AGE STRUCTURED POPULATION MODELS

William D. Stone
February 24, 1997

Age Structured Population Models

William D. Stone

Contents

1 Introduction

In this module we will consider several ways to model population growth in birds. (Of course, similar methods could be used for other types of animals.) We will start with a very simple linear model, then using information about birds we will build an age-structured population model. After analyzing our linear model we will consider several nonlinear effects, and how to model and analyze them. Finally, we will consider how to add some random effects.

This sort of population modeling has many uses. We can get a better understanding of the system by modeling it, and we can examine the affects of different parameters. Models are used to make wildlife management decisions. Further, modeling can help determine what information is important, and thus influence field work.

2 A Very Simple Model

First, let us consider a species that reproduces once a year. There is some average number of offspring per female, and some average fraction of animals that survive the year. In many species the number of males and females are approximately equal, so we will keep track only of the females.

If each female gives birth to an average of b females per year and a fraction of the population s survive the year, we can calculate the next year's population from this year's:

$$P_{n+1} = s(1+b)P_n$$

where P_n = the female population in the n^{th} year. If P_0 is the population we start with, after one year we have

$$P_1 = s(1+b)P_0.$$

A year later we have

$$P_2 = s(1+b)P_1 = [s(1+b)]^2 P_0.$$

Try a couple more steps. The pattern becomes clear,

$$P_n = [s(1+b)]^n P_0.$$

Examples

2.1 Suppose a nest survey shows an average of 3.6 eggs per nest, and banding data indicates a 50% survival rate each year. What happens to the population size? Assuming an equal number of males and females, we have a female birth rate $b = 1.8$, with a survival rate $s = .5$. Thus

$$P_{n+1} = .5(1 + 1.8)P_n = 1.4P_n$$

$$P_1 = 1.4P_0, P_2 = 1.4P_1 = 1.96P_0,$$

$$\vdots$$

$$P_5 = (1.4)^5 P_0 = 5.376P_0.$$

Our population is growing.

2.2 If a population has a female birth rate of 1.1 and a survival rate of 45%, what happens to the population size?

$$b = 1.1 \text{ and } s = .45 \text{ gives}$$

$$P_{n+1} = (.45)(1 + 1.1)P_n = .945P_n$$

Each population is smaller than the one before; our population is decreasing.

Exercises

2.1 *Suppose the average number of female births is 1.5, and 75% of the population survives each year. What happens to the population size?*

2.2 *Suppose the average number of female births is 1.2 and 40% of the population survives each year. What happens to the population size?*

2.3 *What is the critical difference in problems 1 and 2?*

2.4 *Suppose you have a population where 60% survive each year. If you start with 100 newborn individuals, how many live to be one year old? How many to two? To three? Approximately, what is the average life span of these animals?*

3 The Birds and the Bees, for Birds

The simple model we developed in the previous section may be all right for some species, but many have a more complicated life cycle. Many bird species have three distinct life stages: chicks, juveniles, and adults.

A chick is a young bird, still being tended by her parents. The period of being a chick varies considerably among different species of birds. We will consider a species that stay with their parents for one full season.

When chicks are ready to leave their parents, they become juveniles. Although not ready to reproduce, they are no longer being tended by their parents. In some species, juveniles have the lowest survival rates; their parents are not looking after them the way the chicks' parents are, but the juveniles haven't established their territory and learned how to survive the way the adults have.

Juveniles who survive a season become adults. Adults have a relatively high survival rate and, of course, lay eggs and raise chicks.

It seems, then, that we need four numbers: the average number of chicks per adult, and the survival rates of chicks, juveniles, and adults. Biologists measure these rates by counting chicks in the nest and doing cohort studies. We will consider this in the next section.

Once we have birth rates and survival rates, we can construct a basic linear model. The number of chicks next year will be the per capita birth rate times the number of adults this year. The number of chicks this year times the survival rate for chicks gives next year's juveniles. The adults next year will be this year's adults that survive plus the juveniles that survive. Our model is

$$C_{n+1} = bA_n$$

$$J_{n+1} = s_C C_n$$

$$A_{n+1} = s_J J_n + s_A A_n.$$

Examples

3.1 Given the data

	Year 1	*Year 2*	*Year 3*
Chicks	110	120	140
Juveniles	40	65	70
Adults	50	55	75

estimate b, s_C, s_J and s_A.
The first season, 50 adults produced 120 chicks or $\frac{120}{50} = 2.4$ chicks per adult. The next season we had $\frac{140}{55} = 2.55$ chicks per adult. Averaging we estimate $b \approx 2.47$.
The first season $\frac{65}{110}$ chicks survived to become juveniles, the next season, $\frac{70}{120}$.
Averaging gives $s_C \approx .59$.
Survival rates for juveniles and adults are trickier, since the next year both are adults. Going from year 1 to year 2, we have

$$40s_J + 50s_A = 55.$$

Similarly, the next year gives

$$65s_J + 55s_A = 75.$$

Solving simultaneously gives $s_J = .69$, $s_A = .55$.

Exercises

3.1 *Suppose you are given the following population data.*

	Year 1	Year 2	Year 3
Chicks	*200*	*210*	*220*
Juveniles	*120*	*120*	*125*
Adults	*105*	*110*	*115*

Estimate b, s_C, s_J *and* s_A.

