. Thus, the likelihood that up to 25% of the small population is lost in one year is much higher than for the large population.

Demographic variation can be incorporated into spreadsheet models by using the binomial distribution. To use an example from the age-structured model of mule deer described above, instead of multiplying $N_{Y,t} \times S_Y$ to get $N_{A2,t+1}$, we assume that on average S_Y animals live, but for any specific year, some random value is observed. The CRITBINOM function of the spreadsheet software is used, i.e., $N_{A2,t+1} = @CRITBINOM(N_{Y,t}, S_Y, @RAND)$. The @RAND function provides a random variable distributed uniformly between 0 and 1, with the result that the observed value of $N_{A2,t+1}$ will vary around a mean of $N_{Y,t}S_Y$ with variance $N_{Y,t}S_Y(1 - S_Y)$. Thus, demographic variation could be included in all the survival rates of the age-structured model. Demographic variation should also be incorporated into the reproduction process. Instead of applying the birth rate of B_{A2} to $N_{A2,t+1}$ directly, use the binomial distribution:

$CRITBINOM(N_{A2,t+1}, B_{A2}, @RAND)$. Reproduction for the adults >2 age class is more problematic, but a reasonable model would be to assume all adults >2 years old have 1 fawn, and some random proportion have 2 fawns. The following statement would achieve this result:

$$N_{A>2,t+1} + @CRITBINOM(N_{A>2,t+1}, B_{A>2} - 1, @RAND).$$

Knight and Eberhardt (1985) developed a stochastic model of grizzly bear populations in Yellowstone National Park. Their model only incorporated demographic variation (see Box 5).

Another form of stochasticity to incorporate into a model is **temporal variation** (i.e., making the parameters random variables that assume new values each year). Such variation would be exemplified by weather in real populations. Some years, winters are mild and survival and reproduction are high. Other years, winters are harsh and survival and reproduction are poor. Another form of environmental stochasticity is **spatial variation** (i.e., variation of population parameters across the landscape). Factors causing geographic variation include geologic

differences that affect soil type, and thus habitat, and weather patterns (e.g., differences in rainfall across the landscape). If the immigration and emigration rates are high across the landscape, so that subpopulations that are depleted because of local conditions, high spatial variation can lead to higher persistence. This is because the probability of all the subpopulations of a population being affected simultaneously by some catastrophe is low when high spatial variation exists. In contrast, with low spatial variation, the likelihood of a bad year affecting the entire population is high. Thus, in contrast to temporal variation, where increased variation leads to lowered persistence, increased spatial variation leads to increased persistence given that immigration and emigration are effectively mixing the subpopulations. If immigration and emigration are negligible, then spatial variation divides the population into smaller subpopulations, which are more likely to suffer extinction from the effect of demographic variation on small populations.

The combination of temporal and spatial variation is termed **environmental variation**.

Both dictate the animal's environment, one in time, one in space.

Box 5. Stochastic models. Knight and Eberhardt (1985) developed a stochastic model of the grizzly bear population in Yellowstone National Park. Their model assumed only demographic variation (i.e., no other sources of stochasticity were included). The model included age structure, with age-specific rates of survival and reproduction. The purpose of the model was to assess the probability of persistence of the population for 30 years, and estimate likely future populations. The critical assumption made with their approach is that the population parameters used in the model are not changing with time or density. I consider these assumptions acceptable for the intended purpose of the model.

With Tom Beck and Bruce Gill, Colorado Division of Wildlife, I extended the Knight and Eberhardt approach to examine the question of how much the Colorado black bear population would expand with the closure of spring bear hunting in the state. A range of hunting scenarios were explored with the model, including no harvest, 2 spring seasons with 30 and 35% of the harvest consisting of females, and 3 fall seasons with 35, 40, and 45% of the harvest consisting of females. I incorporated temporal variation to account for changes in survival and reproduction in response to failures in mast and berry crops from late spring frosts, plus temporal variation in annual harvest rates because of hunting conditions. One year in 10 was assumed to have optimal hunting conditions. At the time I built this model, spreadsheet technology had not yet reached the level where stochastic models could be easily implemented. Thus I used SAS (SAS Institute 1990) to implement the model. The SAS code is available at <http://www.cnr.colostate.edu/~gwhite/bgmodel>, along with a description of the model.

Although our black bear harvest model was interesting and fun to build and play with, I found the results of little value in answering the questions that motivated the model's construction. The nagging question that the model could not answer for lack of data was the role of density dependence in a burgeoning bear population. This question became increasingly apparent as we examined the various scenarios predicted by the model, and thus focused our thinking on a critical issue where more research and data are required. Because our model was looking at increases in the population, density dependence was an important issue. In contrast, Knight and Eberhardt were more concerned with declines in an already small population, where the role of density dependence is likely negligible. Thus, in one case, a stochastic model was useful in answering the motivating question, in another, useful in focusing our attention on a deeper question.

Environmental stochasticity can be incorporated into a model by making the parameters random variables. As an example, consider making the reproductive rate of adults >2 years old a random variable with a normal distribution with mean $B_{A>2}$ and standard deviation $SD(B_{A>2})$. The NORMINV function of spreadsheet software can produce random normal deviates with the

statement: $\text{@NORMINV}(\text{@RAND}, B_{A>2}, \text{SD}[B_{A>2}])$. Thus, year-specific reproductive rates would be generated randomly for each year, and then applied to the population. The result would be a model that exhibited year-to-year differences in population growth. Another distribution useful for generating random survival rates (and possibly reproductive rates in some circumstances) is the beta distribution. Random beta variables can be generated in spreadsheets with the BETAINV function. Advantages of the beta distribution are that random values can be constrained to specified intervals. For example, survival rates can be constrained to the interval 0-1. Transformations can also be useful in constraining random variables to specified intervals. The logistic transform, $\log[S/(1 - S)] = f(\text{random variables})$ is a useful method. The logistic function was used to model density dependence in fawn survival rates above. An advantage of using the logistic transform is that correlated random variables can be generated. That is, fawn survival and adult survival logically are not independent. A severe winter with poor survival for adults guarantees a low survival rate for fawns. With the logistic function, 2 random normal deviates can be used to generate survival rates. The first deviate (D_1) would provide the year-to-year variation, with a large standard deviation. The second deviate (D_2) would provide minor variation of fawn survival from adult survival. The functions might be:

$$\log[S_A/(1 - S_A)] = \beta_A + D_1, \text{ and}$$

$$\log[S_F/(1 - S_F)] = \beta_F + D_1 + D_2.$$

Another approach to incorporating environmental stochasticity into a model is to use the bootstrap technique to sample from observed parameter values for the population of interest. The VLOOKUP or HLOOKUP functions in spreadsheets, combined with a random integer, can be used to effectively bootstrap observations. The correlation of parameters can be maintained by

selecting a year-specific set of values (i.e., the fawn and adult survival rates from one year are selected together).

