# 1

# Dynamic Modeling with Difference Equations

Whether we investigate the growth and interactions of an entire population, the evolution of DNA sequences, the inheritance of traits, or the spread of disease, biological systems are marked by change and adaptation. Even when they appear to be constant and stable, it is often the result of a balance of tendencies pushing the systems in different directions. A large number of interactions and competing tendencies can make it difficult to see the full picture at once.

How can we understand systems as complicated as those arising in the biological sciences? How can we test whether our supposed understanding of the key processes is sufficient to describe how a system behaves? Mathematical language is designed for precise description, and so describing complicated systems often requires a *mathematical model*.

In this text, we look at some ways mathematics is used to model dynamic processes in biology. Simple formulas relate, for instance, the population of a species in a certain year to that of the following year. We learn to understand the consequences an equation might have through mathematical analysis, so that our formulation can be checked against biological observation. Although many of the models we examine may at first seem to be gross simplifications, their very simplicity is a strength. Simple models show clearly the implications of our most basic assumptions.

We begin by focusing on modeling the way populations grow or decline over time. Since mathematical models should be driven by questions, here are a few to consider: Why do populations sometimes grow and sometimes decline? Must populations grow to such a point that they are unsustainably large and then die out? If not, must a population reach some equilibrium? If an equilibrium exists, what factors are responsible for it? Is such an equilibrium so delicate that any disruption might end it? What determines whether a given population follows one of these courses or another?

To begin to address these questions, we start with the simplest mathematical model of a changing population.

## 1.1. The Malthusian Model

Suppose we grow a population of some organism, say flies, in the laboratory. It seems reasonable that, on any given day, the population will change due to new births, so that it increases by the addition of a certain multiple $f$ of the population. At the same time, a fraction $d$ of the population will die.

Even for a human population, this model might apply. If we assume humans live for 70 years, then we would expect that from a large population roughly $1/70$ of the population will die each year; so, $d = 1/70$. If, on the other hand, we assume there are about four births in a year for every hundred people, we have $f = 4/100$. Note that we have chosen *years* as units of time in this case.

- Explain why, for any population, $d$ must be between 0 and 1. What would $d < 0$ mean? What would $d > 1$ mean?
- Explain why $f$ must be at least 0, but could be bigger than 1. Can you name a real organism (and your choice of units for time) for which $f$ would be bigger than 1?
- Using *days* as your unit of time, what values of $f$ and $d$ would be in the right ballpark for elephants? Fish? Insects? Bacteria?

To track the population $P$ of our laboratory organism, we focus on $\Delta P$, the *change* in population over a single day. So, in our simple conception of things,

$$\Delta P = fP - dP = (f - d)P.$$

What this means is simply that given a current population $P$, say $P = 500$, and the fecundity and death rates $f$ and $d$, say $f = .1$ and $d = .03$, we can predict the change in the population $\Delta P = (.1 - .03)500 = 35$ over a day. Thus, the population at the beginning of the next day is $P + \Delta P = 500 + 35 = 535$.

Some more notation will make this simpler. Let

$$P_t = P(t) = \text{the size of the population measured on day } t,$$

so

$$\Delta P = P_{t+1} - P_t$$

Table 1.1. *Population Growth According to a Simple Model*

| Day | Population |
|---|---|
| 0 | 500 |
| 1 | $(1.07)500 = 535$ |
| 2 | $(1.07)^2 500 = 572.45$ |
| 3 | $(1.07)^3 500 \approx 612.52$ |
| 4 | $(1.07)^4 500 \approx 655.40$ |
| ⋮ | ⋮ |

is the *difference* or change in population between two consecutive days. (If you think there should be a subscript $t$ on that $\Delta P$, because $\Delta P$ might be different for different values of $t$, you are right. However, it's standard practice to leave it off.)

Now what we ultimately care about is understanding the population $P_t$, not just $\Delta P$. But

$$P_{t+1} = P_t + \Delta P = P_t + (f - d)P_t = (1 + f - d)P_t.$$

Lumping some constants together by letting $\lambda = 1 + f - d$, our model of population growth has become simply

$$P_{t+1} = \lambda P_t.$$

Population ecologists often refer to the constant $\lambda$ as the *finite growth rate* of the population. (The word "finite" is used to distinguish this number from any sort of instantaneous rate, which would involve a derivative, as you learn in calculus.)