3.2 *How would this model change for species that are adults immediately after their year of being a chick?*

4 Population Measurement

How does one measure a population of birds? Going out and counting, you don't know if you saw them all, and you don't always know if you've counted the same one more than once.

One method that field biologists use to count a population is called *mark and release* counting. A sample of the population is captured and tagged. In the case of birds, they are ringed by attaching light metal rings to the bird's foot. This sample is counted and released. Then another sample is captured. The fraction of marked individuals in the new sample should approximate the fraction of marked individuals in the entire population.

For example, suppose we catch and mark 276 individuals. Next time, we catch 315 individuals, 24 of which are marked. From our second sample $\frac{24}{315}$, or about 7.6% are marked. If 7.6% of our whole population is marked, then 276 is 7.6% of the whole population. We can estimate our population, then, by $\frac{276}{.076} = 3623$. To improve our estimate, we could mark the remaining 291 individuals we have captured and repeat the process.

By counting or estimating the number of individuals of different ages each year, we can develop a cohort study. Starting with a group of individuals we keep track of how many are alive after one year, two years, etc. From this sort of information we derive our survival rates.

Examples

4.1 Suppose we start with 200 chicks. Each year 80% of the chicks survive, 60% of the juveniles, and 75% of the adults. What happens to the cohort?

Year 1	200 Chicks
Year 2	200 x $s_C = 160$ Juveniles
Year 3	160 x $s_J = 96$ Adults
Year 4	96 x $s_A = 72$ Adults
Year 5	74 x $s_A \cong 54$ Adults
Year 6	56 x $s_A \cong 41$ Adults
Year 7	42 x $s_A \cong 31$ Adults
	$\vdots$

Exercises

4.1 *Five cohorts, each starting with 200 individuals were followed for four years. From the data, estimate* s_C, s_J, s_A.

	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 5
Year 1	*118*	*120*	*120*	*122*	*115*
Year 2	*35*	*36*	*35*	*40*	*31*
Year 3	*28*	*29*	*28*	*30*	*25*
Year 4	*22*	*23*	*21*	*23*	*19*

4.2 *This exercise requires, for each group of students, 1-2 cups of dry beans (light colored) and markers. Take your population of beans and capture some (aim for about 10%). Tag your captured beans with a dot from your marker. Count and return the tagged individuals to the pile and mix. Capture another sample and estimate the total number of beans. Tag the unmarked members of your new sample and repeat. Use another color marker and repeat the entire process. Finally, count your beans and compare your four estimates with the actual population.*

5 The Linear Model

We return to our linear model:

$$C_{n+1} = bA_n$$

$$J_{n+1} = s_C C_n$$

$$A_{n+1} = s_J J_n + s_A A_n$$

or in matrix form:

$$\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{n+1} = \begin{pmatrix} 0 & 0 & b \\ s_C & 0 & 0 \\ 0 & s_J & s_A \end{pmatrix} \begin{pmatrix} C \\ J \\ A \end{pmatrix}_n \tag{1}$$

Examples

5.1 Considering again the parameters we derived in example 3.1, in matrix form we have

$$\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{n+1} = \begin{pmatrix} 0 & 0 & 2.47 \\ .59 & 0 & 0 \\ 0 & .69 & .55 \end{pmatrix} \begin{pmatrix} C \\ J \\ A \end{pmatrix}_{n}$$

Starting with 50 individuals in each age group, and multiplying by our matrix we get

$$\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{0} = \begin{pmatrix} 50 \\ 50 \\ 50 \end{pmatrix}, \begin{pmatrix} C \\ J \\ A \end{pmatrix}_{1} = \begin{pmatrix} 124 \\ 30 \\ 62 \end{pmatrix}, \begin{pmatrix} C \\ J \\ A \end{pmatrix}_{2} = \begin{pmatrix} 153 \\ 73 \\ 54 \end{pmatrix},$$

$$\ldots, \begin{pmatrix} C \\ J \\ A \end{pmatrix}_{10} = \begin{pmatrix} 649 \\ 315 \\ 331 \end{pmatrix}$$

clearly, our population is growing.
5.2 Considering the same model we use in example 5.1, we obtain the stable age distribution.

$$\frac{1}{P_0}\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{0} = \begin{pmatrix} .33 \\ .33 \\ .33 \end{pmatrix}, \frac{1}{P_1}\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{1} = \begin{pmatrix} .57 \\ .14 \\ .29 \end{pmatrix}, \frac{1}{P_2}\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{2} = \begin{pmatrix} .55 \\ .26 \\ .19 \end{pmatrix},$$

$$\ldots, \frac{1}{P_{10}}\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{10} = \begin{pmatrix} .50 \\ .24 \\ .26 \end{pmatrix}, \ldots, \frac{1}{P_{20}}\begin{pmatrix} C \\ J \\ A \end{pmatrix}_{20} = \begin{pmatrix} .51 \\ .24 \\ .25 \end{pmatrix}$$

Exercises

5.1 *Let* $b = 2$, $s_C = .6$, $s_J = .3$, $s_A = .7$. *Choose a reasonable starting value (no negative populations, at least some birds to start with) and run the model for several generations. What is happening to your population?*

5.2 *Repeat the previous exercise with* $b = 1.5$, $s_C = .6$, $s_J = .2$, $s_A = .7$.