All the models examined so far assume that each animal in the population has exactly the same chance of survival and reproduction, even though these rates are changing with time. What happens if each animal in the population has a different rate of survival and reproduction?

Differences between the individuals in the population are termed individual heterogeneity, and creates **individual variation**. Many studies have demonstrated individual heterogeneity of individual survival and reproductions. Clutton-Brock (1982) demonstrated lifetime reproductive success of female red deer varied from 0 to 13 calves reared per female. Differences in the frequency of calf mortality between mothers accounted for a larger proportion of variance in success than differences in fecundity. Bartmann et al. (1992) demonstrated that overwinter survival of mule deer fawns was a function of the fawn's weight at the start of the winter, with larger fawns showing better survival.

Individual variation is caused partially by **genetic variation** (i.e., differences between individuals because of their genome). Individual heterogeneity is the basis of natural selection (i.e., differences between animals is what allows natural selection to operate). However, **phenotypic variation** also is possible, where individual heterogeneity is not a result of genetic variation. Animals that endure poor nutrition during their early development may never be as healthy and robust as animals that are on a higher nutritional plane, even though both are genetically identical. Animals with access to more and better resources have higher reproductive rates, as shown for red deer (Clutton-Brock et al. 1982). Thus, individual heterogeneity may

result from both genetic and phenotypic variation. Lomnicki (1988) developed models of resource partitioning that resulted in phenotypic variation of individuals.

Undoubtedly, natural selection plays a role in the genetic variation left in a declining population. Most populations where biologist are concerned about extinction probabilities have suffered a serious decline in numbers. The genotypes remaining after a severe decline are unlikely to be a random sample of the original population. I would expect that the genotypes persisting through a decline are the “survivors”, and would have a much better chance of persisting than would a random sample from the population prior to the decline. Of course, this argument assumes that the processes causing the decline remain in effect, so that the same natural selection forces continue to operate.

The reason that increased individual heterogeneity increases population persistence is that increased variation results in more chance a few animals have exceptionally high reproductive potential and high survival. Therefore, these animals are unlikely to suffer mortality and be removed from the population, and also can be relied upon to contribute new births each year. As a result, the population may remain small, but will not go extinct as often. Individual heterogeneity has seldom, if ever, been included in a population viability analysis. Yet, as simple examples show, individual heterogeneity is a very important element in maintaining viability (White 1998).

The combined effects of demographic, temporal, spatial, and individual variation are termed **process variation**. That is, each of these sources of variation affect population processes. Process variation is used as a general term for the inherent stochasticity of changes in the population level. Process variation is in contrast to **sampling variation**, which is the variation

contributed when biologists attempt to measure population processes. That is, researchers are unable to measure the exact survival rate of a population. Rather, they observe realizations of the process, but not the exact value. Thus, we observe only estimates of population size, \hat{N}_t , instead of true population size N_t . Even if the fate of every animal in the population is observed, the resulting estimate of survival is only an estimate of the true, but unknown, population survival rate, because of demographic variation. We only observe the outcome of the stochastic process, and can never measure the underlying parameters.

In reality, we may be fortunate and have a series of survival or reproduction estimates across time that provides information about the temporal variation of the process. However, the variance of this series is not the proper estimate of the temporal variation of the process. This is because each of our estimates includes sampling variation (i.e., we only have an estimate of the true parameter, not its exact value). To properly estimate the temporal variation of the series, the sampling variance of the estimates must be removed. Procedures to remove the sampling variance from a series of estimates and obtain an estimate of the underlying process variation (which might be temporal or spatial variation) are available. Simple method of moment estimators are explained in Burnham et al. (1987:260-278) and Burnham (1998). For some kinds of data, where sampling variation is assumed constant, analysis of variance techniques can be used to estimate the underlying process variance. However, these techniques are beyond the scope of this chapter, so will not be considered further here. White (1998) provides a review of methods to estimate process variance and then incorporate the estimate into a population model.

Problem 5. Add stochasticity to a model.

A. Incorporate demographic variation into the age-structured model of problem 4. Use the CRITBINOM function to produce demographic stochasticity in survival and reproductive rates. Note how you get a different population growth curve each time you recalculate the spreadsheet. Explain why the population is now always an integer value. Change the initial population to 1,000. Note how the population growth function smooths out, demonstrating how demographic variation is only important at small population sizes.

B. Incorporate temporal variation into the demographic stochasticity spreadsheet by making the survival and reproductive rates vary by year. Assume that the standard deviation for each parameter is equal to 10% of its mean value, although White and Bartmann (1998a) reported that the standard deviation of over-winter fawn survival is closer to 50% of its mean value for a population in northwest Colorado. Note how much more variable the resulting population growth curves are than the model with just demographic variation, especially when the initial population size is set at 1,000.

C. For the courageous, modify the age-structured model with density dependence with demographic and temporal variation.

FITTING MODELS TO DATA

Often, data are available from a population, and we desire estimates of the underlying parameters that govern the population. Typically, regression methods are used, but more complex procedures often are required (Pascual et al. 1997). The optimization procedures of spreadsheets allow sophisticated nonlinear parameter estimation, methods that are far beyond the scope of this chapter. However, some exposure to parameter estimation methods is needed to develop useful population models. An example that compares two models is useful in demonstrating the capabilities of these techniques.

To illustrate the possible methods, data from McCorquodale et al. (1988) and Eberhardt et al. (1996) will be used. These studies report on the growth of an isolated elk population in the shrub-steppe region of southcentral Washington. The elk population colonized the area about 1975. The following population estimates are provided:

Year	Estimated Population
1975	8
1976	13
1977	15
1978	
1979	16
1980	
1981	25
1982	27
1983	40
1984	55
1985	71
1986	89
1987	94
1988	95
1989	102
1990	115
1991	133
1992	190
1993	238

An interesting question posed by these data is whether the population has shown any decline in its rate of growth, or, in other words, is the population exhibiting density dependence? One approach is to fit the two models, density independence and density dependence, and compare the results. Does the density-dependence model provide an improved fit compared to the density independence-model?

