Population growth in fluctuating environments and measures of fitness

We now come to one of the most misunderstood topics in evolutionary ecology, although Danny Cohen and Richard Lewontin set it straight many years ago (Cohen 1966, Lewontin and Cohen 1969). I include it here because at my university in fall 2002, there was an exchange at a seminar between a member of the audience and the speaker which showed that neither of them understood either the simplicity or the depth of these ideas.

This section will begin in a deceptively simple way, but by the end we will reach deep and sophisticated concepts. So, to begin imagine a population without age structure for which $N(t)$ is population size in year t and $N(0)$ is known exactly. If the per capita growth rate is λ, then the population dynamics are

$$N(t+1) = \lambda N(t) \tag{2.17}$$

from which we conclude, of course, that $N(t) = \lambda^t N(0)$. If the per capita growth rate is less than 1, the population declines, if it is exactly equal to 1 the population is stable, and if it is greater than 1 the population grows. Now let us suppose that the per capita rate of growth varies, first in space and then in time. Because there is no density dependence, the per capita growth rate can also be used as a measure of fitness.

Spatial variation

Suppose that in every year, the environment consists of two kinds of habitats. In the poor habitat the per capita growth rate is λ_1 and in the better habitat it is λ_2. We assume that the fraction of total habitat that is poor is p, so that the fraction of habitat that is good is $1 - p$. Finally, we will assume that the population is uniformly distributed across the entire habitat. At this point, I am sure that you want to raise various objections such as ‘‘What if p varies from year to year?’’, ‘‘What if individuals can move from poorer to better locations’’, etc. To these objections, I simply ask for your patience.

Given these assumptions, in year t the number of individuals experiencing the poor habitat will be $pN(t)$ and the number of individuals experiencing the better habitat will be $(1 - p)N(t)$. Consequently, the population size next year is

$$N(t+1) = (\lambda_1 pN(t) + \lambda_2(1-p)N(t)) = \{p\lambda_1 + (1-p)\lambda_2\}N(t) \tag{2.18}$$

The quantity in curly brackets on the right hand side of this equation is an average. It is the standard kind of average that we are all used to (think about how your grade point average or a batting average is calculated). If we had n different habitat qualities, instead of just two habitat qualities, and let p_i denote the fraction of habitat in which the growth rate is λ_i, then it is clear that what goes in the { } on the right hand side of Eq. (2.18) will be $\sum_{i=1}^{n} p_i \lambda_i$. We call this the arithmetic average. (I am tempted to put "arithmetic average" into bold-face or italics, but Strunk and White (1979) tell me that if I need to do so – to remind you that it is important – then I have not done my job.) Our conclusion thus far: if variation occurs over space, then the arithmetic average is the appropriate description of the growth rate.

Temporal variation

Let us now assume that per capita growth rate varies over time rather than space. That is, with probability p every individual in the population experiences the poorer growth rate in a particular year and with probability $1-p$ every individual experiences the better growth rate. Let us suppose that t is very big; it will be composed of t_1 years in which the growth rate was poorer and t_2 years in which the growth rate was better. Since there is no density dependence in this model, it does not matter in what order the years happen and we write

$$N(t) = (\lambda_1)^{t_1} (\lambda_2)^{t_2} N(0) \tag{2.19}$$

If the total time is large, then t_1 and t_2 should be roughly representative of the fraction of years that are poorer or better respectively. That is, we should expect $t_1 \sim pt$ and $t_2 \sim (1-p)t$. How should you interpret the symbol $\sim$ in the previous sentence? If you are more mathematically inclined, then the law of large numbers allows us to give precise interpretation of what $\sim$ means. If you are less mathematically inclined, this is a case where you can count on your intuition and the world being approximately fair.

Adopting this idea about the good and bad years, Eq. (2.19) becomes

$$N(t) = \lambda_1^{pt} \lambda_2^{(1-p)t} N(0) = \left[\lambda_1^{p} \lambda_2^{1-p}\right]^{t} N(0) \tag{2.20}$$

The quantity in square brackets on the right hand side of this equation is a different kind of average. It is called the geometric mean (or geometric average) and it weights the good and bad years differently than the arithmetic average does. Perhaps the easiest way to see the differences is to think about the extreme case in which the poorer growth rate is 0. According to the arithmetic average, individuals who find themselves in the better habitat will contribute to next year's population and those who find themselves in the poorer habitat will not. On the other hand, if the fluctuations are temporal, then when a poor year occurs, there is no reproduction for the population as a whole and thus the population is gone.

Exercise 2.6 (E/M)

Suppose that λ_1 is less than 1 (so that in poor years, the population declines). Show that the condition for the population to increase using the geometric mean is that $\lambda_2 > \lambda_1^{-p/(1-p)}$. Explore this relationship as λ_1 and p vary by making appropriate graphs. (Do not use three dimensional graphs and recall the advice of the Ecological Detective (Hilborn and Mangel 1997) that you should expect to make 10 times as many graphs for yourself as you would ever show to others.) Compare the results with the corresponding expression making the arithmetic average greater than 1.

If instead of just two kinds of years, we allow n kinds of years, the extension of the square brackets in Eq. (2.20) will be $\prod_{i=1}^{n} \lambda_i^{p_i}$ where the $\prod$ denotes a product (much as $\sum$ denotes a sum, as used above).

Now let us return to Eq. (2.17) for which $N(t) = \lambda^t N(0)$ and recall that the exponential and logarithm are inverse functions, $\lambda = \exp(\log(\lambda))$, which allows us to write $N(t)$ in a different way. In particular we have $N(t) = \mathrm{e}^{[\log(\lambda)]t} N(0)$, and if we define $r = \log(\lambda)$, then we have come back to our old friend from introductory ecology $N(t) = \mathrm{e}^{rt} N(0)$. That is, if time were continuous, this looks like population growth satisfying $\mathrm{d}N/\mathrm{d}t = rN$, in which r is the growth rate. But we can actually learn some new things about fluctuating environments from this old friend, because we know that $r = \log(\lambda)$. In Figure 2.6a, I have plotted growth rate as a function of λ and I have shown two particular values of λ that might correspond to good years and poor years. Note that the line segment joining these two points falls below the curve (such a curve is called concave). This means that the growth rate at the arithmetic average of λ is larger than the average value of the growth rates. This phenomenon is called Jensen's inequality.

If we have more than two growth rates, then the expression in square brackets in Eq. (2.20) is replaced by $\prod_{i=1}^{n} \lambda_i^{p_i}$ and if we rewrite this in terms of logarithms we see that

$$N(t) = \exp\left[t \sum_{i=1}^{n} p_i \log(\lambda_i)\right] N(0) \qquad (2.21)$$

From this equation, we conclude that the growth rate in a fluctuating environment is $r = \sum_{i=1}^{n} p_i \log(\lambda_i)$, which is the arithmetic average of the logarithm of the per capita growth rates. We thus conclude that for a fluctuating environment, one either applies the geometric mean directly

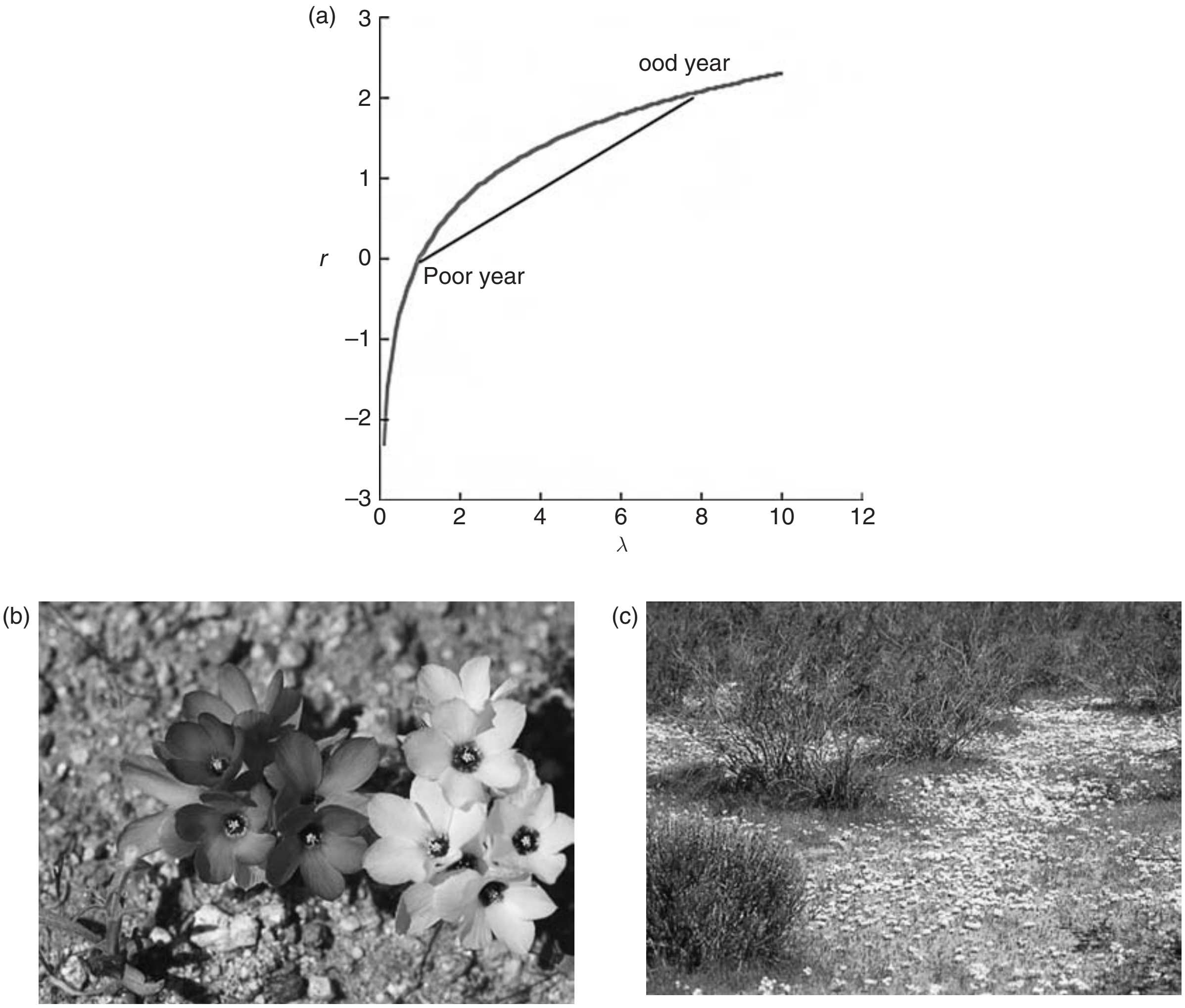


Figure 2.6. (a) The function $r = \log(\lambda)$ is concave. This implies that fluctuating environments will have lower growth rates than the growth rate associated with the average value of λ. (b) The two color morphs of desert snow *Linanthus parryae* are maintained by fitness differences in fluctuating environments. (c) An example of why this plant is called desert snow. Photos courtesy of Paulette Bierzychudek.

to the per capita growth rates or the arithmetic mean to the logarithm of per capita growth rates.

