

Chapter 3

Single-species Population Dynamics

In this chapter we move up to the level of the population. The models we consider here attempt to explain and predict patterns of change over time in population *density*, the number of individuals per unit area or volume.

Population dynamics has always been a core topic in theoretical ecology. One of the original – and still strong – motivations for developing mathematical models is to understand the cause of cycles in particular populations, such as those shown in Figure 3.1. Is the famous lynx cycle the result of the trophic link between lynx and hare, or is it a cycle driven by the interaction between hares and their food resources with the lynx just “along for the ride” as their food source waxes and wanes? We could imagine experimental approaches to this question, but their practicality is a serious issue, and even when such experiments have been attempted their interpretation is not always clear (Turchin 2003). Models are therefore play two important roles: they identify classes of population interactions that could lead to the observed type of dynamics, and they may be able to identify unique predictions of each competing hypothesis that can be tested using observational data.

We are also interested in understanding patterns in cross-species comparisons – how do macroscopic properties such as the cycle period depend on properties of the individual organisms? For example, Figure 3.2 shows that when the period of population cycles is scaled relative to the individual maturation time (the time between birth and sexual maturity), some scaled periods are not observed (the INT category), and there is a clear difference in scaled period between specialists and generalists (a specialist feeds almost exclusively on just one species, a generalist feeds on many species). At the end of a long road that we are now starting, we will understand how this pattern was predicted *a priori* using models that account for individual growth and development, and their interactions with competition for resources.

Population modeling is also important for species management: managing fisheries for the highest possible sustainable yield, developing recovery plans for species threatened by extinction, or trying to contain or prevent the spread of invasive species. For these questions, we are often interested in how a population, or set of interacting populations, responds to a change in system parameters. For example: how

does a change in harvesting effort affect an exploited population, or how does a reduction in some cause of juvenile mortality affect a species at risk of extinction? How sure can we be about our predictions, or (more importantly) about the degree of uncertainty in our predictions?

3.1 Unstructured populations in continuous time

“Unstructured” means that we ignore differences between individuals, and pretend that a total headcount – irrespective of age, sex, breeding status, disease state, etc. – provides all the necessary information for predicting future population changes. You have to start somewhere, this is the easiest place to start, and easy is where you always start when you’re trying to develop something new.

The starting point for modeling population change is the fundamental “BIDE” Balance Law for total population size $N(t)$:

$$N(t+h) = N(t) + \text{Births} + \text{Immigration} - \text{Deaths} - \text{Emigration} \quad (3.1)$$

Equation (3.1) is always true, but it is vacuous until we specify the values of B,I,D, and E over the time interval $(t, t+h)$.

3.1.1 First simple models

Exponential growth results from the simplest possible assumptions, constancy of the per-individual birth and death rates:

Births = (# parents) \times (births/parent/time) \times (length of time interval)

$$B = N(t) \times b \times h$$

and similarly

$$D = N(t) \times d \times h$$

and $I = E = 0$ (closed population). Then

$$\begin{aligned} N(t+h) &= N(t) + N(t)bh - N(t)dh \\ \frac{N(t+h) - N(t)}{h} &= (b-d)N(t) \end{aligned} \quad (3.2)$$

Now we let $h \rightarrow 0$ to get

$$\frac{dN}{dt} = (b-d)N(t) = rN(t) \quad \text{where } r = (b-d). \quad (3.3)$$

This is the differential equation every ecologist can solve,

$$N(t) = N(0)e^{rt}. \quad (3.4)$$

The above is a paradigm of how a model is created.

1. The *state variable(s)* of interest are specified: here just $N(t)$, total population size, based on the “unstructured” assumption.
2. The *processes* affecting the state variable are specified, here by the general BIDE equation.
3. The *process rates* (how many births per time interval?, etc.) are specified as functions of the state variables to give a closed system of equations.
4. The final result is a *dynamic equation* specifying how the state variables change over time, that can be solved (analytically or numerically) to determine what the model predicts

It often helps the modeling process to build up a compartment (“box and arrow”) diagram of the model as you proceed, with boxes representing state variables and arrows the processes that cause a state variable to increase or decrease. For example, Figure 3.3 shows the diagram for the exponential growth model:

The solution (3.4) says that if $r > 0$ (i.e. if $b > d$) the population grows exponentially without limit, and if $r < 0$ it decreases to 0. The latter is all too credible nowadays for nonhuman species, but even for humans the former is not (regardless of what Julian Simon would like us to believe). A more plausible model has to put limits on growth.

The *logistic model* assumes that the net birth-death rate decreases linearly with N . The traditional form is

$$dN/dt = rN \left(1 - \frac{N}{K} \right), \quad r, K > 0. \quad (3.5)$$

This has a long history and remains a favorite representation of limited growth. But despite early (1930’s) claims that it was a general quantitative law, it really is just a convenient, simple model: linear decrease is sometimes seen, sometimes not. Note that the model makes no sense biologically if $r < 0$, since then a population with $N(0) > K$ would increase without limits.

The behavior of solutions to the logistic model can be found by a simple graphical analysis.

1. Graphing dN/dt versus N we have a parabola, with zeros at $N = 0$ and $N = K$ and maximum at $N = K/2$.
2. Any N where $dN/dt = 0$ is an *equilibrium = steady state = fixed point = critical point*. The equilibria for the logistic model are therefore at $N = 0$ and $N = K$.
3. We can also determine the *stability* of fixed points: 0 is unstable, K is stable (N^* stable means: if $N(0)$ is near N^* , then $N(t) \rightarrow N^*$ as $t \rightarrow \infty$. Unstable means: not stable).
4. The graph of dN/dt also allows us to sketch the qualitative form of solutions $N(t)$.
 - If a solution starts at $0 < N(0) < K/2$, then $N(t)$ is an increasing function of t because $dN/dt > 0$. Moreover, as $N(t)$ increases, so does dN/dt until $N(t)$ reaches $K/2$; after that dN/dt decreases over time while $N(t)$ continues to increase up to K . The graph of $N(t)$ is therefore sigmoid, with an inflection point when $N(t) = K/2$.

- If a solution starts at $K/2 < N(0) < K$, then dN/dt is always decreasing while $N(t)$ increases to K , so the solution curve is concave down.
- What is the shape of solutions when $N(0) > K$?

5. The fixed points and their stability can also be found by graphing the net (birth rate - death rate) $r(N) \equiv (1/N)dN/dt = r(1 - N/K)$, so long as we remember that there is an equilibrium at $N = 0$ even though $r(0) > 0$. Positive values of $r(N)$ imply that the population will grow, negative values imply that it will shrink, and any nonzero N^* where $r(N^*) = 0$ will be an equilibrium.

Exercise 3.1 Analyze graphically the dynamics of the following equations. In each case, plot dx/dt versus x , find all the equilibria, determine their stability, and sketch the qualitative shape of $x(t)$ versus t for various starting values, as we did for the logistic equation in lecture. You may find it useful to use **R** for plotting dx/dt versus x .

- (a) $dx/dt = 1 - x^2$ (consider also $x < 0$)
 (b) $dx/dt = x(x - 0.5)(2 - x)$ (consider only $x \geq 0$)

3.1.2 Scaling out parameters

Numerical solutions of a model depend on the values of all its parameters. However, qualitative features of model behavior are usually controlled by a smaller number of parameter combinations. One way to find these useful quantities is by re-scaling the model into dimensionless form.

For the logistic model, we first define a new state variable $x = N/K$. We rescale in this way because N and K are in the same units, so this makes x a dimensionless quantity, meaning that its value does not depend on the units in which N and K are measured. Then

$$\frac{dx}{dt} = \frac{1}{K} \frac{dN}{dt} = r \frac{N}{K} \left(1 - \frac{N}{K}\right) = rx(1 - x).$$

Next we rescale time. r is in units 1/time (WHY?) so rt is dimensionless. Let $\tau = rt$. Then

$$\frac{dx}{d\tau} = \frac{dx}{d(rt)} = \frac{1}{r} \frac{dx}{dt} = x(1 - x).$$

(this calculation can be justified formally using the Chain Rule: $\frac{dx}{d\tau} \frac{d\tau}{dt} = \frac{dx}{dt}$).