For the values $f = .1$, $d = .03$, and $P_0 = 500$ used previously, our entire model is now

$$P_{t+1} = 1.07 P_t, \quad P_0 = 500.$$

The first equation, relating $P_{t+1}$ and $P_t$, is referred to as a *difference equation* and the second, giving $P_0$, is its *initial condition.* With the two, it is easy to make a table of values of the population over time, as in Table 1.1.

From Table 1.1, it's even easy to recognize an explicit formula for $P_t$,

$$P_t = 500(1.07)^t.$$

For this model, we can now easily predict populations at any future times.

It may seem odd to call $P_{t+1} = (1 + f - d)P_t$ a difference equation, when the difference $\Delta P$ does not appear. However, the equations

$$P_{t+1} = (1 + f - d)P_t$$

and

$$\Delta P = (f - d)P$$

are mathematically equivalent, so either one is legitimately referred to by the same phrase.

**Example.** Suppose that an organism has a very rigid life cycle (which might be realistic for an insect), in which each female lays 200 eggs, then all the adults die. After the eggs hatch, only 3% survive to become adult females, the rest being either dead or males. To write a difference equation for the females in this population, where we choose to measure $t$ in generations, we just need to observe that the death rate is $d = 1$, while the effective fecundity is $f = .03(200) = 6$. Therefore,

$$P_{t+1} = (1 + 6 - 1)P_t = 6P_t.$$

- ► Will this population grow or decline?
- ► Suppose you don't know the effective fecundity, but do know that the population is stable (unchanging) over time. What must the effective fecundity be? (*Hint*: What is $1 + f - d$ if the population is stable?) If each female lays 200 eggs, what fraction of them must hatch and become females?

Notice that in this last model we ignored the males. This is actually a quite common approach to take and simplifies our model. It does mean we are making some assumptions, however. For this particular insect, the precise number of males may have little effect on how the population grows. It might be that males are always found in roughly equal numbers to females so that we know the total population is simply double the female one. Alternately, the size of the male population may behave differently from the female one, but whether there are few males or many, there are always enough that female reproduction occurs in the same way. Thus, the female population is the important one to track to understand the long-term growth or decline of the population.

- ► Can you imagine circumstances in which ignoring the males would be a bad idea?

**What is a difference equation?** Now that you have seen a difference equation, we can attempt a definition: a difference equation is a formula expressing values of some quantity $Q$ in terms of previous values of $Q$. Thus, if $F(x)$ is any function, then

$$Q_{t+1} = F(Q_t)$$

is called a difference equation. In the previous example, $F(x) = \lambda x$, but often $F$ will be more complicated.

In studying difference equations and their applications, we will address two main issues: 1) How do we find an appropriate difference equation to model a situation? 2) How do we understand the behavior of the difference equation model once we have found it?

Both of these things can be quite hard to do. You learn to model with difference equations by looking at ones other people have used and then trying to create some of your own. To be honest, though, this will not necessarily make facing a new situation easy. As for understanding the behavior a difference equation produces, usually we cannot hope to find an explicit formula like we did for $P_t$ describing the insect population. Instead, we develop techniques for getting less precise qualitative information from the model.

The particular difference equation discussed in this section is sometimes called an *exponential* or *geometric model*, since the model results in exponential growth or decay. When applied to populations in particular, it is associated with the name of Thomas Malthus. Mathematicians, however, tend to focus on the form of the equation $P_{t+1} = \lambda P_t$ and say the model is *linear*. This terminology can be confusing at first, but it will be important; *a linear model produces exponential growth or decay.*

## Problems

1.1.1. A population is originally 100 individuals, but because of the combined effects of births and deaths, it triples each hour.
   a. Make a table of population size for $t = 0$ to 5, where $t$ is measured in hours.
   b. Give two equations modeling the population growth by first expressing $P_{t+1}$ in terms of $P_t$ and then expressing $\Delta P$ in terms of $P_t$.
   c. What, if anything, can you say about the birth and death rates for this population?

1.1.2. In the early stages of the development of a frog embryo, cell division occurs at a fairly regular rate. Suppose you observe that all cells divide, and hence the number of cells doubles, roughly every half-hour.

  a. Write down an equation modeling this situation. You should specify how much real-world time is represented by an increment of 1 in $t$ and what the initial number of cells is.
  b. Produce a table and graph of the number of cells as a function of $t$.
  c. Further observation shows that, after 10 hours, the embryo has around 30,000 cells. Is this roughly consistent with your model? What biological conclusions and/or questions does this raise?