To fit the models, I assumed that the estimated population is the true population, i.e., that the count is the actual population. Using these values as N_t , I fit the following models:

density independence: $\widehat{N}_{t+1} = N_t(1 + R)$, and

density dependence: $\widehat{N}_{t+1} = N_t[1 + R(1 - N_t / K)]$.

For each model, the sum of the differences $[\log(\hat{N}_{t+1}) - \log(N_{t+1})]^2$ was minimized. I used logarithms of the observed and predicted values to standardize the variance of the residuals across the nearly two orders of magnitude of the observed data. For the years 1979 and 1981, each model was applied twice to the preceding year to obtain the predicted population size.

The result was that the density-dependent model did not improve the fit over the density-independent model ($P = 0.979$). The estimate of K was $>8,000$, but was basically not estimable from these data, consistent with no evidence of density dependence in these data. The fit of the two models was so close that the lines cannot be distinguished on a graph (Figure 7). The estimate of λ was 1.194, very similar to the values obtained by the original authors. However, a conceptually different model was fit to produce their estimate. The observed population sizes are assumed to have no sampling error, in contrast to the approach used by McCorquodale et al. (1988) and Eberhardt et al. (1996), where all the variation in the data was assumed to be sampling error.

Problem 6. Use a spreadsheet to fit the models of density independence and density dependence to the ALE elk data.

A. Graph the 2 models with the observed data to produce a plot similar to Figure 7.

Box 6. Complex example of fitting a model to data. Data have been collected on the Piceance mule deer herd in northwestern Colorado (Table 1). When a 2-age class model (fawns, adults) with sex-specific classes for adults is built from this data, the modeled population crashes. The initial population was computed from the 1981 population estimate assuming that 67% of the animals were counted on the quadrats sampled, based on the work of Bartmann et al. (1986). Age structure was computed from the 1981 age ratios. Years with missing fawn:doe ratios were replaced by the mean of the series. With these inputs, the buck:doe ratio becomes negative and the population goes to zero. Although the population had been thought to be declining during the 1990s, the decline wasn't observed to be that severe. Details are provided in the spreadsheet available from <http://www.cnr.colostate.edu/~gwhite/bgmodel>, including graphs of the model and observed values.

The problem identified with this model is that the data are not totally consistent with themselves. That is, sampling variation in the parameter estimates causes the model to crash. We must now fit a model to the observed values that makes the model produce reasonable predictions. The strategy taken was to minimize the weighted least squares between the observed population size and buck:doe ratios and the predicted values. The weight of each of these observations was taken as the reciprocal of the variance. Thus, for each of these observations, the quantity $\left[(q_i - \hat{q}_i) / SE(q) \right]^2$ was computed to create an objective function to minimize. The parameters changed to improve the fit were the fawn and adult survival rates, December fawn:doe ratios, and population size. For each of these parameters, a penalty was added to the objective function of the form $\left[(q_i - \hat{q}_i) / SE(q) \right]^2$. That is, any change in one of these parameters from its observed value increased the size of the objective function, and thus penalizes the optimization for the change. The resulting fit of the model is a balance between fitting the observed buck:doe ratios and population sizes corrected for sightability and changing the observed data more than can be justified given its precision. The optimization spreadsheet is included with the spreadsheet mentioned above. Results from this procedure were a much-improved fit of the model to the observed data (Figure 8). The predicted decline in the population is now consistent with other observations of population size taken as part of a research study (White and Bartmann 1998b).

PHILOSOPHY ABOUT THE USE OF POPULATION MODELS

There are numerous reasons for constructing models. First, models provide an explicit statement of assumptions about the species of interest. Thus, a realistic model summarizes existing knowledge about a population. Second, models provide predictive capability. This

predictive capability is useful for setting harvest levels to meet herd objectives, and for resolving controversies. Finally, models allow biologists to play “what if” games. Modeling will highlight your ignorance – parameters in the model that are just guesses become obvious when you are building the model. Models will expose your ignorance as you recognize the lack of data available for managing a population

However, the very reasons that models are useful are also why they are dangerous. One of the most common abuses of models is in using them for purposes they were not intended. Too often, a model is constructed with the intention of playing “what if” games, but then is used to make predictions about the population. A second abuse of models is not understanding the limitations of the data when building a model. Examples are using the wrong variance component (e.g., sampling variation in place of temporal variation), and improper sampling frame when data are collected, resulting in biased estimates used in the model.

I try to adhere to the following criteria when using models. First, models test hypotheses about models, not about actual populations. Inferences made to real populations from models are conditional on the assumptions and data used to build the model. Too often in the literature, we find statements made about model results that get interpreted as statements about real systems. Second, models should be developed from data taken on a population if you are going to use the model to make predictions about that population. Third, models used for prediction should be kept simple, and used only within the breath of the data used to develop them (i.e., no extrapolation). Building a model from data will generally mean the model is simple because we seldom have enough data to justify a complex model.

The crucial philosophy underlying the last two points above is that management decisions must be based on data. In other words, the management of a population should not be based on model predictions where the model inputs are not provided from measurements made in the field. Complex models of population dynamics may capture most of our knowledge of this system, but such models do not provide reliable predictions of year-to-year dynamics because of the lack of annual information on required inputs.

The issue of model complexity is better comprehended with an analogy to an auto trip from New York City to Los Angeles. No reasonable driver would start this trip with 7.5 minute USGS topographic quadrangles as his/her model. Certainly the topographic quadrangles contain all the necessary information, but the detail is considerably more than needed. A simpler model will suffice, such as state road maps, and is more likely to result in success. An even simpler model of just a single map of the interstate highways would suffice, but would not provide all the details we might like. Unfortunately, costs usually limit the amount of information available, even though we may desire more. In summary, models are a useful and powerful tool. But like all sharp tools, you can easily cut yourself if you misuse them.

CONCLUSIONS

Population modeling provides a mathematical tool to predict the trajectory of a population, or to evaluate potential management strategies. Computer spreadsheets provide a powerful tool for population modeling, including stochastic models and graphical presentations. Density-independent and density-dependent models of populations with single and multiple age classes are developed in this chapter. Difference equation models are employed. Stochastic models can include process variation, such as environmental (temporal and spatial), individual

(genetic and phenotypic), and demographic variation, but should not incorporate sampling variation of the estimates used to construct the model into the stochasticity of population growth. The random number generators of modern spreadsheets provide the tools to build reasonable stochastic population models. The numerical optimization capabilities in spreadsheets provide the tools needed to fit complex models to observed data.