As before, we see that populations can grow or decline. Of course things are not as simple as with our basic model, but we can still consider the overall growth rate. Let $P_n = C_n + J_n + A_n$. The ratio $\frac{P_{n+1}}{P_n}$ is not a constant as it was in section 2, but it approaches one.

5.3 *Consider the ratio* $\frac{P_{n+1}}{P_n}$ *as* n *gets large for the models in exercise 5.1 and 5.2. What do these ratios approach?*

5.4 *Compare your results in 5.3 to the results of someone who used a different starting population than you in 5.1 and 5.2.*

More is going on now than just the population growth; the population distribution is changing. If we divide each vector of population by the total population,

$$\frac{1}{P_n}\begin{pmatrix} C_n \\ J_n \\ A_n \end{pmatrix},$$

we can see what happens to the age distribution.

5.5 *Consider the age distributions for the models in 5.1 and 5.2. What happens as* n *gets large?*

5.6 *Compare your results in 5.5 to the results of someone who used a different starting population than you in 5.1 and 5.2.*

What we have just computed is called the *stable age distribution* for the population.

6 Decreased Egg Production

The simple model we considered in section 2 had three basic possible behaviors. Unbounded growth, decay to zero, or (if s(1+b) was exactly one) constant. This third situation is structurally unstable. Any change in the coefficients will almost certainly move the system into one of the other two cases. Since we only have estimates on birth rates and survival rates, this means our solution is very unreliable in this situation.

Despite this, most real world populations seem to settle down to a constant level if left alone. If we were to suddenly double the population, there wouldn't be enough food and the survival rate would go down. In other words, we expect that the survival rates s_C, s_J and s_A, and possibly the birth rate, b, are not constants, but functions of the population size.

Our model will still give us C_{n+1}, J_{n+1} and A_{n+1} as functions of C_n, J_n and A_n, but the functions will now be more complicated than the simple linear functions we had before. Such a system is called *nonlinear*. Analyzing nonlinear systems is a bit more complicated than linear systems, but numerical simulation is not much different.

To improve our model, then, we must consider how birth rates and survival rates will be affected by population size. These effects vary from species to species. In some kinds of birds, the juveniles are not completely on their own; they still depend partially on their parents. In these cases, egg production is often inhibited in parents with juveniles.

We will assume, then, that the number of (female) eggs produced per (female) adult is a function of the number of juveniles. We expect this to be a decreasing function, with a maximum at $J = 0$.

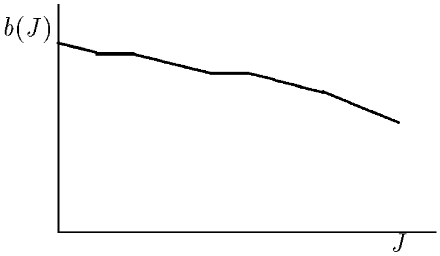

Figure 1

If we say the average clutch for a pair of adults with no juveniles is 4 eggs (2 females) then we expect b to be 2 when $J = 0$.

What else do we know about $b(J)$? If we had lots of data we could consider various functions. Such data, however, is not always easy to get. Lacking any reason or data for a fancier model, we will approximate $b(J)$ with a linear function, $b(J) = b_0 - mJ$. A few data points would be enough to approximate m.

Examples

6.1 Suppose $b(J) = 2 - .02J, s_C = .7, s_J = .2$, and $s_A = .8$. Starting with a population of 10 adults, what happens?

$$C_{n+1} = (2 - .02J_n)A_n$$

$$J_{n+1} = .7C_n$$

$$A_{n+1} .2J_n + .8A_n$$

$$\begin{pmatrix} C \\ J \\ A \end{pmatrix}_0 = \begin{pmatrix} 0 \\ 0 \\ 10 \end{pmatrix}, \begin{pmatrix} C \\ J \\ A \end{pmatrix}_1 = \begin{pmatrix} 20 \\ 0 \\ 8 \end{pmatrix}, \begin{pmatrix} C \\ J \\ A \end{pmatrix}_2 = \begin{pmatrix} 16 \\ 14 \\ 6.4 \end{pmatrix},$$

$$\begin{pmatrix} C \\ J \\ A \end{pmatrix}_3 = \begin{pmatrix} 11 \\ 11.2 \\ 7.9 \end{pmatrix}, \cdots, \begin{pmatrix} C \\ J \\ A \end{pmatrix}_{20} = \begin{pmatrix} 22.4 \\ 15.4 \\ 13.6 \end{pmatrix},$$

$$\cdots, \begin{pmatrix} C \\ J \\ A \end{pmatrix}_{100} = \begin{pmatrix} 40.2 \\ 28.1 \\ 28.0 \end{pmatrix}$$

The population settles down to a steady level.