What about measuring the growth rate of an actual population? Data in a situation such as this one would be population sizes over time $N(0)$, $N(1), \dots N(t)$ from which we could compute the per capita growth rate as the ratio of population size at two successive years. We would then replace the frequency average by a time average and estimate the growth rate according to

$$r \approx \frac{1}{t}[\log(\lambda(0)) + \log(\lambda(1)) + \cdots + \log(\lambda(t-1))] \tag{2.22}$$

with the understanding that t is large. Since the sum of logarithms is the logarithm of the product, the term in square brackets in Eq. (2.22) is the same as $\log(\lambda(0)\lambda(1)\lambda(2)\ldots\lambda(t-1))$. But $\lambda(s) = N(s+1)/N(s)$, so that when we evaluate the product of the per capita growth rates, the product is

$$\begin{aligned}&\log(\lambda(0)\lambda(1)\lambda(2)\ldots\lambda(\mathrm{t}-1))\\&\quad=\log\{(N(1)/N(0))(N(2)/N(1))\ldots(N(t)/N(t-1))\}=\log\{N(t)/N(0)\}\end{aligned}$$

However, in a fluctuating environment, the sequence of per capita rates (and thus population sizes) is itself random. Thus, Eq. (2.22) provides the value of r for a specific sequence of population sizes. To allow for others, we take the arithmetic average of Eq. (2.22) and write

$$r = \lim_{t\to\infty}\frac{1}{t}E\left\{\log\left(\frac{N(t)}{N(0)}\right)\right\} \tag{2.23}$$

This formula is useful when dealing with data and when using simulation models (for a nice example, see Easterling and Ellner (2000)). A wonderful application of all of these ideas is found in Turelli *et al*. (2001), which deals with the maintenance of color polymorphism in desert snow *Linanthus parryae*, a plant (Figure 2.6b, c) that plays an important role in the history of evolutionary biology (Schemske and Bierzychudek 2001). If you stop reading this book now, and choose to read the papers, you will also encounter the "diffusion approximation." We will briefly discuss diffusion approximations in this chapter and then go into them in great detail in the later chapters on stochastic population theory.

Before leaving this section, I want to do one more calculation. It involves a little bit of probability modeling, so you may want to hold off until you've been through the next chapter. Suppose that we do not know the probability distribution of the per capita growth rate, but we do know the mean and variance of λ, which I shall denote by $\bar{\lambda}$ and $\mathrm{Var}(\lambda)$. We begin by a Taylor expansion of $r = \log(\lambda)$ around its mean value, keeping up to second order terms:

$$\log(\lambda) = \log(\bar{\lambda}) + \frac{1}{\bar{\lambda}}(\lambda-\bar{\lambda}) - \frac{1}{\bar{\lambda}^2}(\lambda-\bar{\lambda})^2 \tag{2.24}$$

and we now take the expectation of the right hand side. The first term is a constant, so does not change, the second term vanishes because $E\{\lambda\} = \bar{\lambda}$ and the expectation of the quantity in round brackets in the last term is the variance of the per capita growth rate. We thus conclude

$$r \sim \log(\bar{\lambda}) - \frac{1}{\bar{\lambda}^2}\mathrm{Var}(\lambda) \tag{2.25}$$

This is a very useful expression for fitness or growth rate in a fluctuating environment. The method is often called Seber's delta method, for G. A. F. Seber who popularized the idea in ecology (Seber 1982). I first learned about it while working in the Operations Evaluation Group of the Center for Naval Analyses (Mangel 1982), so I tend to call it the "method of Navy math." Whatever you call it, the method is handy.

The logistic equation and the discrete logistic map – on the edge of chaos

It is likely true that every reader of this book – and especially any reader who has reached this point – has encountered the logistic equation previously. Even so, by returning to an old friend, we have a good starting point for new kinds of explorations. As in the previous section, we will begin with relatively simple material but end with remarkably sophisticated stuff.

The logistic equation

We allow $N(t)$ to represent population size at time t and assume that it changes according to the dynamics

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) \tag{2.26}$$

In this equation, r and K are parameters; K is the population size at which the growth rate of the population is 0. It is commonly called the carrying capacity of the population. When the growth rate is 0, births and deaths are still occurring, but they are exactly balancing each other. The right hand side of Eq. (2.26) is a parabola, with zeros at $N = 0$ and $N = K$ and maximum value $rK/4$ when $N = K/2$, which is called the population size that provides maximum net productitivity (MNP); see Figure 2.7a.

In order to understand the parameter r, it is easiest to consider the per capita growth rate of the population

$$\frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t} = r\left(1 - \frac{N}{K}\right) \tag{2.27}$$

Inspection of the right hand side of Eq. (2.27) shows that it is a decreasing function of population size and that its maximum value is r, occurring when $N = 0$. Of course, if $N = 0$, this is biologically meaningless – there won't be any reproduction if the population size is 0. What we mean, more precisely, is that in the limit of small population size, the per capita growth rate approaches r – so that r is the maximum per capita growth rate.

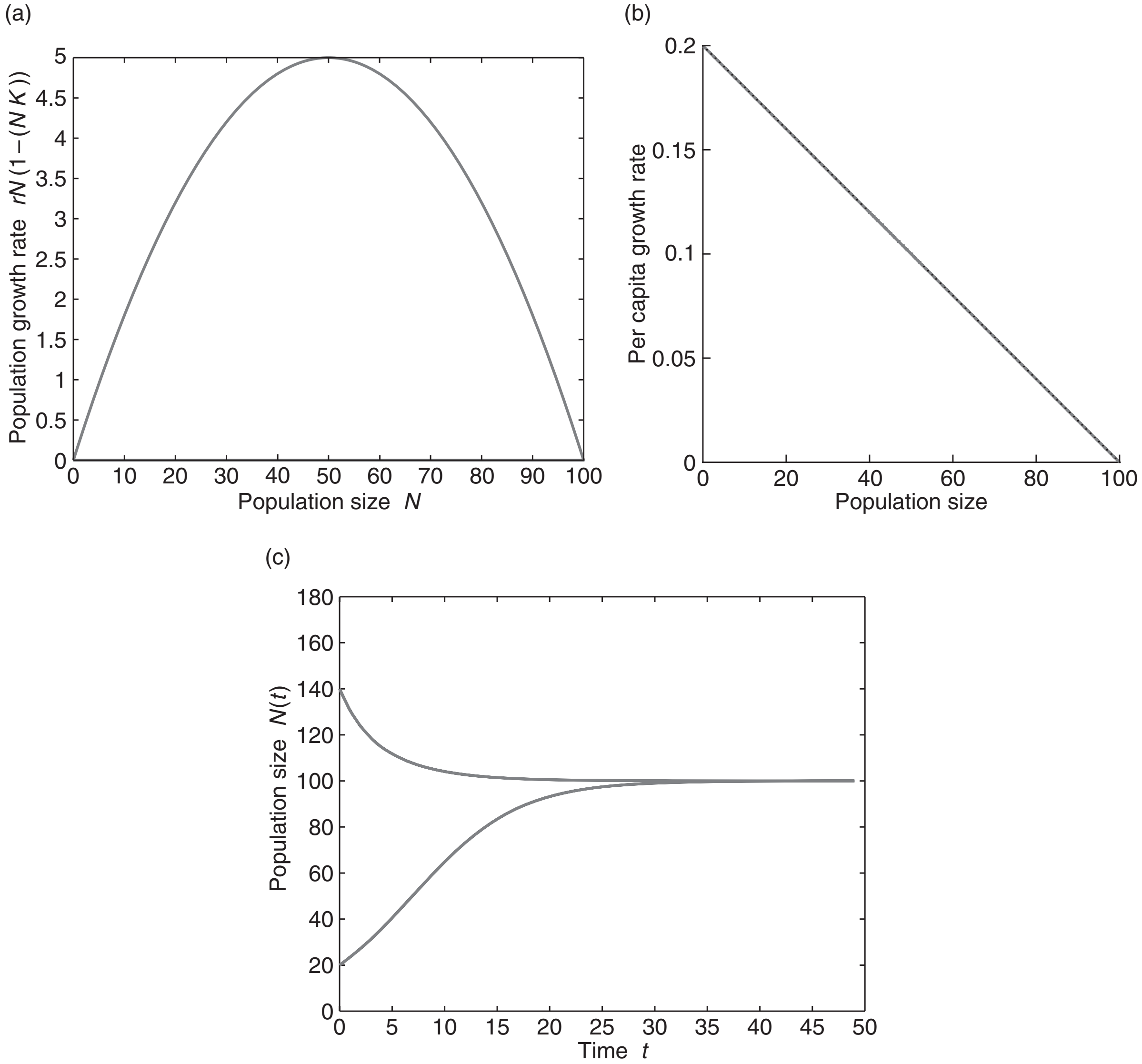


Figure 2.7. An illustration of logistic dynamics when $r = 0.2$ and $K = 100$. (a) Population growth rate as a function of population size. (b) Per capita growth rate as a function of population size. (c) Population size versus time for populations that start above and below the carrying capacity.