LITERATURE CITED

- Bartholow, J. 1992. POP-II system documentation.. IBM-PC Version 7.00 Fossil Creek Software, Fort Collins, Colorado. 50 pp.
- Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monograph* 121:1-39.
- Bartmann, R. M., L. H. Carpenter, R. A. Garrott, and D. C. Bowden. 1986. Accuracy of helicopter counts of mule deer in pinyon-juniper woodland. *Wildlife Society Bulletin* 14:356-363.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and Analysis Experiments for Fish Survival Experiments Based on Capture-Recapture. *American Fisheries Society Monograph No. 5*, Pages 260-278.
- Burnham, K. P. 1998. Shrinkage estimators. Submitted.
- Caswell, H. 1989. *Matrix population models*. Sinauer, Sunderland, Massachusetts 328 pp
- Caughley, G. 1974. Interpretation of age ratios. *Journal of Wildlife Management* 38:557-562.

- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer behavior and ecology of two sexes. University of Chicago Press, Chicago, Illinois. 378 pp.
- Eberhardt, L. E., L. L. Eberhardt, B. L. Tiller, and L. L. Cadwell. 1996. Growth of an isolated elk population. *Journal of Wildlife Management* 60:369-373.
- Fowler, C. W. 1981. Density dependence as related to life history strategy. *Ecology* 62:602-610.
- Gross, J. E., J. E. Roelle and G. L. Williams. 1973. Program ONEPOP and information processor : a systems modeling and communications project. Colorado Cooperative Wildlife Research Unit, Colorado State University, Fort Collins, Colorado. 327 pp.
- Hassel, M. P. 1975. Density-dependence in single-species populations. *Journal of Animal Ecology* 44:283-295.
- Hassell, M. P., J. H. Lawton, and R. M. May. 1976. Patterns of dynamical behaviour in single-species populations. *Journal of Animal Ecology* 45:471-486.
- Knight, R. R., and L. L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology* 66:323-334.
- Lefkovich, 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.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213-245.

- Łomnicki, A. 1988. Population ecology of individuals. Princeton Univ. Press, Princeton, New Jersey. 223 pp.
- Lubow, B., G. C. White, and D. R. Anderson. 1996. Evaluation of a linked-sex harvest strategy for cervid populations. *Journal of Wildlife Management* 60:787-796.
- Manly, B. F. J. 1990. Stage-structured population Sampling, analysis and simulation. Chapman and Hall, London, United Kingdom. 187 pp.
- May, R. M. 1976. Models for single populations. Pages 4-25 *In* Theoretical Ecology: Principles and Applications. R. M. May, editor. Blackwell, Oxford, Great Britain.
- McCorquodale, S. M., L. L. Eberhardt, and L. E. Eberhardt. 1988. Dynamics of a conlonizing elk population. *Journal of Wildlife Management* 52:309-313
- McCullough, D. R., editor. 1996. Metapopulations and wildlife conservation. Island Press, Washington, D.C. 429 pp.
- Noon, B. R. and J. R. Sauer. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441-464 In D. R. McCullough and R. H. Barrett, eds. *Wildlife 2001: Populations*. Elsevier Applied Science, New York, New York.
- Pascual, M. A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology* 11:966-976.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada* 11:624-651.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bull. 191. Ottawa, Canada.

SAS Institute. 1990. SAS® Language: Reference, Version 6, First Edition. SAS Institute Inc., Cary, North Carolina. 1042 pp.

Usher, M. B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. *Journal of Applied Ecology* 3:355-367.

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

White, G. C. 1998. Population viability analysis. Pages ???-??? in Proceedings of Conference on Ecological Methods, Palermo, Sicily.

White, G. C., and R. M. Bartmann. 1998A. Mule deer management — what should be monitored? Pages ???-??? in Proceedings Joint Mule Deer and Elk Symposium, Tucson, Arizona.

White, G. C., and R. M. Bartmann. 1998B. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. *Journal of Wildlife Management* 62:214-225.

ANIMAL SCIENTIFIC NAMES

Common Name	Scientific Name
Mule deer	<i>Odocoileus hemionus</i>
Red deer	<i>Cervus elaphus</i>
Black bear	<i>Ursus americanus</i>

Table 1. Estimates of fawn and adult survival, fawn:doe, buck:doe, and population size collected on the Piceance mule deer herd, northwestern Colorado, from 1981-1995. Missing data are shown as blank entries.

Year	Fawns:100 does		Bucks:100 does		Fawn survival		Adult survival		Population size		Buck harvest		Doe harvest	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1981	77.7	5.78	13.8	1.95	0.48	0.068	0.86	0.049	21103	3592	2293		19	
1982	75.5	4.34	11.4	1.34	0.36	0.044	0.81	0.048	16004	2425	3072		10	
1983	78.8	4.83	11.4	1.45	0.05	0.021	0.83	0.045	27309	3129	3512		64	
1984	70.2	4.49	7.4	1.16	0.19	0.039	0.88	0.040	21723	2387	2017		12	
1985	72.5	5.57	7.2	1.38	0.41	0.039	0.92	0.038	21657	2822	1849		30	
1986	63.5	4.11	14.0	1.62	0.42	0.038	0.76	0.068			931		21	
1987					0.15	0.033	0.88	0.083			1326		24	
1988	74.2	4.66	13.9	1.63	0.35	0.064	0.83	0.108	25248	2517	1449	75	585	19
1989	65.7	3.97	12.4	1.42	0.77	0.049	0.90	0.051			2227	95	1512	59
1990	61.2	3.92	16.2	1.72	0.32	0.069	0.94	0.035			1822	92	1691	48
1991	46.4	2.65	11.9	1.17	0.49	0.072	0.77	0.052			1917	92	1238	45
1992	45.5	3.61	10.5	1.51	0.14	0.029	0.71	0.048			1310	68	1296	70
1993	42.6	3.50	10.1	1.50	0.65	0.038	0.84	0.038			1041	63	777	53
1994	46.1	4.05	7.8	1.43	0.76	0.034	0.88	0.035			1210	65	221	17
1995	47.6	3.81	10.7	1.56	0.70	0.038	0.93	0.029			1489	68	182	16
1996											1631	69	206	18
Mean	62.0	4.24	11.3	1.49	0.42	0.045	0.85	0.051	22174	2812				
SD	13.6		2.7		0.23		0.07		3886					