So apart from the scaling of the axes, the behavior of the logistic model is independent of the values of r and K (though note that we use the assumptions of the logistic model that r and K are both positive – otherwise the rescaled model would have time running backwards rather than slower or faster, and negative numbers of individuals).

A general – though not universal – rule is that rescaling can be used to “eliminate” one parameter per state variable, and one more for the time variable in a continuous time model. In a discrete time model

you can knock out one per state variable and that's it. Once all the variables (including time) in a model are dimensionless (like $x = N/K$), you can't get any more simplifications by rescaling. However there may be several different ways of rescaling a model into dimensionless form, and some may be more helpful than others for the tasks at hand.

Exercise 3.2 Show how the following model for a harvested population

$$dN/dt = rN \left(1 - \frac{N}{K}\right) - H \frac{N}{A + N}, \quad r, K, A, H > 0.$$

can be re-scaled into the dimensionless form

$$\frac{dx}{d\tau} = x(1 - x) - h \frac{x}{a + x}$$

and give the expressions for τ, x, h, a in terms of the variables and parameters of the original model. In the second term of the model H is a measure of fishing effort (e.g. proportional to the number of boat-days per fishing season), and A is the fish population density at which the capture rate per unit of fishing effort reaches half its maximum possible value.

3.1.3 Spruce Budworm

The graphical analysis of equilibrium stability suggests that single-species models $dN/dt = f(N)$ are totally boring. That's not true once you consider how the population can respond to changes in parameter values. As an example, we consider now a classical model for the dynamics of spruce budworm (Ludwig et al. 1978). The goal of the model was to explain the qualitative pattern that budworm exhibits sudden outbreaks from low to high density, which causes defoliation of the forest, and then a sudden collapse back to very low numbers, rather than either gradual oscillations or convergence to a steady balance between bugs and trees. Our presentation draws on Strogatz (1994) and the original article by Ludwig et al.

The model for the insect (budworm) assumes that the population is regulated by two things: competition for resources (foliage) and predation. Competition is modeled by the logistic equation (as usual, because it's the easiest thing to use). Predation is modeled by a loss term depending on budworm density N ,

$$dN/dt = RN \left(1 - \frac{N}{K}\right) - \frac{BN^2}{A^2 + N^2}.$$

The predation term is a so-called "type III" functional response representing a generalist predator at constant density that switches among potential prey items as they change in abundance. Despite optimal foraging theory, this is often observed. $\frac{N^2}{A^2 + N^2}$ represents how much "attention" the predator is paying to budworm.

In the logistic growth term, we think of K as depending on the foliage level in the trees. A more complete model, developed by Ludwig et al. (1978), includes a dynamic equation for changes in foliage. Here we will treat foliage level as a parameter, and think about how gradual changes in foliage level will affect the insect population.

First we need to non-dimensionalize; there are many options. In this case it is convenient to let $x = N/A$ (we'll see why later) so

$$\frac{N^2}{A^2 + N^2} = \frac{x^2}{1 + x^2}.$$

This results in

$$\frac{dx}{dt} = Rx \left(1 - \frac{x}{k}\right) - \frac{B}{A} \frac{x^2}{1 + x^2} \quad (3.6)$$

where $k = K/A$. Now we want to re-scale time. We have a choice: “kill R ” or “kill B/A ”. It is convenient (for the same reason) to kill B/A . So we let

$$\tau = (B/A)t$$

and get

$$\frac{dx}{d\tau} = \frac{dx}{(B/A)dt} = \frac{A}{B} \frac{dx}{dt} = \frac{RA}{B} x \left(1 - \frac{x}{k}\right) - \frac{x^2}{1 + x^2} \quad (3.7)$$

$$\Rightarrow \frac{dx}{d\tau} = rx \left(1 - \frac{x}{k}\right) - \frac{x^2}{1 + x^2} \quad (3.8)$$

where $r = RA/B$.

To analyze the model, we start by looking for fixed points and analyzing their stability.

1. There is always a fixed point of (3.8) at $x = 0$, and it is always unstable (because the linear term dominates near $x=0$, giving $\dot{x} > 0$ (**Warning:** \dot{x} denotes the derivative of x with respect to time. This notation is convenient because it lets us gloss over whether time is t or τ ; but at the end you do have to remember how you scaled things).
2. Positive fixed points ($x > 0$) occur where $\dot{x}/x = 0$, i.e. where

$$r \left(1 - \frac{x}{k}\right) = \frac{x}{1 + x^2} \quad (3.9)$$

This is equivalent to a cubic equation, so there can be at most 3 solutions. There has to be at least one (since a cubic tends to opposite signs as $x \rightarrow \pm\infty$ but there can be 1,2 or 3 depending on the values of r and k (see Figure 3.4).

We can study fixed points and their stability graphically by graphing the two sides of equation (3.9) versus x , on the same graph; see Figure 3.4. Fixed points then occur where the graphs of the two sides intersect. In Figure 3.4 k is constant and r varies, but the same happens as k varies with r held fixed: starting from the bottom dashed line where there are 3 fixed points, as k decreases we go to 2 fixed points and then to 1.

We can determine the stability of fixed points by graphing the flow on the x axis, as usual. From the expression for \dot{x} we see that \dot{x} is positive where the line (the left hand side in (3.9)) is above the curve (the right hand side), and negative where the line is below the curve. Doing this for the possible cases in Figure 3.4, we find that

1. When there are 3 fixed points $a < b < c$, we have bistability: the largest and smallest are stable, the intermediate fixed point is unstable.
2. When there is only one fixed point, it is stable.

We get from 3 fixed points to 1 when the fixed points b collides with one of the others, and they mutually self-destruct. This is called a *saddle-node bifurcation* – because in two-dimensional systems the colliding fixed points are a (stable) node and (unstable) saddle. A *bifurcation* is the term for a change in the qualitative nature of the solutions to a dynamical system. So long as all 3 fixed points are present, the qualitative picture is the same (the system tends to fixed points a or c depending on where it starts); after the bifurcation things are different.

It is useful to study bifurcations because they let us map out where in “parameter space” (the (k, r) plane) we have 1 versus 2 versus 3 fixed points. The model goes from 1 to 3 fixed points along the curve in parameter space where there are exactly 2 fixed points. This occurs at parameters where the two rate functions are tangent (see Figure 3.4). We find these tangencies by requiring that the curves be equal in both value and derivative:

$$r \left(1 - \frac{x}{k}\right) = \frac{x}{1 + x^2} \quad (3.10)$$

$$-r/k = \frac{1 - x^2}{(1 + x^2)^2} \quad (3.11)$$

The best way to express this is by solving for r and k as a function of x , the (scaled) budworm density at which the tangency occurs. It goes like this: from the condition (3.10) we have

$$r = \frac{r}{k}x + \frac{x}{1 + x^2}.$$

The condition (3.11) gives us r/k as a function of x . Plug that into the expression above for r and simplify:

$$r = \frac{2x^3}{(1 + x^2)^2}. \quad (3.12)$$

Then take this expression for r as a function of x and plug it into (3.11), and simplify to get

$$k = 2x^3/(x^2 - 1). \quad (3.13)$$

Equations (3.12) and (3.13) are graphed in Figure 3.5. The cusp in the bifurcation diagram occurs because the maximum of $r(x)$ and the minimum of $k(x)$ occur at the same point, $x = \sqrt{3}$ (proof: $r'(x) = k'(x) = 0$ at $x = \sqrt{3}$). But the slope of r versus k (given by $\frac{dr}{dk} = \frac{dr/dx}{dk/dx}$) is a smooth function at this point. That means that the two branches of the cusp are tangent – they come into the cusp at the same slope.