The word logistic is derived from the French word logistique, which means to compute. The scientist and mathematician Verhulst wanted to be able to compute the population trajectory of France. He knew that using the exponential growth equation $dN/dt = rN$ would not work because the population grows without bound. This happens because with exponential growth the per capita growth rate is a constant (r). We don't know what Verhulst was thinking, but it might have gone something like this: "I know that a constant per capita growth rate will not be a good representation, and it must be true that per capita growth rate declines as population size increases. Suppose that per capita growth rate falls to zero when the population size is K. What is the simplest way to connect the points $(0, r)$ and $(K, 0)$? Of course – a line. C'est bon." Furthermore, there is only one line that connects the maximum per capita growth rate r when $N=0$ and per capita growth rate $=0$ when $N=K$. There are an infinite number of nonlinear ways that we could do it. For example, a per capita growth rate of the form $r(1-(N/K)^{\alpha})$, for any value of $\alpha > 0$, works equally well to achieve the goal of connecting the maximum and zero per capita growth rates. So, the logistic is not a law of nature, but is a simple and somewhat unique representation of nature. In Figure 2.7b, I show the per capita growth rate for the same parameters as in Figure 2.7a.

Let us now think about the dynamics of a population starting at size $N(0)$ and following logistic growth. If $N(0) > K$, then the growth rate of the population is negative and the population will decline towards K. If $N(0) > 0$ but small, the population will grow, albeit slowly at first, but then as population size increases, the growth rate increases too (even though per capita growth rate is always declining, the product of per capita growth rate and population size increases until $N=K/2$). Once the population size exceeds $K/2$, growth rate begins to slow, ultimately reaching 0 as the population approaches K. We thus expect the picture of population size versus time to be S-shaped or sigmoidal and it is (Figure 2.7c).

Exercise 2.7 (M)

Although Eq. (2.26) is a nonlinear equation, it can be solved exactly (that is how I generated the trajectories in Figure 2.7c) and everyone should do it at least once in his or her career. The exercise is to show that the solution of Eq. (2.26) is $N(t) = [N(0)Ke^{rt}] / [K + N(0)(e^{rt}-1)]$. To help you along, I offer two hints (the method of partial fractions, if you want to check your calculus text). First, separate the differential equation so that Eq. (2.26) becomes

$$\frac{\mathrm{d}N}{N\left(1-\frac{N}{K}\right)} = r\mathrm{d}t$$

Second, recognize that the left hand side of this expression looks like a common denominator, so write

$$\frac{1}{N\left(1-\frac{N}{K}\right)} = \frac{A}{N} + \frac{B}{\left(1-\frac{N}{K}\right)}$$

where A and B are constants that you determine by creating the common denominator and simplifying.

The discrete logistic map and the edge of chaos

We now come to what must be one of the most remarkable stories of good luck and good sleuthing in science. To begin this story, I encourage you to stop reading just now, go to a computer and plot the trajectories for $N(t)$ given by the formula for $N(t)$ in the previous exercise, for a variety of values of r – let r range from 0.4 to about 3.5. After that return to this reading.

Now let us poke around a bit with the logistic equation by recognizing the definition of the derivative as a limiting process. Thus, we could rewrite the logistic equation in the following form:

$$\lim_{\mathrm{d}t\to 0}\frac{N(t+\mathrm{d}t)-N(t)}{\mathrm{d}t}=rN\left(1-\frac{N}{K}\right) \tag{2.28}$$

This equation, of course, is no different from our starting point. But now let us ignore the limiting process in Eq. (2.28) and simply set $\mathrm{d}t = 1$. If we do that Eq. (2.28) becomes a difference equation, which we can write in the form

$$N(t+1)=N(t)+rN(t)\left(1-\frac{N(t)}{K}\right) \tag{2.29}$$

This equation is called the logistic map, because it "maps" population size at one time to population size at another time. You may also see it written in the form

$$N(t+1)=rN(t)\left(1-\frac{N(t)}{K}\right)$$

which makes it harder to connect to the original differential equation. Note, of course, that Eq. (2.29) is a perfectly good starting point, if we think that the biology operates in discrete time (e.g. insect populations with non-overlapping generations across seasons, or many species of fish in temperate or colder waters).

Although Eq. (2.29) looks like the logistic differential equation, it has a number of properties that are sufficiently different to make us wonder about it. To begin, note that if $N(t) > K$ then the growth term is negative and if r is sufficiently large, not only could $N(t+1)$ be less than $N(t)$, but it could be negative! One way around this is to use a slightly different form called the Ricker map

$$N(t+1)=N(t)\exp\left[r\left(1-\frac{N(t)}{K}\right)\right] \tag{2.30}$$

This equation is commonly used in fishery science for populations with non-overlapping generations (e.g. salmonids) and misused for other kinds of populations. It has a nice intuitive derivation, which goes like this (and to which we will return in Chapter 6). Suppose that maximum per capita reproduction is A, so that in the absence of density dependence $N(t+1) = AN(t)$, and that density dependence acts in the sense that a focal offspring has probability f of surviving when there is just one adult present. If there are N adults present, the probability that the focal offspring will survive is f^N. Combining these, we obtain $N(t+1) = AN(t)f^{N(t)}$, which surely suggests a good exercise.

Exercise 2.8 (E/M)

Often we set $f^N = \mathrm{e}^{-bN}$, so that the Ricker map becomes $N(t+1) = AN(t)\mathrm{e}^{-bN(t)}$. First, explain the connection between f and B and the relationship between the parameters A, b and r, K. Second, explain why the Ricker map does not have the nasty property that $N(t)$ can be less than 0. Third, use the Taylor expansion of the exponential function to show how the Ricker and discrete logistic maps are connected.

But now let us return to Eq. (2.29) and explore it. To do this, we begin by simply looking at trajectories. I am going to set $K = 100$, $N(0) = 20$ and show $N(t)$ for a number of different values of r (Figure 2.8). When r is moderate, things behave as we expect: starting at $N(0) = 20$, the population rises gradually towards $K = 100$. However, when $r = 2.0$ (Figure 2.8c), something funny appears to be happening. Instead of settling down nicely at $K = 100$, the population exhibits small oscillations around that value. For r slightly larger ($r = 2.3$, panel d) the oscillations become more pronounced, but still seem to be flipping back and forth across $K = 100$. The behavior becomes even more complicated when r gets larger – now there are multiple population sizes that are consistently visited (Figure 2.8e). When r gets even larger, there appears to be no pattern, just wild and erratic behavior. This behavior is called deterministic chaos. It was discovered more or less accidentally in a number of different ways in the 1960s and 1970s (see Connections).

Before explaining what is happening, I want to present the results in a different way, obtained using the following procedure. I fixed r. However, instead of fixing $N(0)$, I picked it randomly and uniformly (all values equally likely) between 1 and K. I then ran the population dynamics for 500 time steps and plotted the point (r, $N(500)$). I repeated this, with r still fixed, for 50 different starting values, then changed r and began the process over again. The results, called a bifurcation (for branching) diagram, are shown in Figure 2.9. When r is small, there is only one place for $N(500)$ to be – at carrying capacity $K = 100$. However, once we enter the oscillatory regime, $N(500)$ is never K – it is either larger or smaller than K. And as r increases, we see that we jump from 2 values of $N(500)$ to 4 values, then on to 8, 16, 32 and so forth (with the transition regions becoming closer and closer). As r continues to increase, virtually all values can be taken by $N(500)$. You may want to stop reading now, go to your computer and create a spreadsheet that does this same set of calculations.

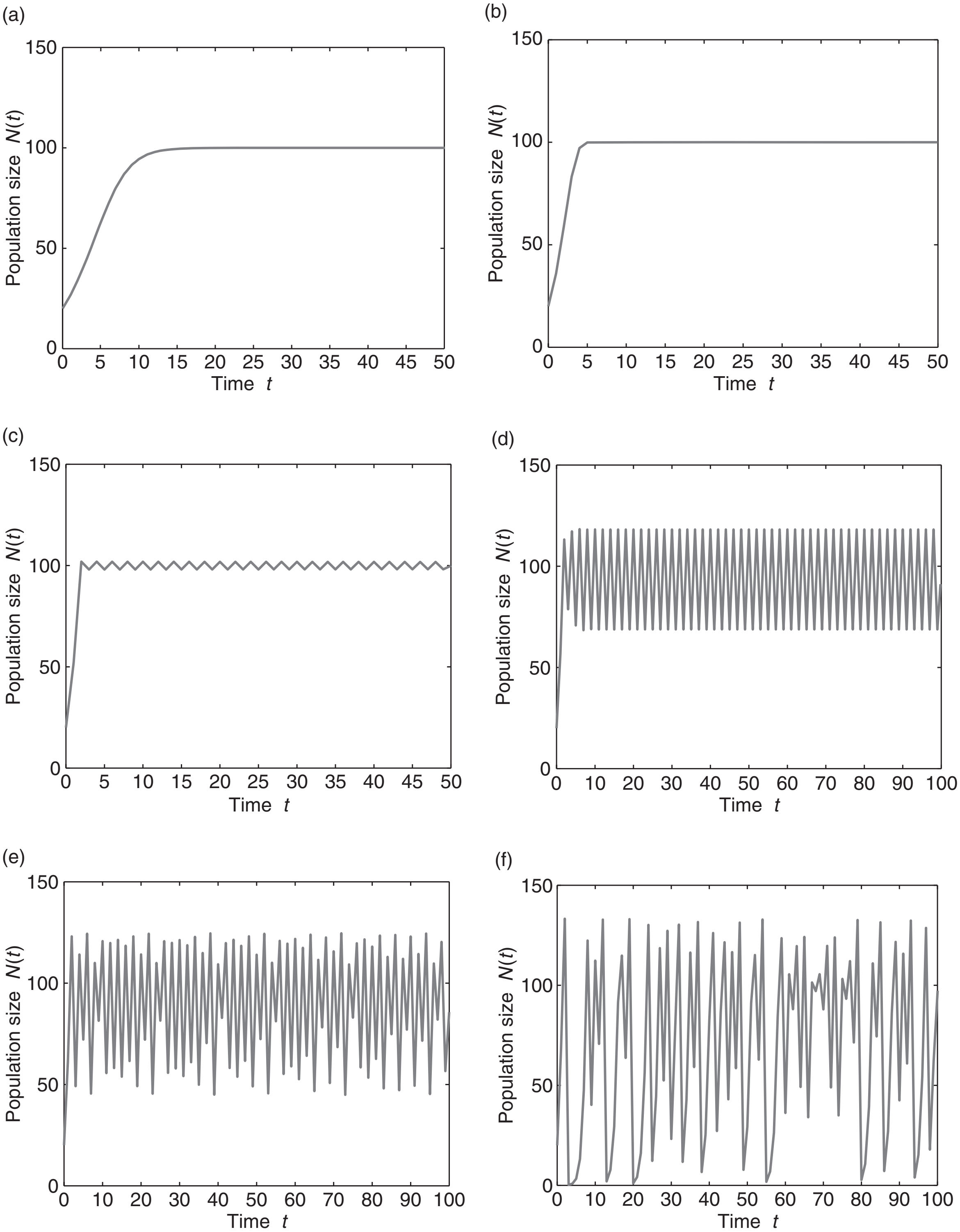


Figure 2.8. Dynamics of the discrete logistic, for varying values of r: (a) $r = 0.4$, (b) $r = 1.0$, (c) $r = 2.0$, (d) $r = 2.3$, (e) $r = 2.6$, (f) $r = 3$.