Exercises

6.1 *Ten years of data on a population of birds is given in the chart. For convenience, the data has been put in order of increasing J. Plot the data on a graph. Does it look roughly linear? Sketch a reasonable line and get its equation. Better yet, if you know linear regression, find the best line to fit the data.*

Juveniles	Average Birth Rate
68	*1.12*
77	*1.20*
79	*1.19*
82	*1.29*
93	*1.44*
104	*1.40*
104	*1.45*
106	*1.56*
108	*1.54*
108	*1.69*

Thus we get our system:

$$C_{n+1} = (b_0 - mJ_n)A_n$$
$$J_{n+1} = s_C C_n$$
$$A_{n+1} = s_J J_n + s_A A_n$$

6.2 *Take the $b(J)$ from exercise 6.1 and use $s_C = .8$, $s_J = .3$, and $s_A = .65$ in this model. Start with a reasonable starting population and iterate 10 times. What is happening? Now iterate 100 times. What do you find?*

6.3 *Compare results with someone who used a different starting value.*

7 Decreased Overall Survival

Another possible effect of increased population is lowered survival rates across the board. This might be the case if food supply were the limiting factor.

Again, we expect the survival rate to be decreasing functions of population. Lacking any reason to the contrary, we will use linear functions. We assume that the population pressure affects all age classes equally, such that the ratios of survival rates is constant. For example, if the juvenile survival rate is .3 for very small populations, and the adult survival rate is .6, we will take the adult survival rate to be always twice the juvenile survival rate. Further, we assume that an individual has roughly the same effect on the food supply, regardless of her age class. Thus the survival rates are functions of $P_n = C_n + J_n + A_n$. Putting this together we get

$$\begin{aligned} C_{n+1} &= b\, A_n \\ J_{n+1} &= \hat{s}_C(1 - \frac{P_n}{K})C_n \qquad (2) \\ A_{n+1} &= \hat{s}_J(1 - \frac{P_n}{K})J_n + \hat{s}_A(1 - \frac{P_n}{K})A_n \end{aligned}$$

where $\hat{s}_C$, $\hat{s}_J$, $\hat{s}_A$ are the (constant) survival rates for low population, P_n is the total population, and K is a constant to be determined from field data.

Examples

7.1 Assuming a model of the form in equation 7.2, and given the following data, estimate the paramters.

n	C	J	A	P
1	37	21	17	75
2	31	16	21	68
3	46	15	18	79
4	35	22	13	70
5	26	18	23	67
6	51	15	20	86
7	35	20	22	77
8	45	17	19	81
9	39	27	22	88
10	47	22	24	93

Using $C_{n+1} = bA_n$ we get 9 estimates for b: 1.82, 2.19, 1.94, 2, 2.22, 1.75, 2.05, 2.05, 2.14. Averaging gives 2.02.
Solving these nonlinear is a little tricky, since $\frac{P_n}{k}$ appears nonlinearly three different places. To simplify the problem, we will solve the J_{n+1} equation for S_c and k, then use this value of k in the A_{n+1} equation to solve for S_j and S_A.
The equation $J_{n+1} = \hat{S}_C(1 - \frac{P_n}{k})C_n$ can be thought of as a linear equation for $\hat{S}_C$ and $\frac{\hat{S}_C}{k}$. Using our data we get

$$\begin{aligned}
16 &= 37S_C - 2775\frac{S_C}{k} \\
15 &= 31S_C - 2108\frac{S_C}{k} \\
22 &= 46S_C - 3634\frac{S_C}{k} \\
18 &= 35S_C - 2450\frac{S_C}{k} \\
15 &= 26S_C - 1742\frac{S_C}{k} \\
20 &= 51S_C - 4386\frac{S_C}{k} \\
17 &= 35S_C - 2695\frac{S_C}{k} \\
27 &= 45S_C - 3645\frac{S_C}{k} \\
22 &= 39S_C - 3432\frac{S_C}{k}
\end{aligned}$$

In matrix form we have

$$\begin{pmatrix} 37 & 2775 \\ 31 & 2108 \\ 46 & 3034 \\ 35 & 2450 \\ 26 & 1742 \\ 51 & 4386 \\ 35 & 2695 \\ 45 & 3645 \\ 39 & 3432 \end{pmatrix} \begin{pmatrix} S_C \\ \frac{-S_C}{k} \end{pmatrix} = \begin{pmatrix} 16 \\ 15 \\ 22 \\ 18 \\ 15 \\ 20 \\ 17 \\ 27 \\ 22 \end{pmatrix}$$

13

When we have an over determined equation of this sort, the least squares solution can be calculated by multiplying both sides by the transpose of the matrix, then solving the resulting system. Thus if we have

$$A\vec{x} = \vec{b}$$

we get

$$A^T A\vec{x} = A^T\vec{b}$$

then the least squares solution is

$$\vec{x} = (A^T a)^{-1} A^T \vec{b}.$$

Here, we get

$$\begin{pmatrix} S_C \\ \frac{-S_C}{k} \end{pmatrix} = \begin{pmatrix} .612 \\ -.0015 \end{pmatrix}$$

Thus $S_C = .612$, $k = 408$.
Now, using this k, we get our equations for S_J and S_A.

$$\begin{array}{c} 21 = 17.1S_J + 13.9S_A \\ 18 = 13.3S_J + 17.5S_A \\ 13 = 12.1S_J + 14.5S_A \\ 23 = 18.2S_J + 10.8S_A \\ 20 = 15.0S_J + 16.7S_A \\ 22 = 11.8S_J + 15.8S_A \\ 19 = 16.2S_J + 17.8S_A \\ 22 = 13.6S_J + 15.2S_A \\ 24 = 21.2S_J + 18.8S_A \end{array}$$