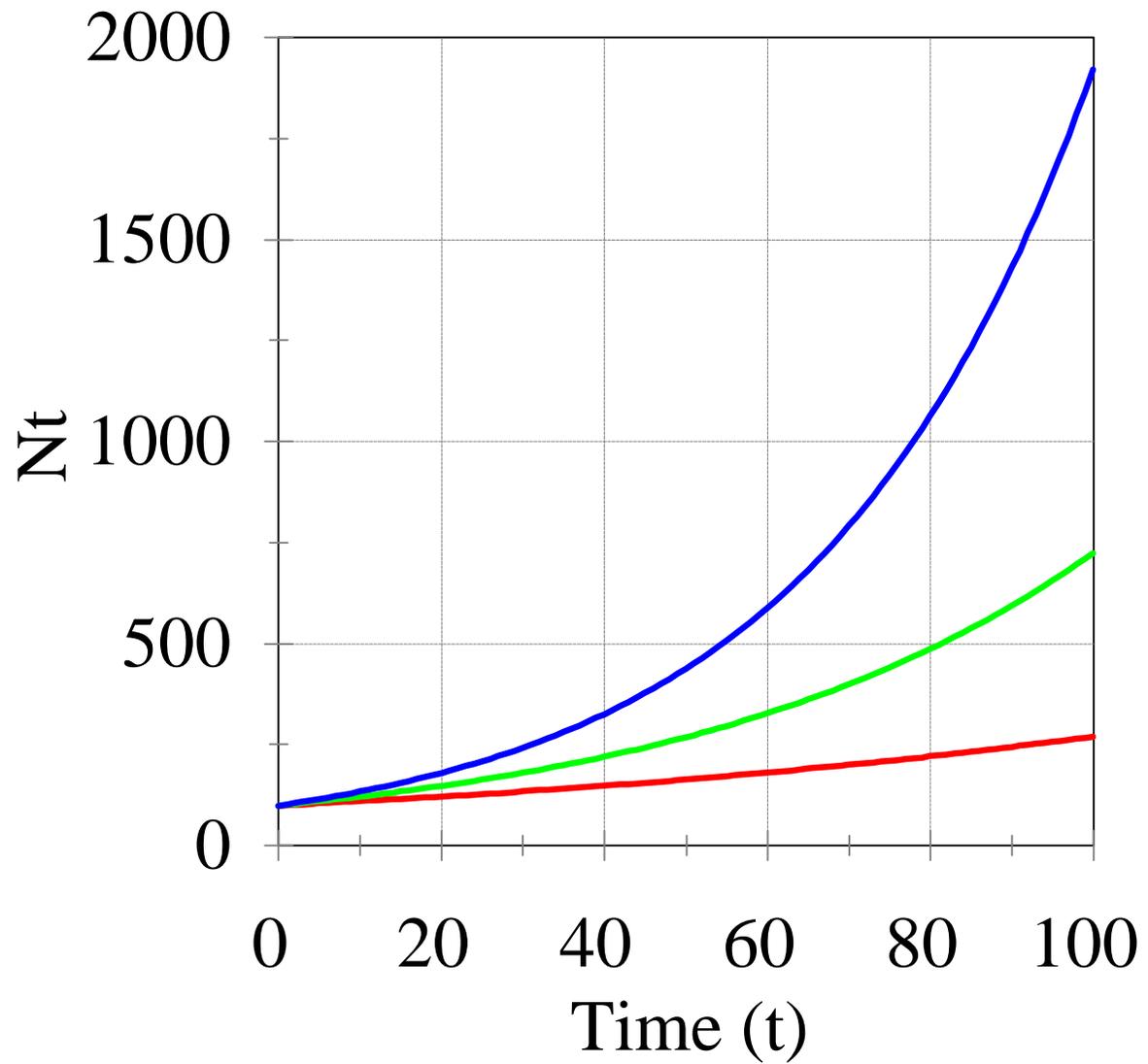


Figure 1. Examples of three density-independent populations with $N_0 = 2$, and different values of $R = 0.01, 0.02,$ and 0.03 , resulting in three different rates of growth.

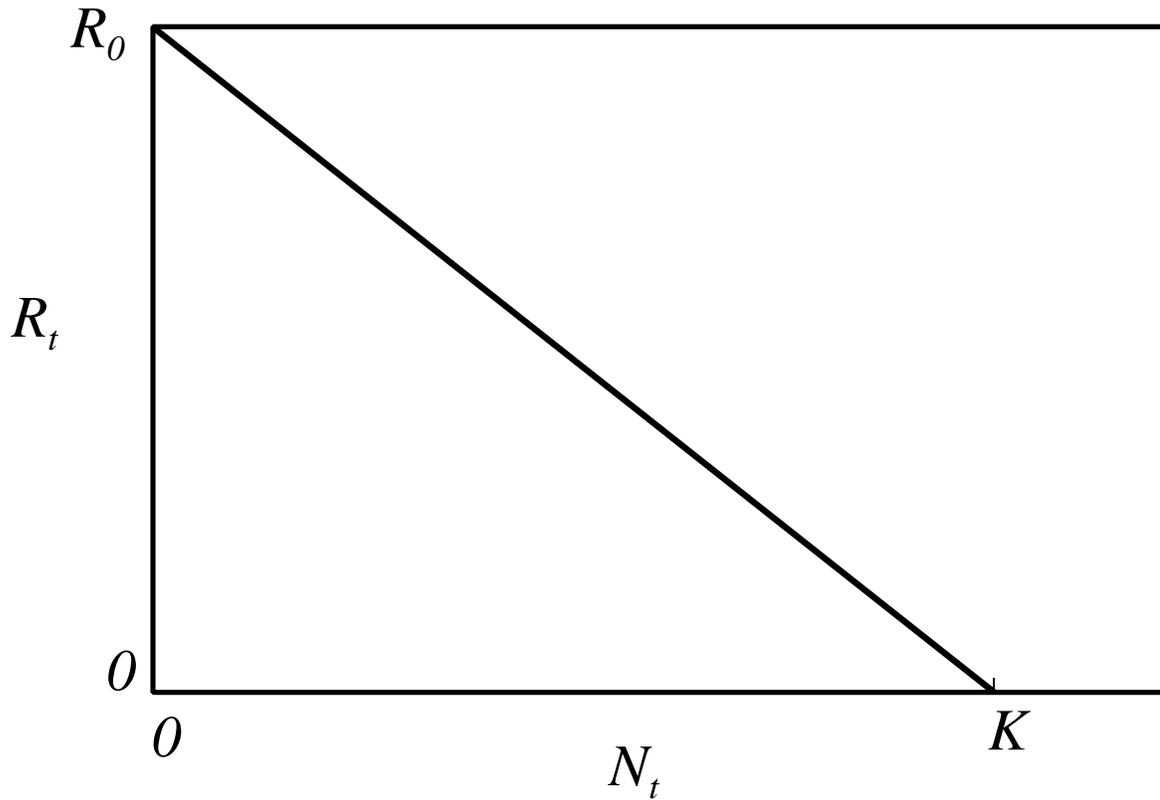


Figure 2. The relation between the finite population growth rate and population size that results in logistic growth. At population size K , the population growth rate is zero. At zero population size, the population growth rate is R_0 .