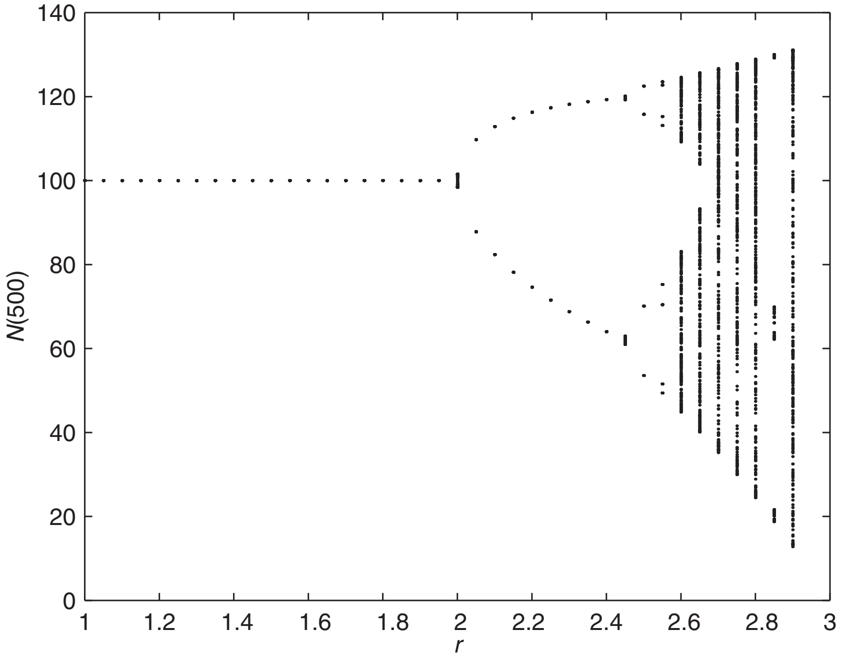


Figure 2.9. The bifurcation plot of *N*(500) versus *r*; see text for details.

How do we understand what is happening? To begin we rewrite Eq. (2.29) as

$$N(t+1) = (1+r)N(t) - \frac{rN(t)^2}{K}$$

and investigate this as a map relating $N(t+1)$ to $N(t)$. Clearly if $N(t) = 0$, then $N(t+1) = 0$; also if $N(t) = K(1+r)/r$, then $N(t+1) = N(t)$. In Figure 2.10, I have plotted this function, for three values of r, when $K = 100$. I have also plotted the 1:1 line. The three curves and the line intersect at the point (100, 100), or more generally at the point (K, K). Using this figure, we can read off how the population dynamics grow. Let us suppose that $N(0) = 50$, and $r = 0.4$. We can see then that $N(1) = 60$ (by reading where the line $N = 50$ intersects the curve). We then go back to the x-axis, for $N(1) = 60$, we see that $N(2) = 69.6$; we then go back to the x-axis for $N(2)$ and obtain $N(3)$. In this case, it is clear that the dynamics will be squeezed into the small region between the curve and the 1:1 line. This procedure is called cob-webbing.

What happens if $N(0) = 50$ and $r = 2.3$? Well, then $N(1) = 107.5$, but if we take that value back to the x-axis, we see that $N(2)$ is about 89. We have jumped right across the steady state at 100. From $N(2) = 89$, we will go to $N(3)$ about 111 and from there to $N(4)$ about 82. The behavior is even more extreme for the case in which $r = 3$: starting at $N(0) = 50$, we go to 125 and from there to about 31; from 31 to about 95, and so forth.

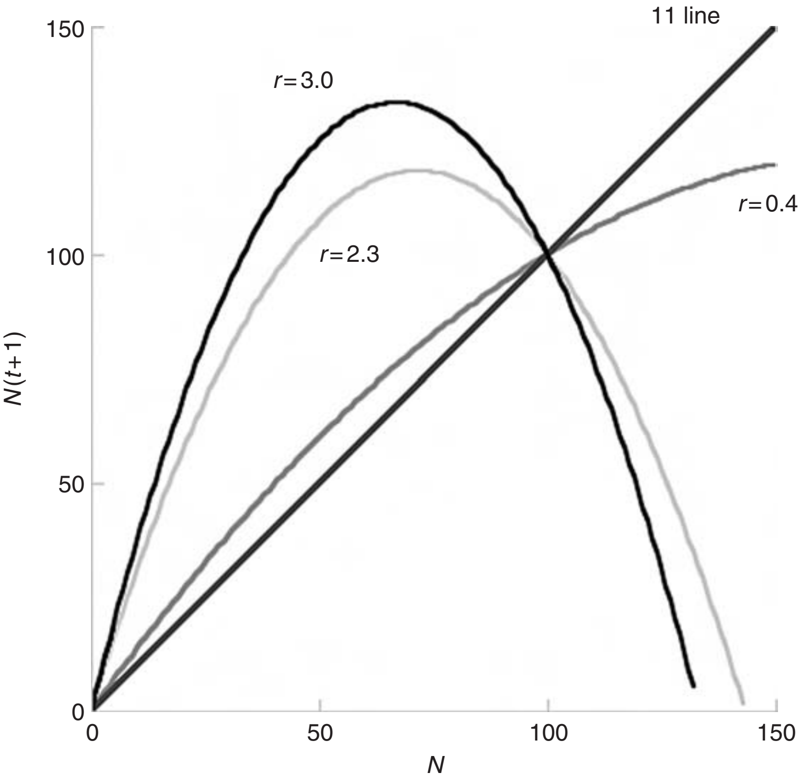


Figure 2.10. Logistic maps for three different values of *r*, allowing us to understand how simple deterministic dynamics can lead to oscillations and to apparently random trajectories.

This is a very interesting process – one in which simple deterministic dynamics can produce a wide range of behaviors, including oscillations and apparently random trajectories. These kinds of results fall under the general rubric of deterministic chaos (see Connections).

A bit about bifurcations

The results of the previous section suggest that when we encounter a differential or difference equation, we should consider not only the solution, but how the solution depends upon the parameters of the equation. This subject is generally called bifurcation theory (because, as we will see, solutions "branch" as parameters vary). In this section, we will consider the two simplest bifurcations and some of their implications. As we discuss the material, do not try to apply biological interpretations to the equations; I have picked them to make illustrating the main points as simple as possible. At the end of this section, I will do one biological example and in Connections point you towards the literature for other ones.

We begin with the differential equation

$$\frac{dx}{dt} = x^2 - \alpha \tag{2.31}$$

for the variable $x(t)$ depending upon the single parameter α. When we first encounter a differential equation, we may ask "What is the solution of this equation?". The trouble is, the vast majority of differential equations do not have explicit solutions. Given that restriction, a good first question is "What are the steady states, that is for what values of x is dx/dt equal to 0?". This is always a good question, and can often be answered. For the dynamics in Eq. (2.31), the steady states are given by $x_s = \pm\sqrt{\alpha}$. We thus conclude that if $\alpha < 0$ there are no steady states (more precisely, there are no real steady states) and that if $\alpha \geq 0$ there are one (when $\alpha = 0$) or two steady states. We will call these steady solutions branches; there are thus two branches, one of which is positive and one of which is negative. Along these branches, $dx/dt = 0$. What about elsewhere in the plane? Between the branches, α is greater than x^2, so we conclude that $dx/dt < 0$ and that $x(t)$ will decrease, thus moving towards the lower branch. Anywhere else in the plane α is less than x^2, so that $dx/dt > 0$ and $x(t)$ will increase; I have summarized this analysis in Figure 2.11.

Before going on with the analysis, a few stylistic comments. First, note that I have put x on the ordinate and α on the abscissa. Thus, one might say "x is on the y axis, how confusing." However, the labeling of axes is a convention, not a rule, and one just needs to be careful when conducting the analysis (more of this to come with the next bifurcation). Second, I have used $x(t)$ and x interchangeably; this is done for convenience (and for avoiding writing things in a more cumbersome manner). Once again, this is not a problem if one is careful in understanding and presentation.

Returning to the figure, imagine that α is fixed, but x may vary, and that we are at some point along the positive branch. Then $dx/dt = 0$ and

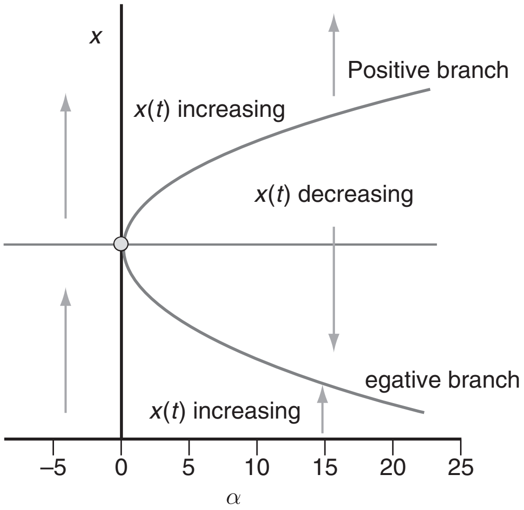


Figure 2.11. The steady states of the differential equation $dx/dt = x^2 - \alpha$, showing the positive and negative branches.