The least squares solution is $S_J = .918$, $S_A = .379$.
7.2 Taking the model from example 7.1, what happens to the population? Using the parameters from example 7.1, we have

$$C_{n+1} = 2.02A_n$$

$$J_{n+1} = .612\left(1 - \frac{P_n}{408}\right)C_n$$

$$A_{n+1} = .918\left(1 - \frac{P_n}{408}\right)J_n + .379\left(1 - \frac{P_n}{408}\right)A_n$$

Starting with 100 adults, after 10 generations we have

$$\begin{pmatrix} C \\ J \\ A \end{pmatrix} = \begin{pmatrix} 44 \\ 17 \\ 26 \end{pmatrix}$$

After 20 generations,

$$\begin{pmatrix} 45 \\ 21 \\ 22 \end{pmatrix}.$$

After 100 generations we have

$$\begin{pmatrix} 44 \\ 21 \\ 22 \end{pmatrix}$$

(rounded to integers).
Our population seems to have settled down to a constant level.

Exercises

7.1 *Take* $b = 2$, $\hat{s}_C = .8$, $\hat{s}_J = .3$, $\hat{s}_A = .65$ *and* $K = 1000$. *Repeat exercises 6.2 and 6.3 for this model.*

7.2 *Assuming a model of the form (2), use linear regression to solve for the constants to fit the data below.*

n	C	J	A
1	*95*	*58*	*40*
2	*77*	*74*	*44*
3	*86*	*61*	*60*
4	*127*	*64*	*67*
5	*133*	*95*	*60*
6	*113*	*102*	*67*
7	*137*	*86*	*73*
8	*149*	*103*	*67*

7.3 *Take the parameters you obtained in 7.2, and repeat exercise 7.1.*

8 Competition for Nesting Sites

In some species, the limiting factor is not food so much as room. Some birds have very specific nesting site requirements, and are very territorial. For a juvenile to survive, she must find an appropriate site, in unoccupied territory. The red cockaded woodpecker [see <http://dataadmin.irm.r9.fws.gov/bio-rcw.html>] and the northern spotted owl are two endangered species for which appropriate territory is a crucial limiting factor. Since adults normally have an established territory, the population pressure falls mainly on the juveniles, and the survival rate is mainly dependent on the number of adults. If we approximate the juvenile survival rate by a linear function of the number of adults we get:

$$C_{n+1} = b\,A_n$$

$$J_{n+1} = s_C C_n$$

$$A_{n+1} = \hat{s}_J(1 - kA_n)J_n + s_A A_n$$

Examples

8.1 Given the following data, and assuming a model of the form given in the equation above, estimate the parameters.

n	C	J	A	P
1	196	143	103	442
2	206	115	109	430
3	229	128	96	453
4	189	140	94	423
5	185	116	96	397
6	182	121	99	402
7	201	111	103	415
8	206	122	106	434

Using $C_{n+1} = bA_n$ we get seven estimates of b: 2.0, 2.10. 1.97, 1.97, 1.90, 2.03, 2. Averaging we get 1.99.
From $J_{n+1} = S_c C_n$ we again get seven estimates of S_c. Averaging gives .615.
Setting up the equation $A_{n+1} = S_J(1-kA_n)J_n+S_A A_n = S_j J_n - kS_j A_n J_n + S_A A_n$ for $S_J, -kS_J, S_A$ gives

$$109 = S_J \cdot 143 - kS_J \cdot 14729 + S_A \cdot 103$$

$$96 = S_J \cdot 115 - kS_J \cdot 12535 + S_A \cdot 109$$

$$94 = S_J \cdot 128 - kS_J \cdot 12288 + S_A \cdot 96$$

$$96 = S_J \cdot 140 - kS_J \cdot 13160 + S_A \cdot 94$$

$$99 = S_J \cdot 116 - kS_J \cdot 11136 + S_A \cdot 96$$

$$103 = S_J \cdot 121 - kS_J \cdot 11979 + S_A \cdot 99$$

$$106 = S_J \cdot 111 - kS_J \cdot 11433 + S_A \cdot 103$$

or in matrix form

$$\begin{pmatrix} 143 & 14729 & 103 \\ 115 & 12535 & 109 \\ 128 & 12288 & 96 \\ 140 & 13160 & 94 \\ 116 & 11136 & 96 \\ 121 & 11979 & 99 \\ 111 & 11433 & 103 \end{pmatrix} \begin{pmatrix} S_J \\ -kS_J \\ S_A \end{pmatrix} = \begin{pmatrix} 109 \\ 96 \\ 94 \\ 96 \\ 99 \\ 103 \\ 106 \end{pmatrix}$$