It has taken a while to understand this model, but the all we’re using is high school algebra, freshman calculus and (crucially) the computer. *The computer changes how we figure out the behavior of models.* We could try to proceed deductively from first principles using pencil and paper. But it’s faster to first

see what happens on the computer screen (e.g., there is a cusp in the bifurcation curve, and it seems to be a tangency), and then use math to understand why those things happen.

So how was this model used to explain budworm outbreak and collapse? In the full model of Ludwig et al. (1978) the budworm population model was linked to a set of two equations for variables characterizing the state of the forest – the size and energy reserves of the trees – in such a way that parallel increases in tree size and health caused both r and k to increase. Both r and k are dimensionless ratios of parameters, and the full Ludwig et al. (1978) model – equations (20)-(22) in that paper – had the property that forest recovery after a budworm outbreak caused both r and k to increase. The referring to figure (3.6) we can have the following scenario:

1. Following an outbreak, the forest has collapsed to a state of low r and k such that there is only a single fixed point a at which budworm density is very low.
2. As the forest matures, r and k increase (more foliage, greater potential for budworm increase). However the budworm remain at a until the saddle-node bifurcation occurs where a and b collide and annihilate each other. The budworm density then suddenly increases to the fixed point c .
3. The same now occurs in reverse: as the forest is defoliated – decreasing r and k – the budworm remain at c until the saddle-node bifurcation occurs at which c is eliminated, and they suddenly collapse down to a .

This is an example of what is called *hysteresis*: as parameters are changed to new values, the system changes; but as parameters change back to old values, the system does not retrace its steps in reverse. Instead it follows a different path, because the change in parameters resulted in it jumping from one stable fixed point to another.

Exercise 3.3 We return here to the (re-scaled) model for a harvested fish population

$$\dot{x} = x(1 - x) - h\frac{x}{a + x}, \quad x > 0$$

with parameters $a, h > 0$. h is a measure of fishing effort (relative to the intrinsic rate of growth of the fish population) and a is the value of (rescaled) fish density at which the harvest per unit of fishing effort reaches half its maximum possible value. Consequently a is “given” by the biology of the system, but h is subject to regulatory control.

(a) As in the budworm model, there is always a fixed point at $x = 0$. Is it always unstable in this model? [HINT: show that for $x > 0$, \dot{x} has the same sign as $g(x) \equiv (a - h) + (1 - a)x - x^2$. Positive fixed points and their stability can therefore be studied as if \dot{x} were equal to $g(x)$].

(b) Graphically show how there can be either 0,1 or 2 fixed points where $x > 0$ [HINT: use $g(x)$ again, and since g is just a parabola you can feel free to draw things freehand rather than using the computer, so long as you get things qualitatively right]

(c) Graphically show how the following scenario can occur: As the fishing rate h is increased, the fish population suddenly collapses and seems to be decreasing exponentially to extinction. When h is

returned to its initial, lower value, the population does not recover, but instead continues to decrease. [HINT: what happens to g if h is changed but all else stays the same?].

(d) Find the expression for the curve in the (a, h) parameter plane where the saddle-node bifurcation occurs (going from 0 to 2 positive fixed points). HINT: use g again, and recall that the solutions of a quadratic equation $Ax^2 + Bx + C = 0$ are

$$\frac{-B \pm \sqrt{B^2 - 4AC}}{2A}.$$

3.1.4 Local stability analysis of fixed points

This section is based on Chapter 2 of Bulmer's book, which can be consulted for additional details.

For the model

$$\dot{n} = f(n)$$

we want to determine the local stability of a fixed point \hat{n} . To study the dynamics near \hat{n} we define $p(t) = n(t) - \hat{n}$ – the deviation from the fixed point. Note that $f(\hat{n}) = 0$ since it is a fixed point. Then

$$\begin{aligned} \dot{p} = \dot{n} &= f(\hat{n} + p) \\ &= f(\hat{n}) + f'(\hat{n})p + \dots \quad [\text{we drop higher order terms in } p] \\ &\doteq f'(\hat{n})p \end{aligned} \tag{3.14}$$

So our equation for the local dynamics is $\dot{p} = rp$ with $r = f'(\hat{n})$. Consequently \hat{n} is

- Stable if $f'(\hat{n}) < 0$
- Unstable if $f'(\hat{n}) > 0$

If $f'(\hat{n}) = 0$ it could be stable or unstable – the linear analysis doesn't tell us.

Example: Spruce budworm model at $x = 0$,

$$\dot{x} = rx \left(1 - \frac{x}{k}\right) - \frac{x^2}{1+x^2}.$$

We could compute $f'(x)$ and set $x = 0$, but there's an easier way for $x = 0$. Quadratic and higher-order terms won't affect the slope at $x = 0$ so we can eliminate them *before* taking the derivative. That leaves us with

$$\dot{x} = rx$$

so $x = 0$ is always unstable (under the model's assumption that $r > 0$).

Example: $dn/dt = rn(1-n)$, $r > 0$. We can find the fixed points and determine their stability by computing the derivatives of $f(n) = rn(1-n)$ at the fixed points. But graphing $f(n)$ versus n it is easy to see that $f'(0) > 0$ (unstable) and $f'(1) < 0$ (stable) – local linearization gives us the same answer as our previous graphical analysis.

Exercise 3.4 (based on Hess 1996). Levins (1966) introduced a simple model for species persistence in a *metapopulation* – a collection of local populations spread across a set of *habitat patches*, and linked through migration of individuals from between patches. The model tracks the fraction of patches that are *occupied* – meaning that some individual of the species is present – but does not pay attention to the variation in population density among occupied patches. The standard form of the model is

$$\dot{p} = mp(1 - p) - xp \quad (3.15)$$

where p is the fraction of habitat patches occupied, m is the migration rate, and x is the extinction rate.

(a) The term $mp(1 - p)$ represents recolonization of empty patches, through the arrival of a migrant. What biological assumptions lead to this expression for the recolonization rate?

(b) The term xp represents extinction of occupied patches. What biological assumptions lead to this expression for the extinction rate?

(c) Find the conditions under which the model (3.15) has a positive equilibrium p^* . Show that there is at most one positive equilibrium, and use local stability analysis to show that that the equilibrium is stable whenever it exists.

(d) What happens to the population when there is no positive equilibrium?

(e) Based on the Levins model (and others), many conservation biologists have suggested that increased connectivity between habitat patches will help the persistence of species whose habitat has become fragmented (a Web search on “conservation corridor” will find many examples where this idea is now being implemented). Hess (1996) pointed out that increased connectivity might also affect the rate of extinctions, by facilitating the spread of predators, pathogens, exotic organisms, and disturbances (fire, toxic waste) that could have negative impacts on the target species. He therefore modified the Levins model to

$$\dot{p} = r(c)p(1 - p) - x(c)p \quad (3.16)$$

where c is the connectivity between patches, and r is the recolonization rate. Suppose that $r(0) = 0$ and r is an increasing function of c . Show that, under some assumptions about how the extinction rate x depends on c , increased connectivity could be beneficial up to a point but then harmful: the species goes extinct if c is too small or too large, and persists at some intermediate range of c values.

3.2 Single unstructured population, discrete time

We continue to follow Chapter 2 of Bulmer’s book. The basic model in discrete time is

$$n_{t+1} = F(n_t) = n_t C(n_t) \quad (3.17)$$

Example: the Ricker map (called the “discrete logistic” in Bulmer),

$$n_{t+1} = n_t e^{r(1-n_t/K)}$$

As usual we rescale the model by setting $x = n/K$, which gives us

$$x_{t+1} = x_t e^{r(1-x_t)}.$$

But note that we can't "kill" r like we did in the continuous time logistic. In discrete-time models you can typically scale out one parameter per state variable, by making each state variable dimensionless. In continuous-time models you can generally scale out one more by making time nondimensional. But in discrete-time models time already is nondimensional – the model describes what happens in one "time step" whether that step is an hour, day, or year.