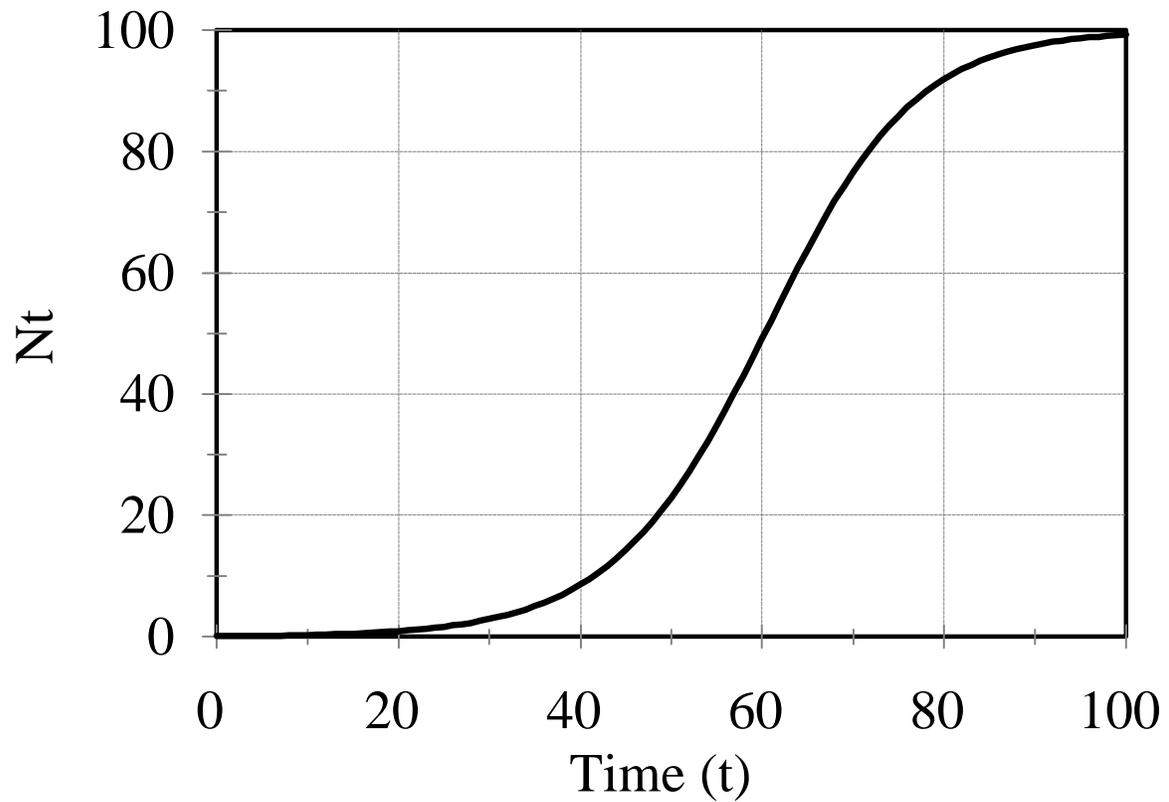


Figure 3. Graph of population size versus time for the logistic population growth model. The logistic model is a special case of density-dependent population growth where the finite population growth rate is a linear function of population size.

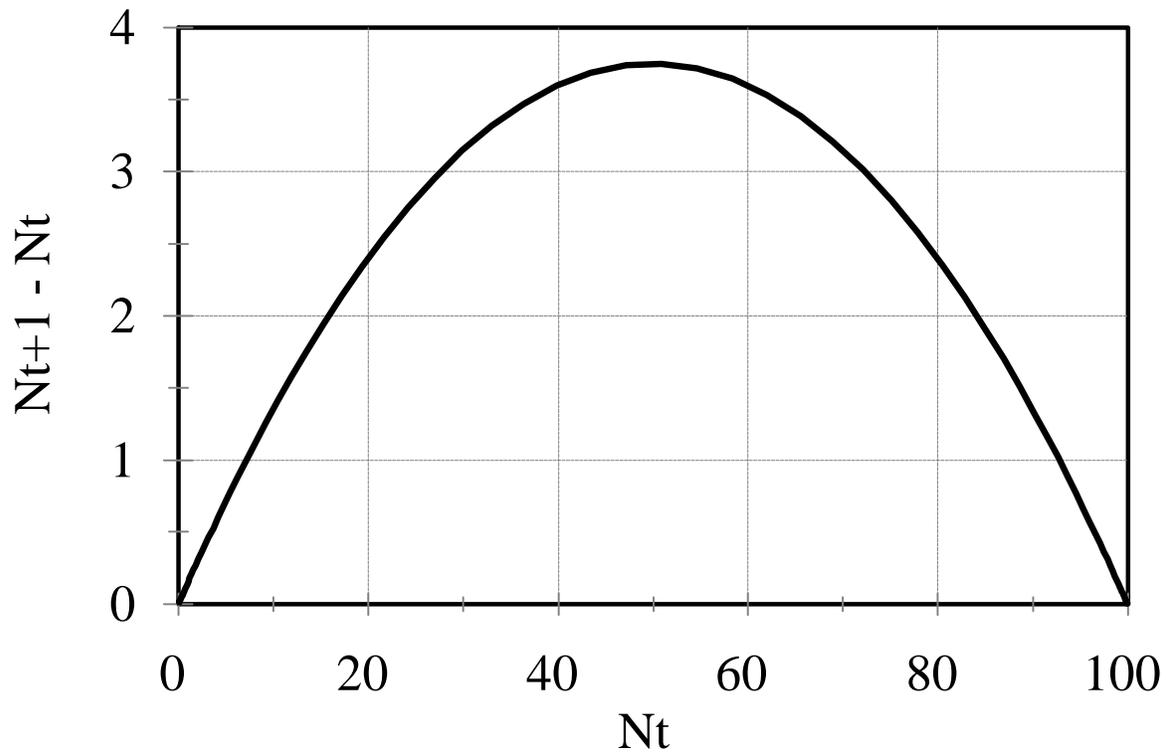


Figure 4. Relation of population size to annual yield for the logistic population growth model.