Multiplying by the transpose of the matrix gives

$$\begin{pmatrix} 110076 & 10973334 & 87260 \\ 10973334 & 1096470636 & 8732666 \\ 87260 & 8732666 & 70168 \end{pmatrix} \begin{pmatrix} S_J \\ -kS_J \\ S_A \end{pmatrix} = \begin{pmatrix} 87812 \\ 8775452 \\ 70358 \end{pmatrix}$$

so the least squares solution is

$$\begin{pmatrix} S_J \\ -kS_J \\ S_A \end{pmatrix} = \begin{pmatrix} .400 \\ -.00273 \\ .844 \end{pmatrix}$$

or

$$S_J = .400$$

$$k = .0068$$

$$S_A = .844$$

8.2 Taking the parameters from example 8.1, what happens to the population? Using the numbers from example 8.1, we have

$$C_{n+1} = 1.99A_n$$

$$J_{n+1} = .615C_n$$

$$A_{n+1} = .40(1 - .0068A_n)J_n + .844A_n$$

starting with 100 adults only, after 10 generations we have

$$\begin{pmatrix} C \\ J \\ A \end{pmatrix} = \begin{pmatrix} 19 \\ 116 \\ 97 \end{pmatrix}$$

After 20, we have

$$\begin{pmatrix} 199 \\ 122 \\ 100 \end{pmatrix}$$

After 100 generations our population seems to have settled down to

$$\begin{pmatrix} 199 \\ 123 \\ 100 \end{pmatrix}$$

(rounded to integers).

Exercises

8.1 *Using the data in table 1 approximate b,* s_C, $\hat{s}_J$, s_A *and k.*

Table 1.

n	C	J	A
1	*219*	*161*	*132*
2	*271*	*181*	*145*
3	*293*	*220*	*162*
4	*314*	*246*	*174*
5	*330*	*251*	*213*
6	*420*	*250*	*224*
7	*441*	*332*	*236*
8	*471*	*359*	*271*

8.2 *Using the data from exercise 8.1, repeat exercises 6.2 and 6.3.*

8.3 *What are the units on the constant k?*

8.4 *What are some other ways population pressure might affect a species? One example might be too many juveniles lowering the chicks' survival rate. Can you think of others? Make up a model to fit the given example or your own example.*

9 Fixed Points

The nonlinear systems we have been considering have tended to settle down to a constant population distribution after several generations. For instance, consider the system

$$C_{n+1} = 2A_n$$
$$J_{n+1} = .8C_n \tag{3}$$
$$A_{n+1} = .4(1 - \frac{A_n}{500})J_n + .7A_n.$$

Let $C_0 = 0 = J_n$, $A_0 = 100$; after five generations we have

$$C_5 = 202,\ J_5 = 147,\ A_5 = 96$$

After ten generations

$$C_{10} = 298,\ J_{10} = 218,\ A_{10} = 163$$

Then

$$C_{20} = 477,\ J_{20} = 373,\ A_{20} = 243$$

After 40 generations or so, the system has settled down to approximately

$$C = 531,\ J = 425,\ A = 266.$$

A constant solution to an interative system is called a *fixed point* or a steady state. Evaluating a system at $(C_n, J_n, A_n) =$ a fixed point, gives the same values for $(C_{n+1}, J_{n+1}, A_{n+1})$.

Let us look for a fixed point to system (3). Setting $C_{n+1} = C_n = C$, and similarly for J and A, we get

$$C = 2A$$
$$J = .8C$$
$$A = .4(1 - \frac{A}{500})J + .7A$$

Substituting $C = 2A,\ J = .8C = 1.6A$, into the third equation gives

$$A = .64(1 - \frac{A}{500})A + .7A$$

or

$$\frac{.64}{500}A^2 - .34A = 0.$$

Thus we get $A = 0$ (which implies $C = J = 0$) or

$$A = \frac{500}{.64}(.34) = 265.625,$$

so

$$C = 2A = 531.25,\ J = .8C = 425.$$

Thus we see there are exactly two fixed points: (0,0,0) and (531,425,266).

Examples

9.1 We had three nonlinear systems in our previous examples. Each of these converged to a constant population. Now we look for the fixed points.
a) Example 6.1 had the system

$$C_{n+1} = (2 - .02J_n)A_n$$

$$J_{n+1} = .7C_n$$

$$A_{n+1} = .2J_n + .8A_n$$

So we look for a solution to

$$C = (2 - .02J)A$$

$$J = .7C$$

$$A = .2J + .8A$$

The third equation implies that $A = J$, so we know $A = J = .7C$ (from the second equation). Using this in the first, we get $C = (2 - .014C).7C$ so $C = A = J = 0$ or $C = 40.8$, $A = J = 28.6$. This agrees with the result in example 6.1.
b) Example 7.2 had the system

$$C_{n+1} = 2.02A_n$$

$$J_{n+1} = .612\left(1 - \frac{P_n}{408}\right)C_n$$

$$A_{n+1} = .918\left(1 - \frac{P_n}{408}\right)J_n + .379\left(1 - \frac{P_n}{408}\right)A_n$$

Again we eliminate subscripts and look for the fixed point, recalling that $P_n = C_n + J_n + A_n$. Eliminating C we get

$$J = 1.23624\left(1 - \frac{J + 3.02A}{408}\right)A$$

$$.918\left(1 - \frac{J + 3.02A}{408}\right)J + .379\left(1 - \frac{J + 3.02A}{408}\right)A$$