For a difference equation like this, fixed points occur where $F(x) = x$, intersections between the graph of $y = F(x)$ and the 45-degree line $y = x$. **(Draw the graph)** Note the potential for overshoot of a fixed point, impossible in $dn/dt = f(n)$. That is, it is possible to have n_t below a fixed point and n_{t+1} above it.

3.2.1 Local stability analysis

As usual we let $n_t = \hat{n} + p_t$ where \hat{n} is a fixed point, meaning that

$$F(\hat{n}) = \hat{n}.$$

Then

$$\begin{aligned} n_{t+1} &= F(n_t) = F(\hat{n} + p_t) \\ &\doteq F(\hat{n}) + F'(\hat{n})p_t \\ &= \hat{n} + F'(\hat{n})p_t \end{aligned} \tag{3.18}$$

and therefore

$$p_{t+1} \doteq F'(\hat{n})p_t.$$

Consequently, \hat{n} is

- Stable if $|F'(\hat{n})| < 1$, and unstable if $|F'(\hat{n})| > 1$. If $F'(\hat{n}) = \pm 1$ we don't know: the local linear analysis is inconclusive.
- Monotonic if $F'(\hat{n}) > 0$, and
- oscillatory if $F'(\hat{n}) < 0$ (oscillatory means that successive values of n_t are on opposite sides of the equilibrium).

Note: all 4 combinations of (Stable, Unstable) \times (Monotonic, Oscillatory) are possible.

Example: what most people call the discrete logistic model,

$$n_{t+1} = rn_t(1 - n_t/K), \quad r > 0.$$

What are the equilibria, and how does their stability depend on parameter values?

The first step is to get rid of one parameter; letting $x_t = n_t/K$ we have

$$x_{t+1} = rx_t(1 - x_t), \quad r > 0. \tag{3.19}$$

Equilibria of (3.19) satisfy the equation

$$\hat{x} = r\hat{x}(1 - \hat{x}).$$

One solution is $\hat{x}_1 = 0$. To find others we divide through by \hat{x} and get

$$1 = r(1 - \hat{x}),$$

so the second equilibrium is

$$\hat{x}_2 = 1 - \frac{1}{r},$$

which is only meaningful when $r > 1$ so that $\hat{x}_2 > 0$.

To examine the stability of these equilibria we need to look at the derivatives of $F(x) = rx(1 - x)$. Expanding the quadratic and differentiating, we have

$$F'(x) = r - 2rx = r(1 - 2x).$$

- Stability of $\hat{x} = 0$: $F'(0) = r$, so this equilibrium is stable when $r < 1$ and unstable for $r > 1$.
- Stability of $\hat{x} = 1 - 1/r$: $F'(1 - 1/r) = r(1 - 2(1 - 1/r)) = r(2/r - 1) = 2 - r$, so this equilibrium is stable whenever

$$\begin{aligned} -1 &< 2 - r < 1 \\ -3 &< -r < -1 \\ 1 &< r < 3 \end{aligned} \tag{3.20}$$

Convergence to \hat{x} will be monotonic if $0 < 2 - r < 1$, which is $1 < r < 2$, and oscillatory for $2 < r < 3$.

This leads us to make the following reasonable guesses:

1. For $0 < r < 1$ all solutions tend to $\hat{x} = 0$, so the population dies out.
2. For $1 < r < 3$ all solutions tend to $\hat{x} = 1 - 1/r$, so the population settles down to a constant value.
3. for $r > 3$ the population doesn't die out and it doesn't settle down, so it must constantly fluctuate.

Exercise 3.5 Do some computer experiments to see how much of our “reasonable” guesswork is correct (answer: almost all of it, but not exactly 100%).

Exercise 3.6 Pulliam (1988) developed a model for populations divided between *source* and *sink* habitat. In source habitat the species is self-sustaining and exports migrants. In sink habitat the species cannot maintain itself unless the local population is augmented by immigrants. Pulliam's (1988) simple didactic model is as follows:

- The source habitat contains \hat{n}_1 breeding sites, which are always fully occupied. Each year the source habitat population grows by a factor $\lambda_1 > 1$, with \hat{n}_1 individuals remaining in the source habitat, and the remaining $(\lambda_1\hat{n} - \hat{n})$ moving to the sink habitat.

• The sink habitat population $n_2(t)$ shrinks by a factor $\lambda_2 < 1$ each year, followed by arrival of the migrants from source habitat.

These give the following equation for the sink habitat population dynamics:

$$n_2(t+1) = \lambda_2 n_2(t) + \hat{n}_1(\lambda_1 - 1)$$

- Find the nonzero fixed point for the sink habitat population n_2 (call it \hat{n}_2) and show that \hat{n}_2 is locally stable by a linearized stability analysis.
- For what values of the model parameters will \hat{n}_2 be greater than \hat{n}_1 ?
- Show that for suitable parameter values, the number of immigrants to the sink population may be far smaller than the number of individuals in the sink population.

The conclusion of this paper – and the reason it got so much attention – are the ways for things to be other than they seem:

- most individuals of a species may be in *unsuitable* habitat where it cannot sustain itself.
- A seemingly trivial number of immigrants, coming from a small fraction of the occupied habitats, may be crucial for a population to persist.

A lot of conservation planning is still based on range maps and the idea that you can preserve a species by preserving the places where it is found. But if source-sink is credible (as may believe), a static picture of “who lives where” may be very misleading. Even if a species and its habitat are protected across most of its range, it may go extinct if most of the protected area is sink habitat.

Exercise 3.7 Here we explore the possible role of *lattice effects* in the dynamics of these simple population models. “Lattice effects” are the consequences of the fact that actual number of individuals in a population must be an integer. For this exercise, look at lattice effects in the unscaled logistic model

$$N_{t+1} = rN_t(1 - N_t/K)$$

with $r = 3.75$, $K = 100$.

(a) Do some computer experiments to compare the dynamics of the logistic model to that of the lattice logistic model

$$N_{t+1} = \text{round}rN_t(1 - N_t/K)$$

(here $\text{round}(x)$ is the integer closest to x), and report what you discover. It will be informative to start by comparing what happens if N_0 is close to the fixed point of the non-lattice model, but don’t stop with that.

(b) For the lattice model, draw a plot of N_{t+1} versus N_t , and add the line $N_{t+1} = Nt$ to the plot. What does that tell you about stability of the fixed point for the lattice model? What else does this explain about your discoveries in part (a)?

(c) How much difference do you think it would make if you rounded down in the lattice model, instead of rounding to the nearest integer?

For more on lattice effects, see Henson et al. (2001) subsequent work citing that paper.

3.3 Fitting the models to data

We now have two different models for the changes in abundance of a single unstructured population

$$\begin{aligned} \dot{n} &= f(n), \\ n_{t+1} &= F(n_t) \end{aligned} \tag{3.21}$$

Both of these are ways to specify “what happens next” – given the current state (population density n at time t), the first gives the instantaneous rate of change dn/dt , the second specifies the finite rate of change $n_{t+1} - n_t$.

Biologically, we think of these as corresponding to overlapping versus discrete generations. In the former case, the ongoing stream of births and deaths is approximated by an equation for the rate of ongoing population change (net (birth rate - death rate) as a function of current population size). In the latter case, the population really jumps from one value (this generation) to another (next generation).

However, any differential equation implicitly determines a difference equation: $n(t+1) =$ where you wind up after one time unit, starting from $n(t)$. So if a continuously growing population can be described by a model of the form $dn/dt = f(n)$, we can also fit a model of the form $n_{t+1} = F(n_t)$, and both models should make the same predictions.