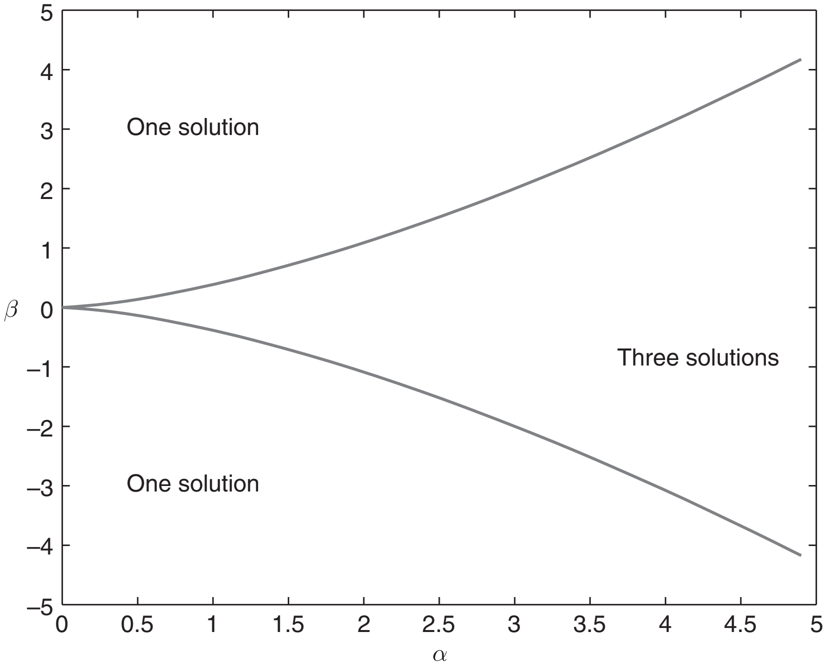
we will stay there forever. However, if we receive a small perturbation off that branch, interesting things happen. If the perturbation (until otherwise notified, all perturbations are small) puts us between the two branches, then $x(t)$ declines and we move towards the negative branch. If the perturbation puts us above the positive branch, then $x(t)$ increases and we move away from the positive branch. So, in either case, a perturbation moves us away from the positive branch. We say that such a branch is dynamically unstable (or just unstable). A similar argument shows that perturbations from the negative branch return to it; we say that the negative branch is stable. What happens when $\alpha = 0$? The differential equation becomes $dx/dt = x^2$, so that $x(t)$ is always increasing. Thus, if $x(0) < 0$, $x(t)$ rises towards 0; however if $x(0) > 0$, $x(t)$ moves away from 0. We say that such a point is marginally stable; we also say that the equation $dx/dt = x^2 - \alpha$ is structurally unstable (these words may appear to be needlessly complex, but think about them and they make sense) when $\alpha = 0$, because small changes of α from the value 0 lead to very different properties of the equation (in this case, either no steady states or two steady states). We also sometimes say that the stable steady state and unstable steady state coalesce and annihilate each other (kind of like matter and antimatter) when $\alpha = 0$.

The next most complicated equation involves two parameters and a cubic in x:

$$\frac{dx}{dt} = -x^3 + \alpha x + \beta \tag{2.32}$$

where α and β are the parameters of interest. The steady states of this equation satisfy the cubic equation $x^3 - \alpha x - \beta = 0$. We will momentarily discuss geometric solutions of this equation, but now begin with a bit of algebra. A cubic equation has three solutions (by the fundamental theorem of algebra), of which one may be real and two complex, three may be real with two equal, or three may be real and unequal. Which case applies is determined by the value of the discriminant $D(\alpha, \beta) = (\beta^2/4) - (\alpha^3/27)$. (You probably once learned this in high school algebra, but most likely don't remember it. This is a case where I ask that you trust me; of course you can also go and check the formula in a book.) If $D(\alpha, \beta) > 0$, then there is one real solution; if $D(\alpha, \beta) = 0$, then there are three real solutions, two of which are equal; if $D < (\alpha, \beta)$ then there are three real, unequal solutions. Thus, in some sense $D(\alpha, \beta) = 0$ is a boundary. So, we need to think about the shape of $\beta^2 = 4\alpha^3/27$, which is shown in Figure 2.12. This kind of equation (in which the independent variable appears as a 3/2 power) is called a cusp; hence this is called the cusp bifurcation or sometimes the cusp catastrophe (see Connections).

Figure 2.12. A plot of the equation $\beta^2 = 4\alpha^3/27$, which is called a cusp. Along the curves, there are two real solutions of the cubic (and thus three steady states of Eq. (2.32)). Elsewhere, there are either one real solution or three real solutions.



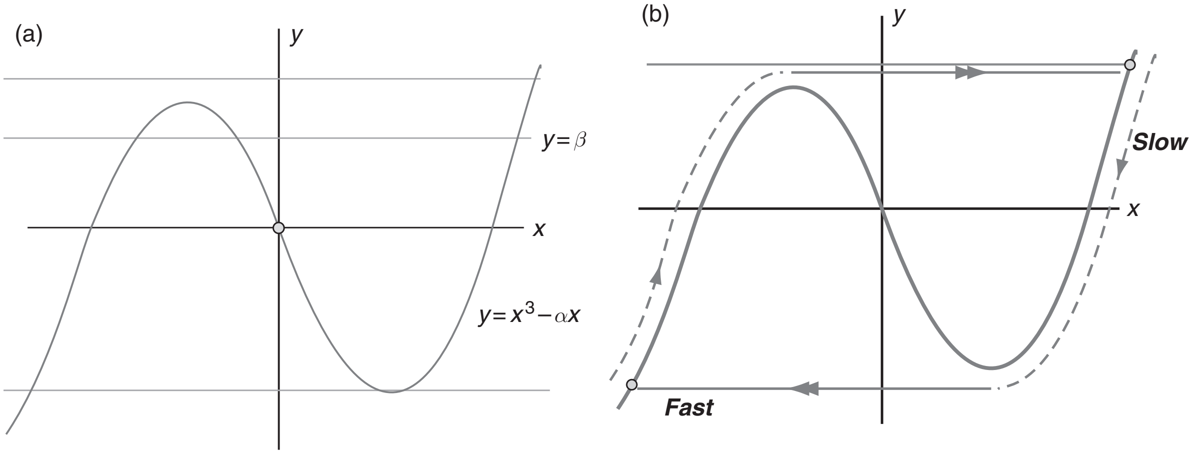


Figure 2.13. (a) The geometric solution of the equation $x^3 - \alpha x = \beta$. (b) When we append dynamics for β, there is no longer a steady state, but both x and β change in time.

Now I want to discuss the solution in a more geometric manner, because learning to think geometrically about these matters is absolutely essential for your understanding of the material. The steady states of the differential equation (2.32) satisfy $x^3 - \alpha x = \beta$. In Figure 2.13a, I plotted the curve $y = x^3 - \alpha x$ and the line (actually a number of lines) $y = \beta$. Since the steady states correspond to values of x where these are equal, we conclude that the steady states are values of x for which the line and the curve intersect. We also see that there may be just one intersection point (on the left hand branch of the curve or on the right hand branch), there may be two intersection points (if the line is tangent to the curve) or three intersection points (if the value of β falls between the local maximum and local minimum of the curve). We thus have a geometric interpretation of the cusp. When the horizontal line is tangent to the curve, the system is once again structurally unstable: at the point of tangency there are two steady states, one of which is marginally stable. However, a small change in either of the parameters leads to a situation in which there are either three or one steady states.

But this really is not the situation that I wanted to consider. Rather, I want to consider the situation in which β varies as well. In particular, let us append the equation $\mathrm{d}\beta/\mathrm{d}t = -\varepsilon x$, in which ε is a new parameter, to Eq. (2.32). We will assume that ε is small (that is much less than 1), and we know that when ε is set equal to 0 we obtain the cusp bifurcation.

The steady state is now $x = 0$, $\beta = 0$, but the dynamics are very interesting. To be explicit, suppose we start on the right hand branch of the cubic, where the line is above the local maximum, as shown in Figure 2.13b. If ε were 0, the system would stay there. But since ε is not 0, things change. In light of $x > 0$, β will decline (since its derivative is negative). Thus in the next bit of time, the line will lower a little. Furthermore, now the line is slightly below the cubic and since $\mathrm{d}x/\mathrm{d}t = \beta - (x^3 - \alpha x)$, x declines slightly too. At this new value of x, $\mathrm{d}\beta/\mathrm{d}t$ is still negative, so that both β and x will continue to decline. We will thus slowly move down along the right hand branch of the cubic (Figure 2.13b). For how long will this go on? Until we reach the local minimum of the cubic at $x = \sqrt{\alpha}$. At this point, β is still declining, but once it does so there is no intersection between the line and the curve for positive values of x. We thus predict a rapid transition from the right hand branch of the cubic to the left hand branch. When we get near the left hand branch, x is negative so that $\mathrm{d}\beta/\mathrm{d}t$ is positive and β begins to rise. Once again, this happens slowly, along the left hand branch, until the local maximum is crossed, at which point there will be a rapid transition back to the right hand branch of the cubic. In other words, we predict oscillations, and that the oscillations will have a shape that involves a slowly changing component and a rapidly changing component.

In Figure 2.14, I show the numerical solution of the differential equations for the case in which $\alpha = 1$, $\varepsilon = 0.005$ with initial values $x(0) = 2$ and $\beta(0) = x(0)^3 - \alpha x(0)$. Starting at $x(0) = 2$, we see a slow decline along the right hand branch of the cubic, until there is a rapid drop, then a slow rise, and oscillations set in. To help make this point clearer, Figures 2.14b and c show just parts of the trajectory; in Figure 2.14c, we most clearly see the slow and fast parts of the oscillation.