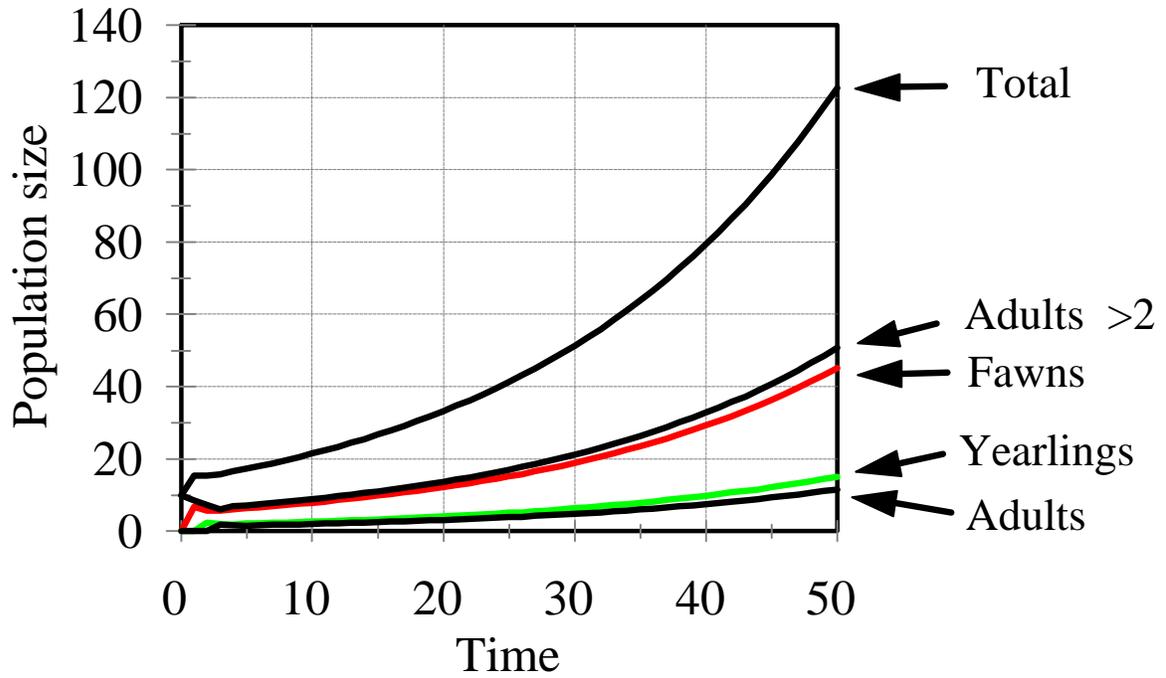


Figure 5. Population growth in an age-structured model of mule deer.

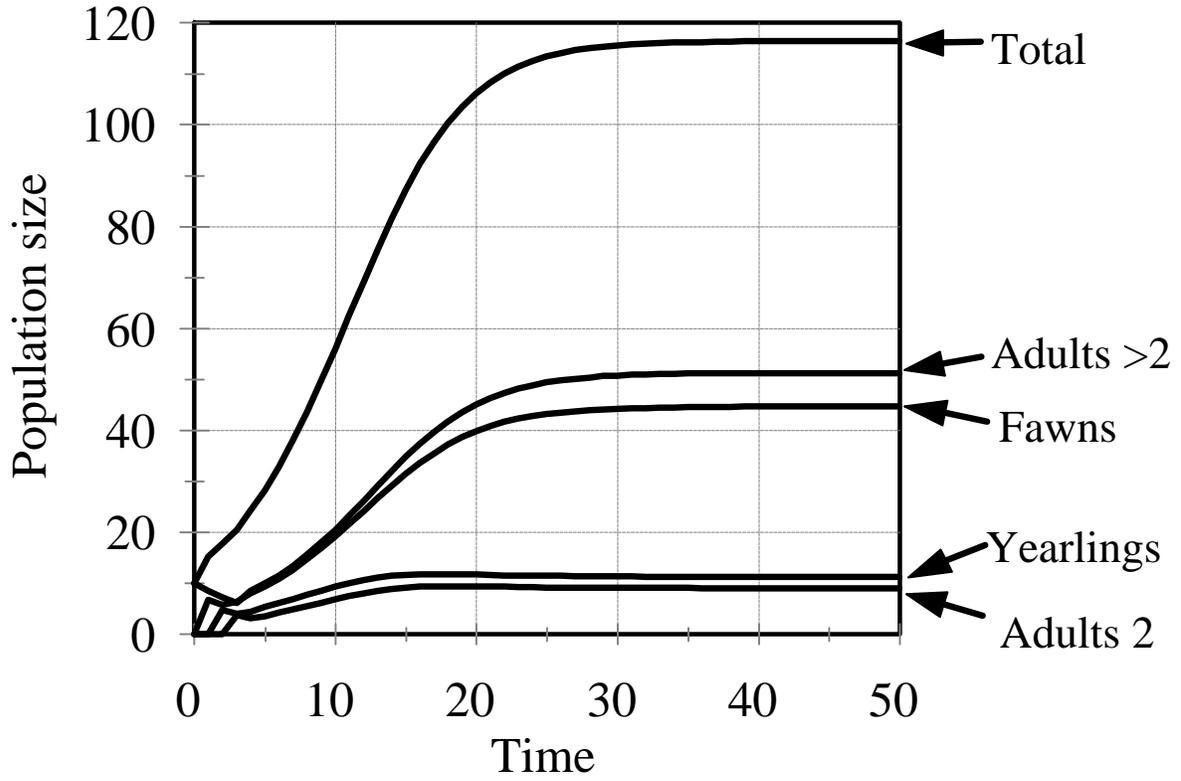


Figure 6. Population growth as a result of incorporating density dependence in fawn survival in the age-structured model of a mule deer population.