Figures 3.7 and 3.8 show an example. The data are from a study by Veilleux (1976, 1979) on a protozoan predator-prey system *Paramecium aurelia* and *Didinium nasutum*, which is a classic model system for population studies. *Paramecium* was grown on Cerophyl medium (which provides nutrients for the bacterial populations upon which the *Paramecium* feed). Varying the Cerophyl concentration corresponds to varying the prey carrying capacity. Methyl cellulose was added to thicken the medium and slow down predator and prey movements. Persistent predator-prey cycles were obtained in this medium for Cerophyl concentrations ranging from 0.675 – 0.9g/l. The data shown in the figures are *Paramecium* growing in the absence of the predators, at 0.9g/l, digitized from Figure 2b in Veilleux (1976). Jost and Ellner (2000) analyzed these data as a step towards estimating a model for the predator-prey dynamics.

The differential equation model requires us to find a smooth function representing \dot{x} as a function of x . A simple approach is to use the $x(t)$ data to estimate \dot{x} ; fitting the model is then a statistical regression problem. The data are at regularly spaced times t_i , so a crude estimate of the derivative at time t_i is the centered difference quotient

$$\dot{x}(t_i) \doteq \frac{x(t_{i+1}) - x(t_{i-1}))}{t_{i+1} - t_{i-1}}.$$

We can then plot these estimated derivative values versus the corresponding x value, and fit a curve (bottom panel in Figure 3.7). A logistic model (quadratic without intercept) fits the \dot{x} data reasonably well, and solutions of the model approximate the data reasonably well.

The difference equation is easier: just plot “next generation” versus “this generation” and fit a curve to it. Again a logistic model is a reasonable fit (the discrete logistic map in the usual sense, $n(t+1) = an(t) - bn(t)^2$), and iterating this model gives a good fit to the data (Figure 3.8).

The **R** code for doing these fits is shown below. In reality (Jost and Ellner 2000) one would go beyond this crude fit of the differential equation model. First, the derivative can be estimated more accurately by fitting a smooth curve through the data, and taking the derivative of the fitted curve. Second, there seems to be overshoot: the population gets above K and then converges with oscillations (this is more pronounced in other data sets, where the simple logistic model consequently is not such a good fit). Jost and Ellner (2000) found that the data from this and other experiments could be fitted better by a logistic model with time delay,

$$\dot{n} = rn(t)(1 - n(t - \delta)/K).$$

Mechanistically this corresponds to individuals alive at time t giving birth and dieing at a rate determined by population density (a surrogate for prey availability?) at time $t - \delta$. If so, we should see in the data that $\log(n(t))$ is a linear function of $n(t - \delta)$. This seems to be true, more or less, for $\delta = 12h$, which was interpreted as corresponding to the time time between cell divisions estimated by Vielleux (9-15h); see Figure 3.9.

3.4 Period doubling bifurcation

We have seen that in the logistic map there is a single fixed point \hat{n} for $r > 1$, which becomes unstable at $r = 3$. Specifically, as r increases past 3, $F'(\hat{n})$ goes from $-1 + \varepsilon$ (stable) to $-1 - \varepsilon$ (unstable).

What happens for $r > 3$, when no fixed point is stable? Look at the second iterate map

$$F_2(x) = F(F(x))$$

[Note: this is also notated as F^2 or $F^{(2)}$. $F_2(x)$ has two humps instead of 1. This is not a special property of the logistic map. It happens because the maximum value of $F(x)$ – the top of the hump – is above 0.5, the value of x at which the hump occurs. So as x increases from 0 to 1, $F(x)$ increases from 0 to something above 0.5, and then decreases back to 0. So $F(F(x))$ climbs up the hump in F and partway down it, but then reverses direction and goes back over the hump.

Note that $F_2(\hat{n}) = F(F(\hat{n})) = F(\hat{n}) = \hat{n}$, so \hat{n} is also a fixed point of F^2 . *Is it stable or unstable?* To answer this question we look at the derivative of F^2 using the chain rule:

$$F_2'(n) = (d/dn)F(F(n)) = F'(F(n))F'(n)$$

For $n = \hat{n}$ we have $F(\hat{n}) = \hat{n}$ so

$$F_2'(\hat{n}) = [F'(\hat{n})]^2$$

Thus $F_2'(\hat{n})$ goes from (1 - a bit) (stable) to (1+ a bit) (unstable) as r increases past 3, and at $r = 3$ the graph of F_2 is exactly tangent to the 45-degree line (slope=1).

So when \hat{n} becomes unstable through the slope of F_2 becoming slightly bigger than 1, this creates two new fixed points of F_2 , say \hat{n}_1 and \hat{n}_2 . The new fixed points are both stable because the slope of F_2 at

```
##### Fitting the logistic ODE by gradient matching
require(odesolve);
# read in the data
x=as.matrix(read.table(file="whatever"));
tvals=x[,1]; xvals=x[,2]; nt=length(xvals);

# Estimate derivatives by centered differences, fit logistic model
xt=xvals[2:(nt-1)];
dxt=(xvals[3:nt]-xvals[1:(nt-2)])/(tvals[3:nt]-tvals[1:(nt-2)]);
fit=lm(dxt~xt+I(xt^2)-1); # "-1" means to omit the intercept

#solve the fitted logistic equation
logist=function(t,x,parms) {
  r=parms[1]; b=parms[2];
  return(list(xdot=r*x+b*x^2));
}
times=(0:65)/10;
parms=fit$coef; x0=xvals[1];
out=lsoda(0.75*x0,times,logist,parms);

# plot the results
par(mfrow=c(2,1),cex.axis=1.25,cex.lab=1.25,cex.main=1.25,mar=c(5,6,4,4));
plot(tvals,xvals,type="o",pch=16,xlab="time t (d)",ylab="Population x(t)")
points(out[,1],out[,2],type="l",lty=2,col="red",lwd=2);
title("Data and fitted solution");

px=0:550; py=fit$coef[1]*px+fit$coef[2]*px^2;
plot(xt,dxt,pch=16,xlim=c(0,550),xlab="Population x(t)",ylab="Estimated dx/dt");
points(px,py,type="l"); title("Fitting logistic to dx/dt vs x")
```

Table 3.1: Fitting the logistic differential equation by gradient matching.

the fixed points is positive but less than 1. Again, these are not special properties of the logistic map. The two fixed new fixed points of F_2 are initially close to \hat{n} , so

$$F_2'(\hat{n}_i) \approx F_2'(\hat{n}) \approx 1 > 0.$$

The fact that $F_2'(\hat{n}_i) < 1$ is a consequence of the double-hump shape of F_2 . At both fixed points the graph of F_2 crosses the 45-degree line from above to below, implying that the slope of F_2 is < 1 . Thus $0 < F_2'(\hat{n}_i) < 1$, so the new fixed points are locally stable.


```

x=as.matrix(read.table(file="whatever",skip=1));
tvals=x[,1]; xvals=x[,2]; nt=length(xvals);

# fit difference equation
xt0=xvals[1:(nt-1)]; xt1=xvals[2:nt];
fit=lm(xt1~xt0+I(xt0^2)-1);

# solve fitted difference equation
r=fit$coef[1]; b=fit$coef[2];
xhat=rep(0,nt); xhat[1]=xvals[1];
for(j in 2:nt) {
  xhat[j]=r*xhat[j-1]+b*xhat[j-1]^2
}

# plot the results
par(mfrow=c(2,1),cex.axis=1.25,cex.lab=1.25,cex.main=1.25,mar=c(5,6,4,4));
plot(tvals,xvals,type="o",pch=16,xlab="time t (d)",ylab="Population x(t)")
points(tvals,xhat,type="o",lty=2,col="red",lwd=2);
title("Data and fitted solution");

px=0:550; py=fit$coef[1]*px+fit$coef[2]*px^2;
plot(xt0,xt1,pch=16,xlim=c(0,550),ylim=c(0,550), xlab="Population x(n)",
ylab="Population x(n+1)");
points(px,py,type="l");
points(px,px,type="l",lty=2,col="red");
title("Fitting quadratic map to x(n+1) vs x(n)")

```

Table 3.2: Fitting the logistic map by ordinary least squares regression.