1.1.3. Using a hand calculator, make a table of population values at times 0 through 6 for the following population models. Then graph the tabulated values.

  a. $P_{t+1} = 1.3P_t$, $P_0 = 1$
  b. $N_{t+1} = .8N_t$, $N_0 = 10$
  c. $\Delta Z = .2Z$, $Z_0 = 10$

1.1.4. Redo Problem 1.1.3(a) using MATLAB by entering a command sequence like:

```
p=1
x=p
p=1.3*p
x=[x p]
p=1.3*p
x=[x p]
⋮
```

(Because this repeats an earlier command, you can save some typing by hitting the "↑" key twice.)

Explain how this works.

Now redo the problem again by a command sequence like:

```
p=1
x=1
for i=1:10
    p=1.3*p
    x=[x p]
end
```

(The indentation is not necessary, but helps make the *for-end* loop clearer to read.)

Explain how this works as well.

Graph your data with:

```
plot([0:10],x)
```

1.1.5. For the model in Problem 1.1.3(a), how much time must pass before the population exceeds 10, exceeds 100, and exceeds 1,000? (Use MATLAB to do this experimentally, and then redo it using logarithms and the fact that $P_t = 1.3^t$.) What do you notice about the difference between these times? Explain why this pattern holds.

1.1.6. If the data in Table 1.2 on population size were collected in a laboratory experiment using insects, would it be consistent with a geometric model? Would it be consistent with a geometric model for at least some range of times? Explain.

1.1.7. Complete the following:

a. The models $P_t = kP_{t-1}$ and $\Delta P = rP$ represent *growing* populations when $k$ is any number in the range ___ and when $r$ is any number in the range ___.

b. The models $P_t = kP_{t-1}$ and $\Delta P = rP$ represent *declining* populations when $k$ is any number in the range ___ and when $r$ is any number in the range ___.

c. The models $P_t = kP_{t-1}$ and $\Delta P = rP$ represent *stable* populations when $k$ is any number in the range ___ and when $r$ is any number in the range ___.

1.1.8. Explain why the model $\Delta Q = rQ$ cannot be biologically meaningful for describing a population when $r < -1$.

1.1.9. Suppose a population is described by the model $N_{t+1} = 1.5N_t$ and $N_5 = 7.3$. Find $N_t$ for $t = 0, 1, 2, 3,$ and 4.

1.1.10. A model is said to have a *steady state* or *equilibrium point* at $P^*$ if whenever $P_t = P^*$, then $P_{t+1} = P^*$ as well.

a. Rephrase this definition as: A model is said to have a *steady state* at $P^*$ if whenever $P = P^*$, then $\Delta P = \ldots.$

b. Rephrase this definition in more intuitive terms: A model is said to have a *steady state* at $P^*$ if ....

c. Can a model described by $P_{t+1} = (1 + r)P_t$ have a steady state? Explain.

Table 1.2. *Insect Population Values*

| $t$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| $P_t$ | .97 | 1.52 | 2.31 | 3.36 | 4.63 | 5.94 | 7.04 | 7.76 | 8.13 | 8.3 | 8.36 |

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Table 1.3. *U.S. Population Estimates*

| Year | Population (in 1,000s) |
|---|---|
| 1920 | 106,630 |
| 1925 | 115,829 |
| 1930 | 122,988 |
| 1935 | 127,252 |
| 1940 | 131,684 |
| 1945 | 131,976 |
| 1950 | 151,345 |
| 1955 | 164,301 |
| 1960 | 179,990 |

1.1.11. Explain why the model $\Delta P = rP$ leads to the formula $P_t = (1 + r)^t P_0$.

1.1.12. Suppose the size of a certain population is affected only by birth, death, immigration, and emigration – each of which occurs in a yearly amount proportional to the size of a population. That is, if the population is $P$, within a time period of 1 year, the number of births is $bP$, the number of deaths is $dP$, the number of immigrants is $iP$, and the number of emigrants is $eP$, for some $b$, $d$, $i$, and $e$. Show the population can still be modeled by $\Delta P = rP$ and give a formula for $r$.

1.1.13. As limnologists and oceanographers are well aware, the amount of sunlight that penetrates to various depths of water can greatly affect the communities that live there. Assuming the water has uniform *turbidity*, the amount of light that penetrates through a 1-meter column of water is proportional to the amount entering the column.

a. Explain why this leads to a model of the form $L_{d+1} = kL_d$, where $L_d$ denotes the amount of light that has penetrated to a depth of $d$ meters.

b. In what range must $k$ be for this model to be physically meaningful?

c. For $k = .25$, $L_0 = 1$, plot $L_d$ for $d = 0, 1, \ldots, 10$.

d. Would a similar model apply to light filtering through the canopy of a forest? Is the "uniform turbidity" assumption likely to apply there?