Oscillations such as the ones described here are called “relaxation oscillations” and they arise in many different ecological contexts,

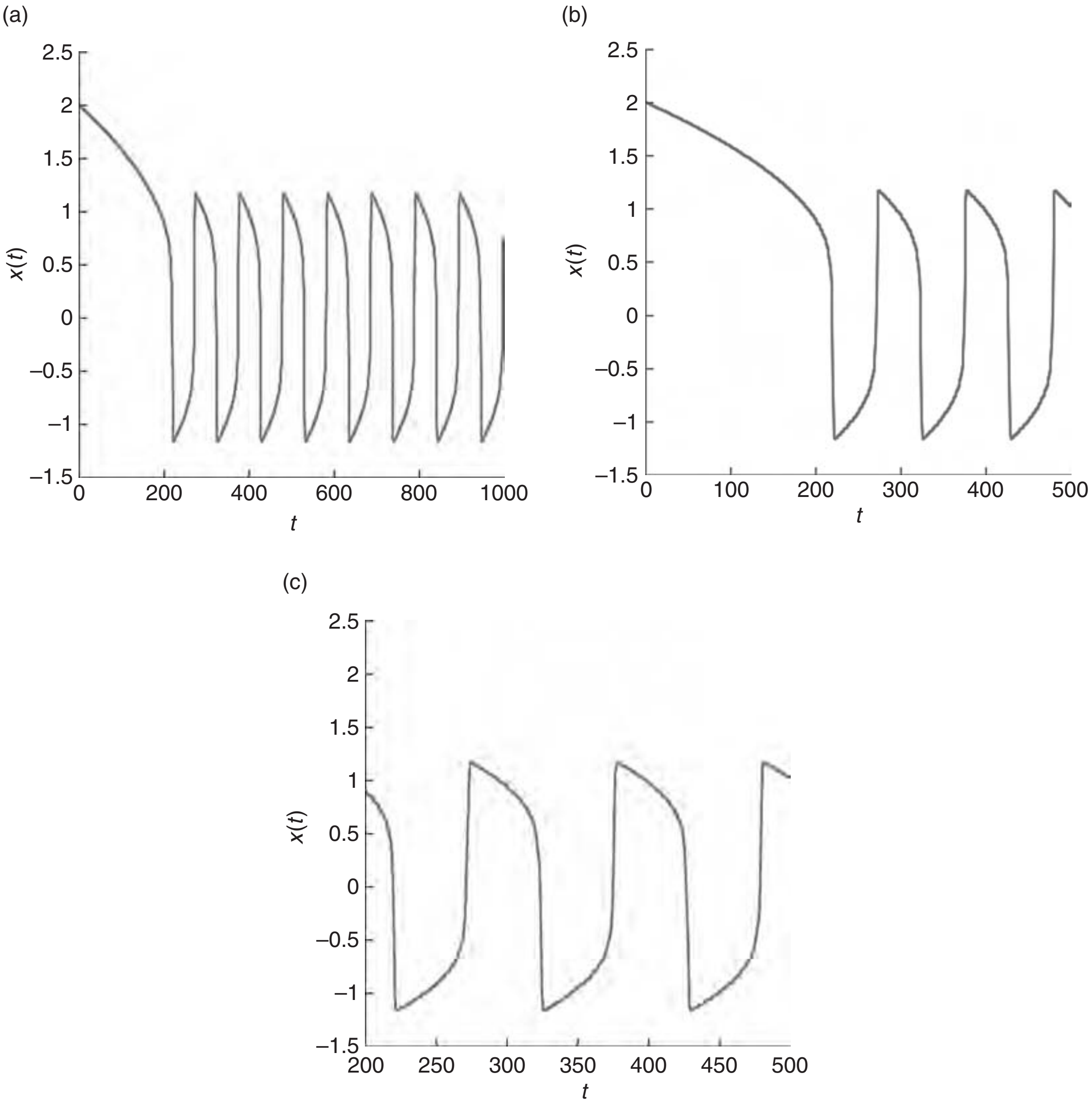


Figure 2.14. The oscillations induced by allowing the parameter β to slowly change, as described in the text. Three panels are shown, with increasingly fine resolution in time, so that we can clearly see the slow and fast parts of the oscillatory system.

typically in relationship to some kind of pest outbreak or plankton bloom (see Connections).

Two dimensional differential equations and the classification of steady states

Many of the models that we encounter in population biology involve two or more differential equations of the form $dx/dt = f(x, y)$ and

$\mathrm{d}y/\mathrm{d}t = g(x,\ y)$. Some examples are the Lotka–Volterra predator (P)–prey (V) equations

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= rV\left(1 - \frac{V}{K}\right) - bPV\\ \frac{\mathrm{d}P}{\mathrm{d}t} &= cPV - mP\end{aligned} \tag{2.33}$$

the Lotka–Volterra competition equations

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= r_1x\left(1 - \frac{x + \alpha y}{K_1}\right)\\ \frac{\mathrm{d}y}{\mathrm{d}t} &= r_2y\left(1 - \frac{y + \beta x}{K_2}\right)\end{aligned} \tag{2.34}$$

and equations that could describe a mutualistic interaction (for example between ants and butterflies, see Pierce and Nash (1999) or Pierce *et al*. (2002); for yuccas and moths see Pellmyr (2003))

$$\begin{aligned}\frac{\mathrm{d}A}{\mathrm{d}t} &= r_aA\left(1 - \frac{A}{K_0 + K_1B}\right)\\ \frac{\mathrm{d}B}{\mathrm{d}t} &= B(r_bA - mB)\end{aligned} \tag{2.35}$$

If these equations are not familiar to you, do not despair, but read on – we shall explicitly consider the first two pairs in what follows.

When considering differential equations such as these in the plane, one can usefully apply a three step procedure (which is generalized to systems of higher dimension): understand the steady states, the qualitative dynamics, and only then the quantitative dynamics. We will approach this procedure slowly, beginning with some very specific examples and then ending with the general case.

We start with a specific example: consider the following system of differential equations for a pair of variables $u(t)$ and $v(t)$ (don't try to ascribe biological meaning to them just now, that will come later on).

$$\begin{aligned}\frac{\mathrm{d}u}{\mathrm{d}t} &= Au\\ \frac{\mathrm{d}v}{\mathrm{d}t} &= Dv\end{aligned} \tag{2.36}$$

The choice of the constants A and D, which may be mysterious now, will also become apparent later.

The steady states of this system are the values in the $(u,\ v)$ plane for which $\mathrm{d}u/\mathrm{d}t = 0$ and $\mathrm{d}v/\mathrm{d}t = 0$. We can determine by inspection that the only steady state is the origin (0, 0). Furthermore, we can determine by inspection that $u(t)$ and $v(t)$ must be exponential functions of time. Thus, we conclude that $u(t) = u(0)\mathrm{e}^{At}$ and that $v(t) = v(0)\mathrm{e}^{Dt}$.

(We could also note that $\mathrm{d}u/\mathrm{d}v = Au/Dv$, which integrates to $A\ln(u) = D\ln(v) + \text{constant}$, and which then becomes $u = cv^{A/D}$, where c is a constant. But we are not going to make a big deal out of this because it does not help us except in the special case).

What does help us, however, is to think about the exponential solutions of time in a plane represented by u on the abscissa and v on the ordinate. This is called the phase plane (Figure 2.15). We will distinguish three cases. First suppose that $A > 0$ and $D > 0$. If we start the system at $u(0) = 0$ and $v(0) = 0$, then it stays there forever. However, if we start it anywhere else, both $u(t)$ and $v(t)$ grow in time. We say that points in the u–v plane "flow away from the origin." This is represented by the arrows in Figure 2.15a pointing away from the origin. Note that we are not trying to characterize the shape of those curves that represent the flow away from the origin, just that points move away. We call this an unstable node. Second, suppose that $A < 0$ and $D < 0$. Then everything that we just concluded applies, but in reverse. If initial values are not at the origin, they decline in time; we say that the flow is towards the origin and that this is a stable node (Figure 2.15b). Third, suppose that one of A or D is positive and that the other is negative. For concreteness, I will do the case $A < 0$ and $D > 0$ and let you draw the picture for the other one. Now some interesting things can happen. Note, if we start exactly on the u-axis, we flow towards the origin. If we start exactly on the v-axis, we flow away from the origin. For any starting point with $u(0) \neq 0$ and $v(0) \neq 0$ but close to the origin, we will first flow towards the origin, kind of "along the u-axis" and then flow away from it "along the v-axis." So we see that the u-axis separates the plane into two regions; these are often called domains of attraction and the u-axis is called the separatrix. In this case the origin is called a saddle point (Figure 2.15c), in analogy to real saddles (Figure 2.15d) in which one falls into the middle of the saddle moving along the back of the horse but off the saddle moving laterally to the back of the horse.

This case was nice, but perhaps a bit too simple because the dynamics of u and v were not connected in any way. The next most complicated case would be linear, but with connection. Here we will go back to x and y and write

$$\begin{aligned}\frac{\mathrm{d}x}{\mathrm{d}t} &= Ax + By\\ \frac{\mathrm{d}y}{\mathrm{d}t} &= Cx + Dy\end{aligned} \tag{2.37}$$

and now I hope you understand my choice of A and D in the previous discussion. How could we analyze these equations? We might try to find some combination of x and y so that new variables $u = \alpha x + \beta y$ and $v = \gamma x + \delta y$ satisfy $\mathrm{d}u/\mathrm{d}t = A'u$ and $\mathrm{d}v/\mathrm{d}t = B'v$ for some constants