The new fixed points of F_2 are then a two-point cycle or period-2 oscillation in F , i.e.

$$F(\hat{n}_1) = \hat{n}_2, \quad F(\hat{n}_2) = \hat{n}_1$$

The population oscillates up and down, alternating between values above and below the unstable fixed point \hat{n} .

GRAPH stable 2-point cycle, n_t versus t , oscillating around \hat{n} .

As r increases further, this process repeats. \hat{n}_1 goes from being a stable fixed point of F_2 (with slope near 1) to unstable (slope < -1), creating a pair of fixed points for $F_2(F_2(n)) = F_4(n)$, i.e. a four-point cycle. Further increases in r give 8,16,32, etc. point cycles, until eventually you reach deterministic chaos at which the oscillations become aperiodic. Quoting Marc Mangel, it is hard to be awake in the 21st Century without being aware of chaos and the interest that it has aroused in many areas of science.

3.5 What really happens?

Even in our simplest population models, we have seen a range of qualitative dynamics: stability, cycles and chaos. So what really happens?

A short answer is that we see stability:cycles:chaos in proportions 2:1:0.

A longer answer is: **Chaos** The appeal to (at least some) ecologists of chaos was the promise that it would provide a simple explanation for complicated population dynamics. That is, a few strong feedbacks of simple form might be all it takes to explain any patterns whatsoever in the dynamics of populations. Figure 3.11 is the kind of thing that got people excited: all the complexities of real data coming from a 1-parameter, one-dimensional map. Maybe life was simple after all.

This has not panned out (Zimmer 1999), but it took a while not to. Early reviews of the available long-term data were essentially negative (Hassell et al. 1976). But the approach used in that study was soon rendered obsolete by developments in “nonlinear time series analysis” as practised by physicists. Those approaches, applied to ecological data, began to produce abundant evidence of chaos. Unfortunately, equally strong evidence could also be obtained using nonchaotic artificial “data” that had been generated on the computer using random numbers to simulate effects of environmental variation superimposed on other factors (seasonality, age structure, etc.). The methods from physics proved to be unreliable when the data did not come from controlled experiments in the laboratory. With more appropriate methods, suitable for data on populations in the wild, one finds a few apparent examples but not many (Ellner and Turchin 1995, Rees et al. 2002, Freckleton and Watkinson 2002). An “optimist” might now think that there are 3–6 solid examples out of the data sets examined for signs of chaos, which would extrapolate to saying that $\frac{1}{2}$ –1% of populations are chaotic. But a “pessimist” could say that there are no solid examples outside of laboratory experiments.

Cycles These are common. The best empirical estimate (Kendall et al. 1998, see Table 3.3 is that about 1/3 of all animal populations show evidence for periodicity in their dynamics. These are not necessarily periodic orbits – they could be damped oscillations that are continually “kicked” into action by exogenous factors that perturb populations away from equilibrium. Nonetheless, the evidence suggests that ecologists’ fascination with population cycles was not misplaced: cycles happen often enough to merit study. There is also a latitudinal trend, with populations near the poles being more likely to show cycles. In particular, the fitted trend line (Kendall et al. 1998, Figure 1) estimates that the majority of mammal populations at 60° latitude or higher exhibit cyclicity. The data base for these estimates suffers from observation bias: interesting data (and cycles are interesting!) are more likely to be collected for long enough to count as a long-term data set (Kendall et al. required 25 or more years of data for inclusion in their survey). On the other hand, given such short series and the high sampling error in population counts, one would expect that many cyclic cases would be missed because the signs were not strong enough to achieve statistical significance. So perhaps these balance out, and 1/3 is a good estimate for the frequency of cycling in natural animal populations.

Stability This is really a catch-all for non-cyclic patterns of population variation, that don’t show any

Taxon	# populations	% Periodic*
Birds	139	13
Mammals	328	33
Fish	129	43
Insects	79	16
Aquatic inverts	18	44
All	693	29

*Significant peak in the power spectrum.

Table 3.3: Fraction of long-term population records showing statistical evidence of cyclic fluctuations, classified by taxonomic group. Retabulated from Table 1 of Kendall et al. (1998)

signs of being chaotic. Stability sounds boring, but in fact is the most problematic pattern for theory, and is still intensely studied despite decades of attention to it already. Exploiter-victim systems are prone to cycling; some of them (host-parasitoid) are, in simple models, prone to extreme cycles. All organisms are either exploiters or victims, or both. So why do we see so much stability in the real world? Maybe the simple models in this chapter are leaving out something essential for understanding real populations.

3.6 References

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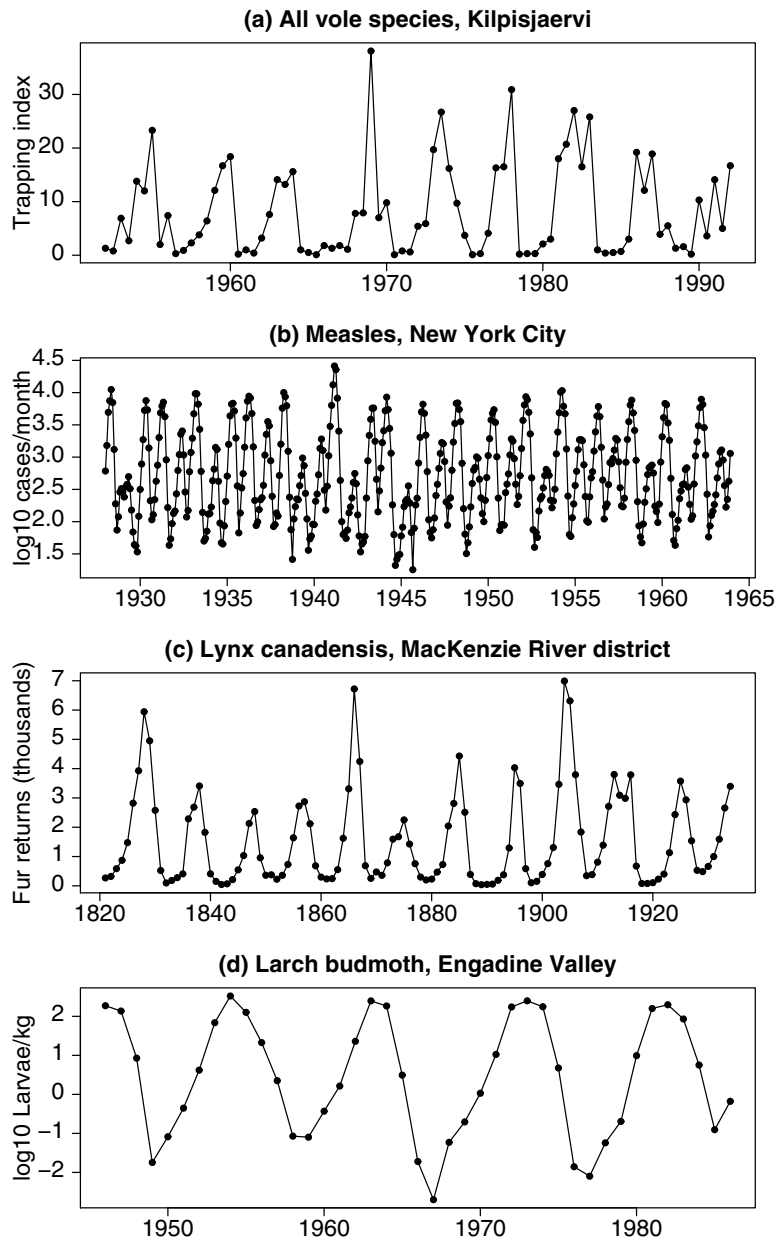


Figure 3.1: Examples of cyclic fluctuations in natural populations. (a) All vole species at Kilpisjärvi, Finnish Lapland. The data are an index of vole abundance based on the number caught in a standardized trapping protocol each Spring and Fall. (b) Monthly case reports of measles in New York City, prior to vaccination. (c) Abundance of *Lynx canadensis* in the MacKenzie River district, Canada, based on annual fur capture records of the Hudson's Bay Company. (d) Number of larvae per kg of foliage of larch budmoth *Zeiraphera didiniana* in the Engadine Valley, Switzerland. A one-stop source for long term population data is the Global Population Dynamics Database [NERC Centre for Population Biology, Imperial College (1999). The Global Population Dynamics Database. <http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>].