Multiplying the second equation by A, and eliminating the $\left(1 - \frac{P}{408}\right)$ terms, gives $1.23624A^2 - .379AJ - .918J^2 = 0$. Solving this quadratic (ignoring the negative root) gives

$$A = .943J.$$

Substituting this back in, we get

$$J = 1.17\,(1 - .00971J)\,J$$

so $J = 0 = A = C$ or $J = 14.6$, $A = .943J = 13.8$, $C = 2.02A = 27.9$. This also agrees with the results from example 7.2.
c) Example 8.2 had the system

$$C_{n+1} = 1.99A_n$$

$$J_{n+1} = .615C_n$$

$$A_{n+1} = .40\,(1 - .0068A_n)\,J_n + .844A_n$$

Using $C = 1.99A$, and $J = .615C = 1.22A$ we get $A = .49(1 - .0068A)A + .844A$ so $.156A = .49(1 - .0068A)A$ and $A = 0 = J = C$ or $A = 100.2$, $J = 1.22A = 122.3$, $C = 199.5$.
Again, this agrees with the results in the example.

Exercises

9.1 *Find the fixed points to the system in exercise 6.2.*

9.2 *Find the fixed points to the system in exercise 7.1.*

9.3 *Find the fixed points to the system in exercise 7.3.*

9.4 *Find the fixed points to the system in exercise 8.1.*

9.5 *How did the fixed points you found compare to your solution after 100 generations?*

10 Stochastic Models

In the modeling we have done so far, all our parameters have been averages. We have taken lots of observations and then fit a number to our data. For large populations this is reasonable. Years with bigger growth and years with smaller growth balance out. For some endangered species, however, the number of individuals is so low that using average values for parameters is not very reliable. Fluctuations around the norm may have important effects. A population where a female sometimes lays 1 egg, sometimes 2 and sometimes more, is different from a population where the females always lay 2 eggs, even if the average is the same. A model that incorporates this kind of uncertainty is called a stochastic model.

To build a model to consider these effects, we have to consider each individual in the population, and model the significant events in their life cycle. For example, our birds are born, some survive from chicks to juveniles, some survive to adulthood, lay eggs, etc. To simplify matters, we will assume these happen at distinct times: nesting in the spring, most death (thus survival) over the winter.

Suppose for our population we expect an average of 80% of our chicks to survive to be juveniles. We need to go through our population of chicks one by one and decide whether or not they survive. We want our model to have an average survival rate for chicks of .8, though some years will be higher and some lower. To do this we choose a random number between 0 and 1. If this number is less than 0.8, the chick survives, otherwise that individual dies. After deciding whether or not each chick survives, we have the next generation's juvenile population.

Similarly, we choose a random number for each juvenile and each adult. Comparing the random number to the average survival rate, we decide whether each individual dies, or becomes part of the next generation's adults.

When it comes to determining the number of eggs, our problem gets a bit more complicated. Just knowing the average number of eggs doesn't tell us the distribution of clutch sizes: what percent of pairs have no female chicks, one, two, three or more.

If we have lots of data, we may be able to approximate this distribution. We seldom have enough information to determine how this distribution changes with population size, so we assume the distribution doesn't change. Nest surveys are made, counting the number of eggs for each nesting pair. For instance, a survey of many nests might give us the data in table 2.

Table 2.

# eggs	0	1	2	3	4	5	6
% nests	3	2	5	12	44	29	5

If we assume equal numbers of males and females, we can calculate the probabilities of no female chicks in a nest, of one female chick, of two, etc.

As an example, suppose a nest has four eggs. Each egg is equally likely to be a female or a male, so there are sixteen equally likely outcomes for the nest:

MMMM	MMMF	MMFM	MMFF
MFMM	MFMF	MFFM	MFFF
FMMM	FMMF	FMFM	FMFF
FFMM	FFMF	FFFM	FFFF

Of these sixteen possibilities, one has no females, four have one female, six have two females, four have three females, and one has four females. Thus the probability of no females in a nest of four eggs is $\frac{1}{16}$; the probability of one female in a nest of four eggs is $\frac{4}{16}$; and so on.

Counting up the possible outcomes for other clutch sizes we can construct table 3.

Table 3. Probabilities for Various Numbers of Females

Eggs in Nest	*Number of Females*						
	0	1	2	3	4	5	6
0	1	0	0	0	0	0	0
1	$\frac{1}{2}$	$\frac{1}{2}$	0	0	0	0	0
2	$\frac{1}{4}$	$\frac{2}{4}$	$\frac{1}{4}$	0	0	0	0
3	$\frac{1}{8}$	$\frac{3}{8}$	$\frac{3}{8}$	$\frac{1}{8}$	0	0	0
4	$\frac{1}{16}$	$\frac{4}{16}$	$\frac{6}{16}$	$\frac{4}{16}$	$\frac{1}{16}$	0	0
5	$\frac{1}{32}$	$\frac{5}{32}$	$\frac{10}{32}$	$\frac{10}{32}$	$\frac{5}{32}$	$\frac{1}{32}$	0
6	$\frac{1}{64}$	$\frac{6}{64}$	$\frac{15}{64}$	$\frac{20}{64}$	$\frac{15}{64}$	$\frac{6}{64}$	$\frac{1}{64}$

Exercises

10.1 *Can you see the pattern in table 3? (Hint: Think about Pascal's triangle.)*

Now we are ready to calculate the distribution of numbers of females. For example, given the information in table 2 and table 3, what is the probability of exactly 2 female chicks in a nest?