1.1.14. The U.S. population data in Table 1.3 is from (Keyfitz and Flieger, 1968).

a. Graph the data. Does this data seem to fit the geometric growth model? Explain why or why not using graphical and numerical

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evidence. Can you think of factors that might be responsible for any deviation from a geometric model?

b. Using the data only from years 1920 and 1925 to estimate a growth rate for a geometric model, see how well the model's results agree with the data from subsequent years.

c. Rather than just using 1920 and 1925 data to estimate a growth parameter for the U.S. population, find a way of using all the data to get what (presumably) should be a better geometric model. (Be creative. There are several reasonable approaches.) Does your new model fit the data better than the model from part (b)?

1.1.15. Suppose a population is modeled by the equation $N_{t+1} = 2N_t$, when $N_t$ is measured in *individuals*. If we choose to measure the population in *thousands of individuals*, denoting this by $P_t$, then the equation modeling the population *might* change. Explain why the model is still just $P_{t+1} = 2P_t$. (*Hint*: Note that $N_t = 1000P_t$.)

1.1.16. In this problem, we investigate how a model must be changed if we change the amount of time represented by an increment of 1 in the time variable $t$. It is important to note that this is not always a biologically meaningful thing to do. For organisms like certain insects, generations do not overlap and reproduction times are regularly spaced, so using a time increment of less than the span between two consecutive birth times would be meaningless. However, for organisms like humans with overlapping generations and continual reproduction, there is no natural choice for the time increment. Thus, these populations are sometimes modeled with an "infinitely small" time increment (i.e., with differential equations rather than difference equations). This problem illustrates the connection between the two types of models.

A population is modeled by $N_{t+1} = 2N_t,\ N_0 = A$, where each increment of $t$ by 1 represents a passage of 1 year.

a. Suppose we want to produce a new model for this population, where each time increment of $t$ by 1 now represents 0.5 years, and the population size is now denoted $P_t$. We want our new model to produce the same populations as the first model at 1-year intervals (so $P_{2t} = N_t$). Thus, we have Table 1.4. Complete the table for $P_t$ so that the growth is still geometric. Then give an equation of the model relating $P_{t+1}$ to $P_t$.

b. Produce a new model that agrees with $N_t$ at 1-year intervals, but denote the population size by $Q_t$, where each time increment of

Table 1.4. *Changing Time Steps in a Model*

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| $t$ | 0 | | 1 | | 2 | | 3 |
| $N_t$ | A | | 2A | | 4A | | 8A |
| $t$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 |
| $P_t$ | A | | 2A | | 4A | | 8A |

$t$ by 1 represents 0.1 years (so, $Q_{10t} = N_t$). You should begin by producing tables similar to those in part (a).

c. Produce a new model that agrees with $N_t$ at 1-year intervals, but denote the population size by $R_t$, where each time increment of $t$ by 1 represents $h$ years (so $R_{\frac{1}{h}t} = N_t$). ($h$ might be either bigger or smaller than 1; the same formula describes either situation.)

d. Generalize parts (a–c), writing a paragraph to explain why, if our original model uses a time increment of 1 year and is given by $N_{t+1} = kN_t$, then a model producing the same populations at 1-year intervals, but that uses a time increment of $h$ years, is given by $P_{t+1} = k^h P_t$.

e. (Calculus) If we change the name of the time interval $h$ to $\Delta t$, part (d) shows that

$$\frac{\Delta P}{\Delta t} = \frac{k^h - 1}{h} P.$$

If $\Delta t = h$ is allowed to become *infinitesimally small*, this means

$$\frac{dP}{dt} = \lim_{h \to 0} \frac{k^h - 1}{h} P.$$

Illustrate that

$$\lim_{h \to 0} \frac{k^h - 1}{h} = \ln k$$

by choosing a few values of $k$ and a very small $h$ and comparing the values of $\ln k$ and $\frac{k^h - 1}{h}$.

This result is formally proved by:

$$\lim_{h \to 0} \frac{k^h - 1}{h} = \lim_{h \to 0} \frac{k^{0+h} - k^0}{h} = \frac{d}{dx} k^x \Big|_{x=0} = \ln k \; k^x \big|_{x=0} = \ln k.$$

f. (Calculus) Show the solution to $\frac{dP}{dt} = \ln k P$ with initial value $P(0) = P_0$ is

$$P(t) = P_0 e^{t \ln k} = P_0 k^t.$$