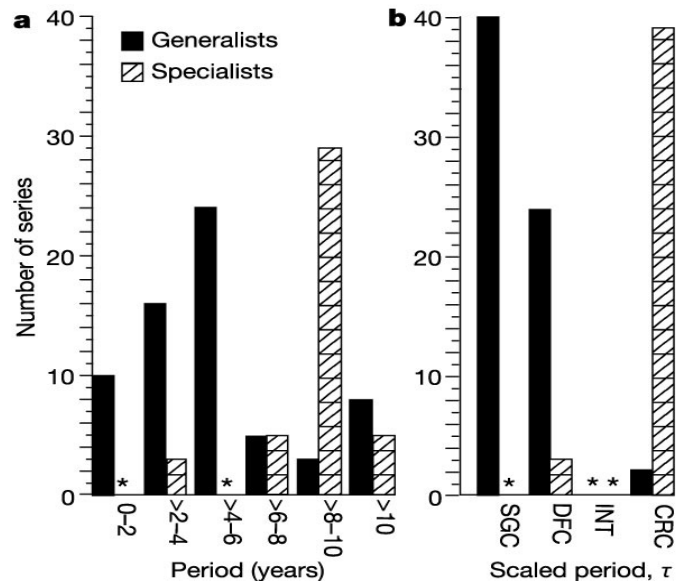


Figure 3.2: Population cycles classified by period, from Murdoch et al. (2002). Asterisk indicates zero in the class. (a) Number of cyclic populations with various periods in years. (b) Distribution of cycles among classes defined by scaled cycle period $\tau = (\text{cycle period}) / (\text{maturation time})$. SGC, single generation cycles ($\tau = 1$); DFC, delayed-feedback cycles ($2 \leq \tau \leq 4$); CRC, consumer-resource cycles (period in years $\geq 4T_C + 2T_R$ where T_C and T_R are the maturation times of consumer and resource species).

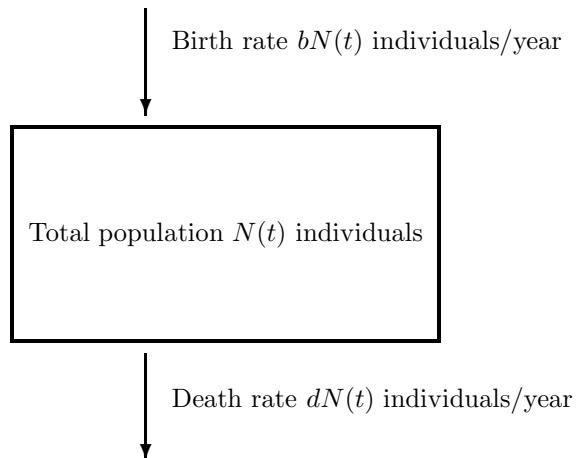


Figure 3.3: Compartment diagram of the exponential growth model. The rectangle denotes the state variable – the number of individuals in the population – and the arrows denote births and deaths.

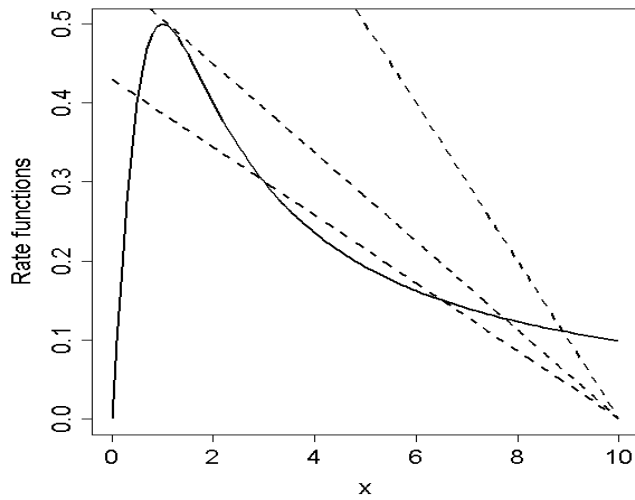


Figure 3.4: Examples of Budworm model with 1,2 or 3 nonzero fixed points for the insect population density. The solid curve is $\frac{x}{1+x^2}$, and the dashed lines are $r(1-x/k)$ for $k = 10$ and three different values of the y -intercept r .