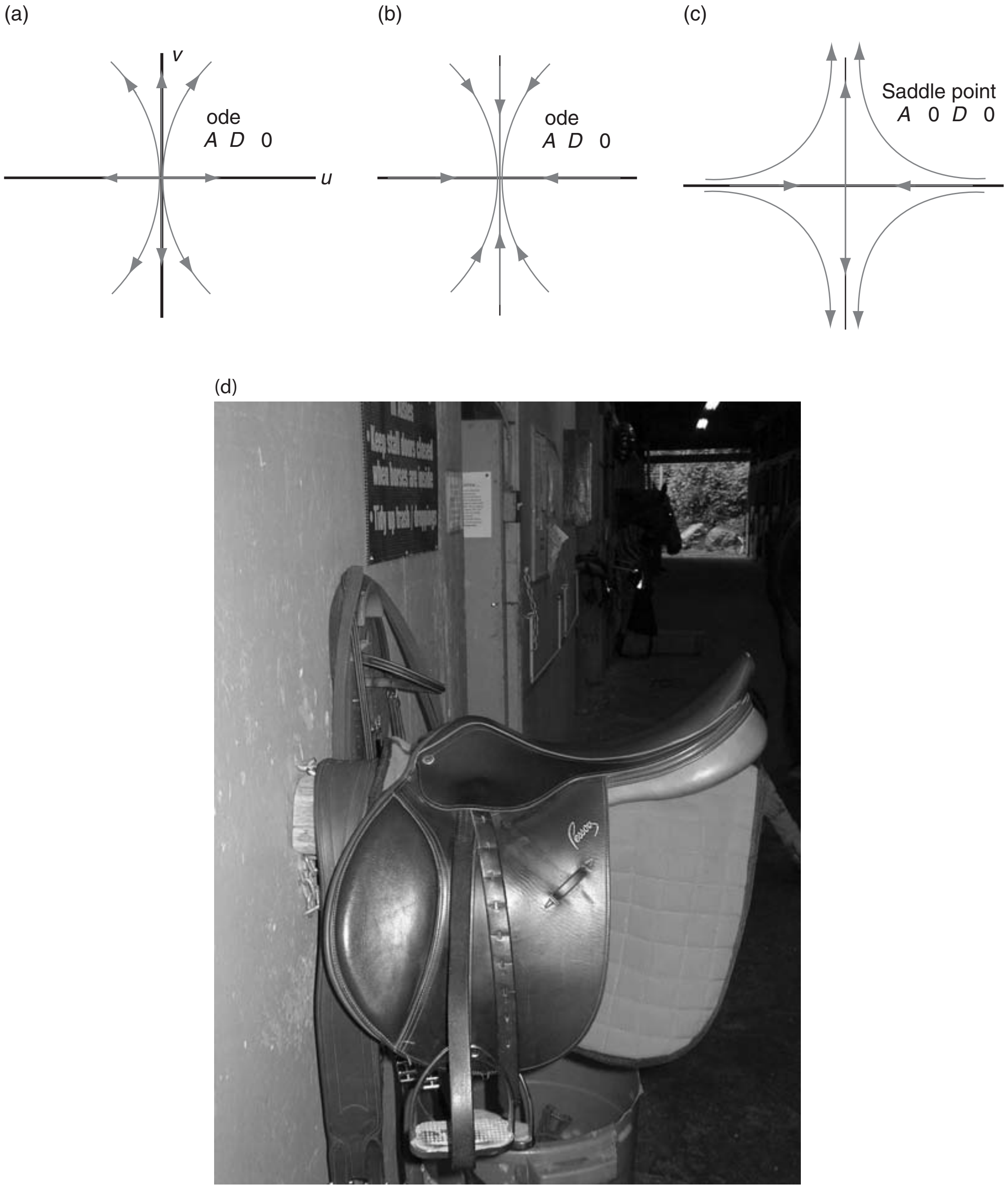


Figure 2.15. The phase plane for the simple dynamical system du/d$t = Au$, dv/d$t = Dv$. If A and D are both greater than 0, the origin is an unstable node (panel a). If A and D are both less than 0, the origin is a stable node (panel b). If one of A or D is positive and the other is negative, the origin is called a saddle point (panel c), in analogy with actual saddles (panel d; compliments of Gabby Roitberg).

A' and B'. Rather than doing that, we will try to generalize what we have already learned.

I will now show two different ways to get to the same answer. The first method is completely independent of anything outside of this book. The second requires that you know a bit of linear algebra. The first method proceeds as follows. We differentiate the first equation in Eq. (2.37) with respect to time to obtain $\mathrm{d}^2x/\mathrm{d}t^2 = A(\mathrm{d}x/\mathrm{d}t) + B(\mathrm{d}y/\mathrm{d}t) = A(\mathrm{d}x/\mathrm{d}t) + B(Cx + Dy)$. Now we use the first equation in (2.37) once again, by noting that $y = (1/B)[(\mathrm{d}x/\mathrm{d}t) - Ax]$. Combining these, we obtain a single, second order differential equation for $x(t)$.

Exercise 2.9 (E)

Show that when we combine the last two equations, we obtain

$$\frac{\mathrm{d}^2x}{\mathrm{d}t^2} - (A + D)\frac{\mathrm{d}x}{\mathrm{d}t} + (AD - BC)x = 0 \tag{2.38}$$

Now, before discussing the solution of this equation, let us think about some of its properties. Since this is a second order differential equation, two constants of integration will appear in the solution. These are called the initial conditions. For the original system, we might specify $x(0)$ and $y(0)$ (for example, two population sizes), but for Eq. (2.38) we might specify $x(0)$ and $\mathrm{d}x/\mathrm{d}t|_{t=0}$ (these are an analogous specification since we know that $y = (1/B)[(\mathrm{d}x/\mathrm{d}t) - Ax]$). Because of the integration constants, there will be many different solutions of Eq. (2.38). The next exercise, which is called the linear superposition of solutions, will be extremely useful for the rest of the chapter.

Exercise 2.10 (E/M)

Suppose that $x_1(t)$ and $x_2(t)$ are solutions of Eq. (2.38). (That is, each of them satisfies the differential equation.) Show that $X(t) = ax_1(t) + bx_2(t)$, where a and b are constants, is also a solution of Eq. (2.38).

We still have to deal with the matter of finding the solution of Eq. (2.38). We know that a first order linear differential equation of the form $\mathrm{d}x/\mathrm{d}t = Ax$ has exponential solutions, so let's guess that the solution of Eq. (2.38) has the form $x(t) = x_0\mathrm{e}^{\lambda t}$ where x_0 is a constant (corresponding to the initial value of x) and we need to find λ. If we accept this guess, then the derivatives of $x(t)$ are $\mathrm{d}x/\mathrm{d}t = \lambda x_0\mathrm{e}^{\lambda t}$ and $\mathrm{d}^2x/\mathrm{d}t^2 = \lambda^2 x_0\mathrm{e}^{\lambda t}$. When we substitute these forms for $x(t)$ and its two derivatives back into Eq. (2.38), note that both x_0 and $\mathrm{e}^{\lambda t}$ will cancel since they appear in all of the terms. We are then left with a quadratic equation for the parameter λ:

$$\lambda^2 - (A + D)\lambda + AD - BC = 0 \tag{2.39}$$

Before interpreting Eq. (2.39), I will show a different way to reach it. For this second method, let us assume that there are certain special initial values of $x(0) = u$ and $y(0) = v$ such that $x(t) = u\mathrm{e}^{\lambda t}$ and $y(t) = v\mathrm{e}^{\lambda t}$. Note that these are clearly not the u and v with which we started this section. I use them here because in life we are symbol-limited. Given this form for $x(t)$ and $y(t)$ the derivatives are $\mathrm{d}x/\mathrm{d}t = \lambda u\mathrm{e}^{\lambda t} = \lambda x(t)$ and $\mathrm{d}y/\mathrm{d}t = \lambda v\mathrm{e}^{\lambda t} = \lambda y(t)$. For this reason, λ is called an eigenvalue (from the German word "eigen" meaning similar or equivalent) of the differential equations (2.37) because when we take the derivatives of $x(t)$ and $y(t)$ we get back multiples of $x(t)$ and $y(t)$. In a geometrical way, we can think of a vector that joins the origin and the point (u, v); it is called the eigenvector, for much the same reason.

Now we substitute these derivatives into Eq. (2.37). Once again, the exponential terms cancel and when we combine terms we obtain

$$\begin{aligned} (A - \lambda)u + Bv &= 0 \\ Cu + (D - \lambda)v &= 0 \end{aligned} \tag{2.40}$$

One solution of these linear algebraic equations is $u = v = 0$. For there to be other solutions, we recall that the determinant of the coefficients of u and v must be equal to 0. That is

$$\begin{vmatrix} A - \lambda & B \\ C & D - \lambda \end{vmatrix} = 0 \tag{2.41}$$

and when we apply the rule for determinants (i.e. that Eq. (2.41) is equivalent to $(A - \lambda)(D - \lambda) - BC = 0$) we obtain the same equation for λ, Eq. (2.39).

Equation (2.39) is a quadratic equation, so that we know there are two solutions, given by the quadratic formula. We will denote these solutions by $\lambda_{1,2}$ and they are

$$\begin{aligned} \lambda_{1,2} &= \frac{(A + D) \pm \sqrt{(A + D)^2 - 4(AD - BC)}}{2} \\ &= \frac{(A + D) \pm \sqrt{(A - D)^2 + 4BC}}{2} \end{aligned} \tag{2.42}$$

where, for convention, we will assume that 1 corresponds to + and 2 to − in the quadratic formula. If we define the discriminant by $\varDelta = (A - D)^2 + 4BC$, then we can write that $\lambda_{1,2} = \left[(A + D) \pm \sqrt{\varDelta}\right]/2$.

We are now able to classify the steady state (0, 0) of the system given in Eq. (2.37). Before doing that, let's have a brief interlude.

Exercise 2.11 (M)

Show that if λ is a solution of Eq. (2.42) and that if we set $u = B$ and $v = \lambda - A$ that Eq. (2.40) is satisfied. Thus, we know how to find the eigenvectors too.

As long as $\Delta \neq 0$, which we will assume in this chapter, the exercises up to this point have allowed us to find the general solution of the system given by Eq. (2.37):

$$\begin{aligned} x(t) &= c_1 B e^{\lambda_1 t} + c_2 B e^{\lambda_2 t} \\ y(t) &= c_1(\lambda_1 - A)e^{\lambda_1 t} + c_2(\lambda_2 - A)e^{\lambda_2 t} \end{aligned} \tag{2.43}$$

Although it is nice to have an explicit form for the solution, what is nicer is that we now know how to classify the steady state.

We begin with the case in which $\Delta > 0$. Then both of the eigenvalues are real. We conclude that if they are both positive, the origin is an unstable node. Since solutions will grow exponentially, whichever eigenvalue is larger will ultimately dominate the behavior of the solution. If both of the eigenvalues are negative, we conclude that the origin is a stable node. If one of the eigenvalues is positive and the other is negative, we conclude that the origin is a saddle point.

When $\Delta < 0$, the eigenvalues are complex numbers, so if we set $q = \sqrt{|\Delta|}$ we can rewrite the eigenvalues as $\lambda_{1,2} = [(A + D) \pm iq]/2$, where $i = \sqrt{-1}$. Consequently, when we compute solutions given by Eq. (2.43), we will need to consider expressions of the form

$$\exp\left(\frac{(A+D)t + iqt}{2}\right) = \exp\left(\frac{(A+D)t}{2}\right)\exp\left(\frac{iqt}{2}\right)$$

From this, we see that if $A + D$, the real part of the eigenvalues, is negative, then whatever else happens solutions will decline in time. If $A + D$ is positive, they will grow in time. The question then becomes how we interpret the exponential of iqt.