We take the probability of 2 females in a nest of k eggs times the probability of a nest with k eggs, and add them up:

$$0 \cdot \frac{3}{100} + 0 \cdot \frac{2}{100} + \frac{1}{4} \cdot \frac{5}{100} + \frac{3}{8} \cdot \frac{12}{100} + \frac{6}{16} \cdot \frac{44}{100} + \frac{10}{32} \cdot \frac{29}{100} + \frac{20}{64} \cdot \frac{5}{100} = .3248$$

In the same way, we calculate the probabilities of other numbers of females in a nest, and obtain table 4.

Table 4.

# of female chicks	0	1	2	3	4	5	6
Probability	.105	.24	.325	.231	.084	.014	.001

10.2 *Calculate table 4 from table 2 and table 3.*

Finally we simulate the number of chicks in our next generation. For each adult female choose a random number. If it is less than .105, this bird has no female chicks this year. If the random number is between .105 and .345 (.105 + .240) she has one female chick; if it is between .345 and .670 (.345 + .325) she has two, and so on.

A sample program, corresponding to the model in section 8, might look like

```
Put in an initial population.
    Input C(0),J(0),A(0)

This calculates the number of female chicks from each adult female, and adds
them up for the next generation of chicks.
    For $K = 1$ to (Number of Generations)
        For $i = 1$ to $A(K-1)$
            $b$ =random #
            if $b \leq .05$, then $e = 0$
            if $.105 < b \leq .345$, then $e = 1$
            if $.345 < b \leq .67$, then $e = 2$
            if $.67 < b \leq .901$, then $e = 3$
            if $.901 < b \leq .985$, then $e = 4$
            if $.985 < b \leq .999$, then $e = 5$
            if $.999 < b$, then $e = 6$
            $C(K) = C(K) + e$
        next i
This counts how many chicks survive to be the next generation of juveniles.
        For $i = 1$ to $C(K-1)$
            $s$ =random #
            if $s < .8$ then $J(K) = J(K) + 1$
        next i
This counts how many juveniles survive, taking into account the nonlinear
survival rate.
        For $i = 1$ to $J(K-1)$
            $s$ =random #
            if $s < .4(1 - \frac{A(K-1)}{500})$ then $A(K) = A(K) + 1$
        next i
This is the survival of the adults.
        For $i = 1$ to $A(K-1)$
            $s$ =random #
            if $s < .7$ then $A(K) = A(K) + 1$
        next i
    Print K, C(K), J(K), A(K)
    Next K
```

10.3 *Write a program to implement the above scheme.*

10.4 *Take the data from a 10 year run of the program you wrote in exercise 10.3. Fit the model parameters from your data. How well did they agree with what was used in the model? Compare your results to other groups. Why is there a difference?*

Since each time we run this program we get different values, due to the randomness in the program, this is not a solution in the same sense as we had before. We can, however, run the program many times and get statistics on the behaviour. We can examine questions such as, "What happens if the available habitat is cut in half? What percent of the time will the population die out?" This kind of information is useful for wildlife managers who need to predict the effect of various actions. With endangered species, particularly, we can't run several experiments, so this sort of probability of survival is the best we can get.

10.5 *Run your program for 100 years, starting with a group of 10 adults, 500 times. Get the following statistics:*

- *i) Probability of survival for 100 years.*
- *ii) Mean and variance of average total population over the last 10 years.*
- *iii) Mean and variance of average adult population over the last 10 years.*

Another possibility with a stochastic model is to add effects due to weather or epidemics, which some years have a much larger affect than others. A "weather multiplier" between 0 and 1 might be multiplied on all the survival rates, and the distribution of harsh winters estimated from past weather data. Similarly, a disease might affect survival rates by a lot in years of epidemic, and not at all other years. This can also be included in a stochastic model given sufficient data.

10.6 *Suppose a frost 2 weeks later than average reduces egg production by 20%, and 4 weeks later than usual reduces eggs by 60%. Look up last frost dates in your area for the last hundred years and add this weather effect to your model. How are your statistics changed?*

10.7 *Suppose (on average) once every 20 years, pneumonia kills $\frac{1}{2}$ of all your birds. Add this effect to your model. How are your statistics changed?*

11 Conclusion

We have gone through several methods to model population growth in our bird population. We started with linear models, getting the ideas of a growth rate and a stable age distribution. Then we looked at several possible nonlinear effects, and their fixed points. Finally, we considered how random effects could be considered.

This sort of modeling can be used to predict how changes in the environment affect populations. This can help with wildlife management. We have looked at fairly simple models, with birth and annual survival rates. Where necessary, more complex models can be built that consider more life stages: birth, fledging, juvenile survival, finding a territory, finding a mate, etc.

How good our predictions are, is dependent on how good our data are. Another way these models are used is in helping to determine what information is most critical, and thus guiding what field work needs to be done. This is another important way that mathematics and science interact.

Of course, we could have used the same techniques for species other than birds. All we need is an understanding of the life cycle of the species, and the data.