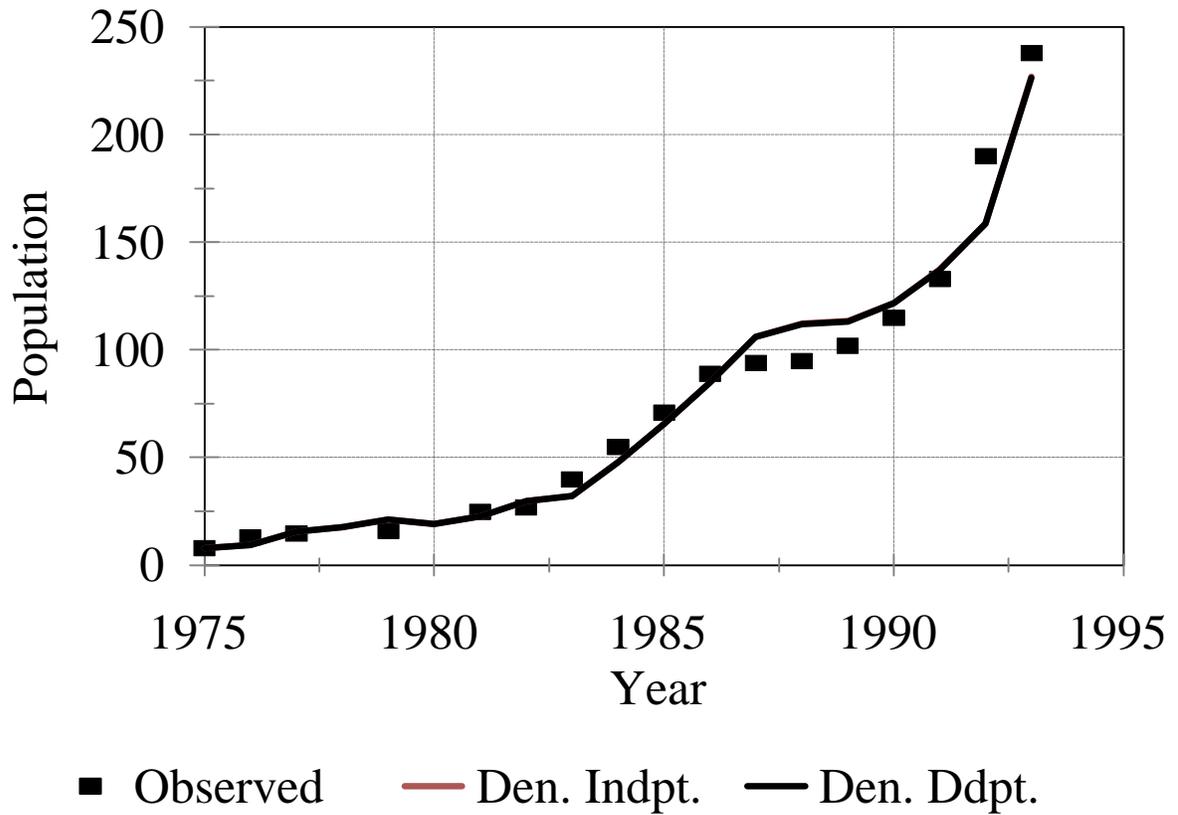


Figure 7. Fit of density-independent and density-dependent models to the data of Mccorquodale et al. (1988) and Eberhardt et al. (1996) from the Arid Lands Ecology Reserve, Washington. The two models are indistinguishable on the graph.

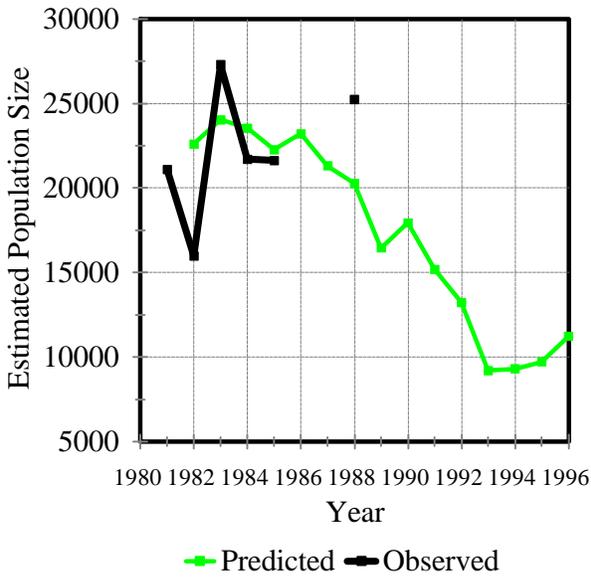
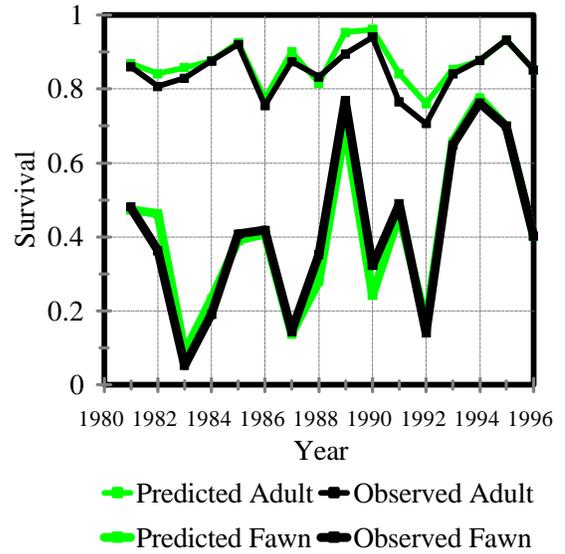
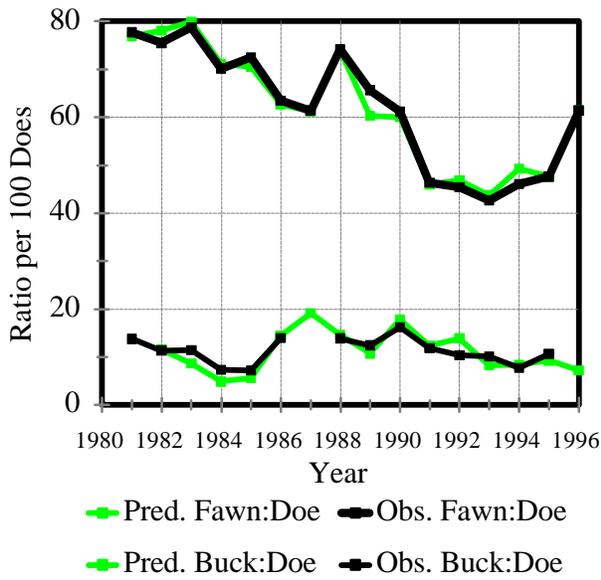


Figure 8. Results of fitting a model to the data in Table 1 on the Piceance mule deer herd in northwestern Colorado.