For this interpretation, we need a brief reminder. Recall that the solution of the differential equation $d^2x/dt^2 = -kx$ involves sines or cosines. (If you do not recall this, confirm that if $x = \sin(\sqrt{k}t)$ or $x = \cos(\sqrt{k}t)$ then the differential equation is satisfied.) Since this is a linear equation, the general solution must be of the form $c_1 \sin(\sqrt{k}t) + c_2 \cos(\sqrt{k}t)$, where the c_i are constants. Suppose that we had guessed an exponential solution for this equation, i.e. that $x = ce^{\lambda t}$. In this case, the second derivative of $x(t)$ is $c\lambda^2 e^{\lambda t}$ so that we conclude λ must satisfy the equation $\lambda^2 = -k$ or that $\lambda = \pm i\sqrt{k}$. In other words, exponentials involving $\sqrt{-1}$ lead to oscillations. Our solution is at hand. If $\Delta < 0$, we now know that the solutions will oscillate. Such a steady state is called a focus or a spiral point. If $A + D < 0$, the focus is stable and if $A + D > 0$ the focus is unstable.

But, of course, all this work (and it is hard work) only corresponds to the linear system of equations (2.37) and the equations that we actually encounter in population biology are nonlinear. What do we do about this? That is, in general we will have a pair of differential equations of the form

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= f(x,y) \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= g(x,y) \end{aligned} \tag{2.44}$$

and let us suppose that the point $(x_\mathrm{s}, y_\mathrm{s})$ is a steady state of this system so that $f(x_\mathrm{s}, y_\mathrm{s}) = g(x_\mathrm{s}, y_\mathrm{s}) = 0$. We go forward from Eq. (2.44) by linearizing the equations around the steady state. That is, we write $x(t) = x_\mathrm{s} + \tilde{x}(t)$ and that $y(t) = y_\mathrm{s} + \tilde{y}(t)$ so that $\tilde{x}(t)$ and $\tilde{y}(t)$ measure the deviations from the steady state. Since the steady states are constant, we know that $\mathrm{d}x/\mathrm{d}t = \mathrm{d}\tilde{x}/\mathrm{d}t$ and $\mathrm{d}y/\mathrm{d}t = \mathrm{d}\tilde{y}/\mathrm{d}t$. Now we will Taylor expand $f(x, y)$ around the steady state and keep only the linear term:

$$\begin{aligned} f(x,y) &\approx f(x_\mathrm{s} + \tilde{x}, y_\mathrm{s} + \tilde{y}) \\ &= f(x_\mathrm{s}, y_\mathrm{s}) + \frac{\partial}{\partial x} f(x,y)|_{(x_\mathrm{s},y_\mathrm{s})}\tilde{x} + \frac{\partial}{\partial y} f(x,y)|_{(x_\mathrm{s},y_\mathrm{s})}\tilde{y} \end{aligned} \tag{2.45}$$

Now let us consider the three terms in the right hand expression of this equation. The first term on the right hand side is identically zero, because $(x_\mathrm{s}, y_\mathrm{s})$ is a steady state. The second term is the partial derivative of $f(x, y)$ with respect to x, evaluated at the steady state. To help simplify what we have to write, we will use subscripts for partial derivatives and, with a slight abuse of notation, replace the second and third terms on the right hand side of Eq. (2.45) by $f_x(x_\mathrm{s}, y_\mathrm{s})\tilde{x}$ and $f_y(x_\mathrm{s}, y_\mathrm{s})\tilde{y}$. A similar argument shows that $g(x,y) \approx g_x(x_\mathrm{s}, y_\mathrm{s})\tilde{x} + g_y(x_\mathrm{s}, y_\mathrm{s})\tilde{y}$. The point of all this work is that we can now replace the nonlinear differential equation (2.44) by a linear system that characterizes the deviations from the steady state

$$\begin{aligned} \frac{\mathrm{d}\tilde{x}}{\mathrm{d}t} &= f_x(x_\mathrm{s}, y_\mathrm{s})\tilde{x} + f_y(x_\mathrm{s}, y_\mathrm{s})\tilde{y} \\ \frac{\mathrm{d}\tilde{y}}{\mathrm{d}t} &= g_x(x_\mathrm{s}, y_\mathrm{s})\tilde{x} + g_y(x_\mathrm{s}, y_\mathrm{s})\tilde{y} \end{aligned} \tag{2.46}$$

and we now compare Eq. (2.46) with Eq. (2.37) to determine the values of A, B, C, and D (note that they are not arbitrary but must match the various partial derivatives in Eq. (2.46)), from which we can determine the stability characteristics of the steady states.

To help make the preceding more concrete, we will first consider an example, then an exercise. A very simple model for competition between two types or species $x(t)$ and $y(t)$ is

$$\begin{aligned}\frac{dx}{dt} &= x(1+a-x-ay)\\ \frac{dy}{dt} &= y(1+a-y-ax)\end{aligned} \tag{2.47}$$

where a is a parameter, which we assume to be positive. From the form of these equations, we see that the presence of x increases the rate of change of x and that the presence of both x and y decreases the rate of change of x (and vice versa for y). We say that x and y are auto-catalysts for themselves and anti-catalysts for the other type. This thinking underlay the work of Sir F. C. Frank in his study of spontaneous asymmetric synthesis (see Connections); Eq. (2.47) is also a simple analog of the Lotka–Volterra competition equations, in which the competition is symmetric.

We find the steady states of Eq. (2.47) by setting $dx/dt = 0$ and $dy/dt = 0$. For the former, we find that $x = 0$ or $x + ay = 1 + a$. For the latter, we find that $y = 0$ or $y + ax = 1 + a$. Thus, (1, 1) is a steady state. Before conducting an eigenvalue analysis, we use the isoclines (or more properly, the nullclines, lines on which $dx/dt = 0$ or $dy/dt = 0$) of the differential equations to understand properties of the solution. These are shown in Figure 2.16. The steady state (1, 1) can be either a node (if $a < 1$) or a saddle point (if $a > 1$). When $a = 1$, the two isoclines sit on top of each other and the system is structurally unstable. Note also that, because x and y are interchangeable in the two equations, the line $y = x$ is a solution of the equations – points on the line $y = x$ move towards (1, 1), regardless of whether it is a node or a saddle point.

We can now conduct the eigenvalue analysis. In this case $f(x,y) = x(1+a-x-ay) = x(1+a) - x^2 - axy$ and $g(x, y) = y(1+a) - y^2 - axy$. The partial derivatives are thus $f_x = 1 + a - 2x - ay$, $f_y = -ax$, $g_x = -ay$, and $g_y = 1 + a - 2y - ax$, and we evaluate these at (1, 1) in order to obtain A, B, C, and D, so that $A = 1 + a - 2 - a = -1$, $B = -a$, $C = -a$, and $D = 1 + a - 2 - a = -1$. We substitute this into Eq. (2.42) and find that $\lambda_{1,2} = -1 \pm \sqrt{a}$. From the eigenvalue analysis, we reach the same conclusion as from the phase plane analysis – that (1, 1) is either a stable node or saddle point, depending upon the value of a. Thus, in this case, the eigenvalue analysis told us little that we could not understand from the phase plane. Here's an example where it tells us much more.

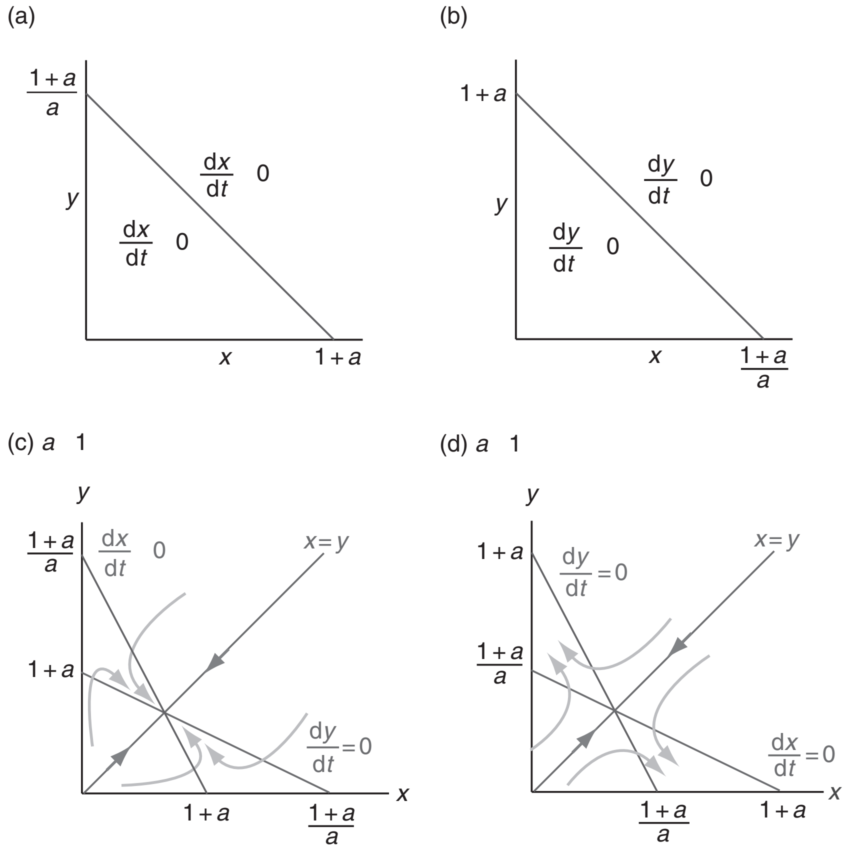


Figure 2.16. The isocline analysis of the equations for spontaneous asymmetric synthesis/symmetric competition. In panels (a) and (b), I show the separate isoclines for dx/dt = 0 and dy/dt = 0 and the flow of points in the phase plane. When these are put together, the resulting phase plane shows either a stable node at (1,1) (panel c) or a saddle point (panel d).

Exercise 2.12 (M → H)

Consider the following predator (P)–prey (V) system

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - bPV \qquad \frac{dP}{dt} = cPV - mP$$

Assume that the biomass of each is measured in numbers of individuals (but treated as a continuous variable) and time is measured in years. It might be helpful for what follows to think of rabbits and foxes as the victims and predators. It might also be helpful, especially for parts (a) and (b), to convert to per capita growth rates. (a) What are the units of all the parameters? (b) Interpret the biology of both predator and prey. What must be true about the relationship between b and c if the system is mammalian predators such as rabbits and foxes? (c) Conduct an isocline analysis. Note: there are two cases, depending upon the relationship between K and m/c. Be sure to get both of them and carefully think about what each means. (d) Classify the steady states of the system according to their eigenvalues. What does the eigenvalue calculation tell you that the isocline analysis did not? Once again, there are two cases that require careful interpretation. (e) What happens to the eigenvalues as $K \to \infty$?