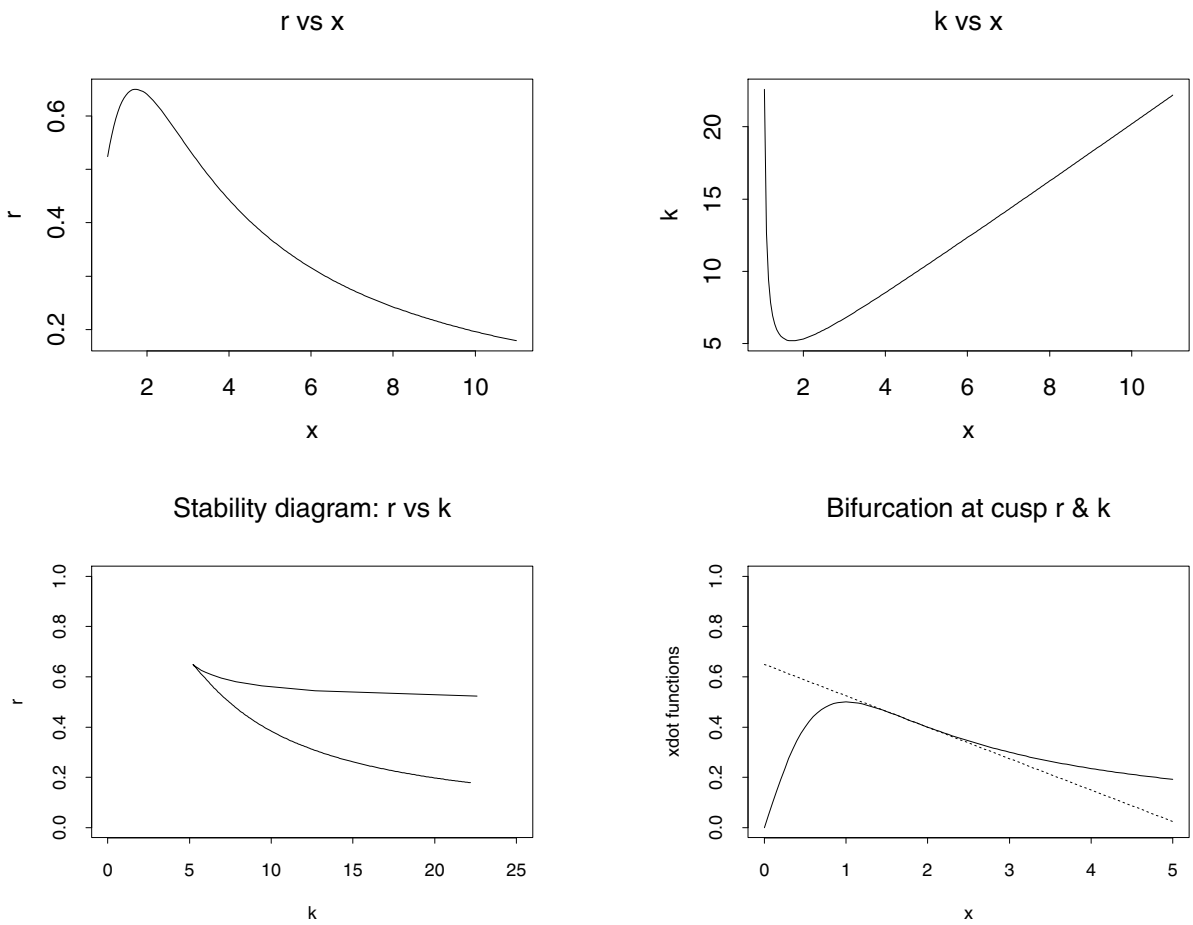


Figure 3.5: Bifurcation curve in budworm model

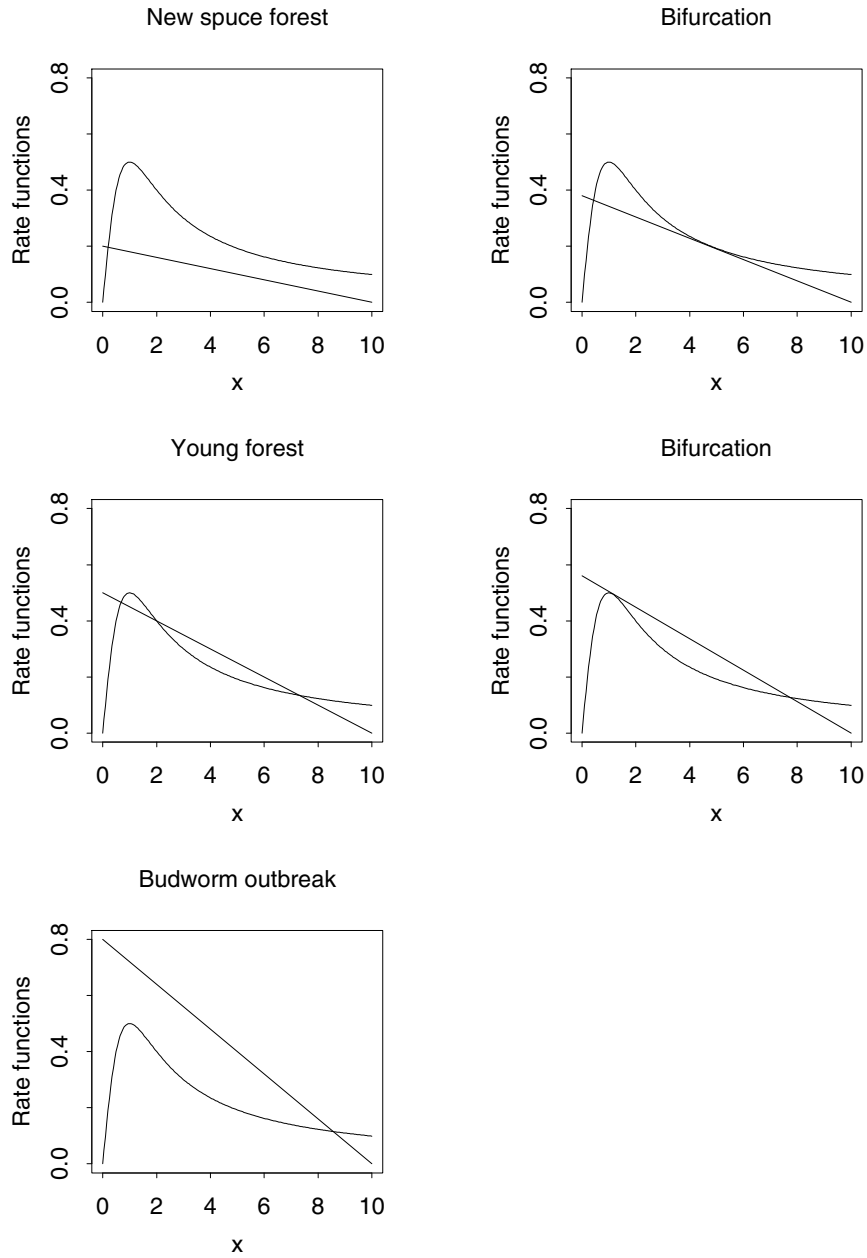


Figure 3.6: Scenario for budworm sudden outbreak and collapse through saddle-node bifurcations, resulting from forest growth and then defoliation by budworm

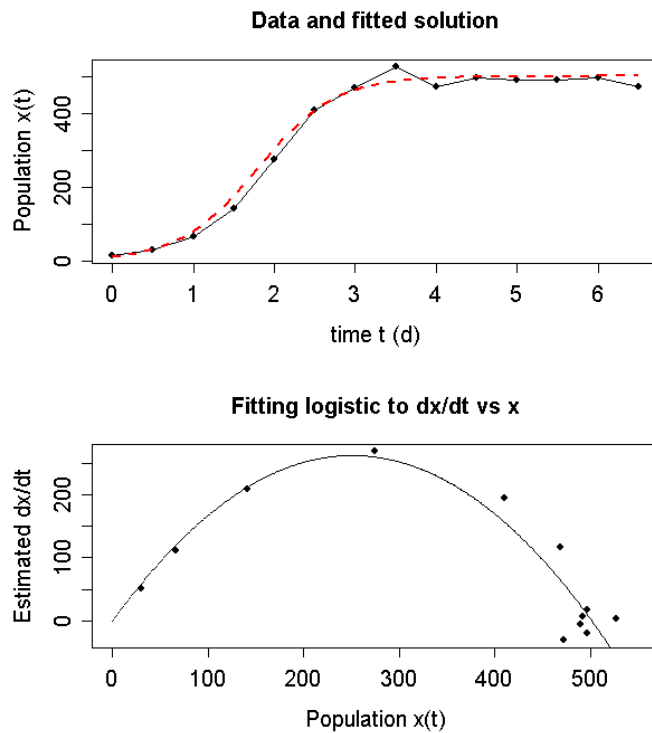


Figure 3.7: Fitting $\dot{x} = f(x)$ to Veilleux (1976) data on growth of *Paramecium* on Cerophyl medium. Top shows the data and a solution trajectory of the fitted model. Bottom shows the plot of estimated \dot{x} versus x on which the model is based, and the fitted logistic model.

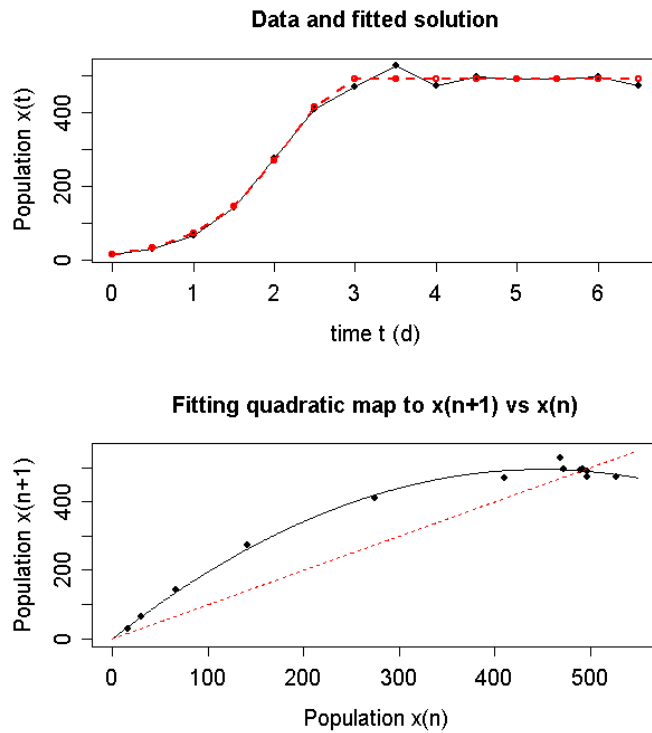


Figure 3.8: Fitting $n_{t+1} = F(n_t)$ to Veilleux (1976) data on growth of *Paramecium* on Cerophyl medium. Top shows the data and a solution trajectory of the fitted model. Bottom shows the plot on which the model is based, and the fitted quadratic (discrete logistic) model.

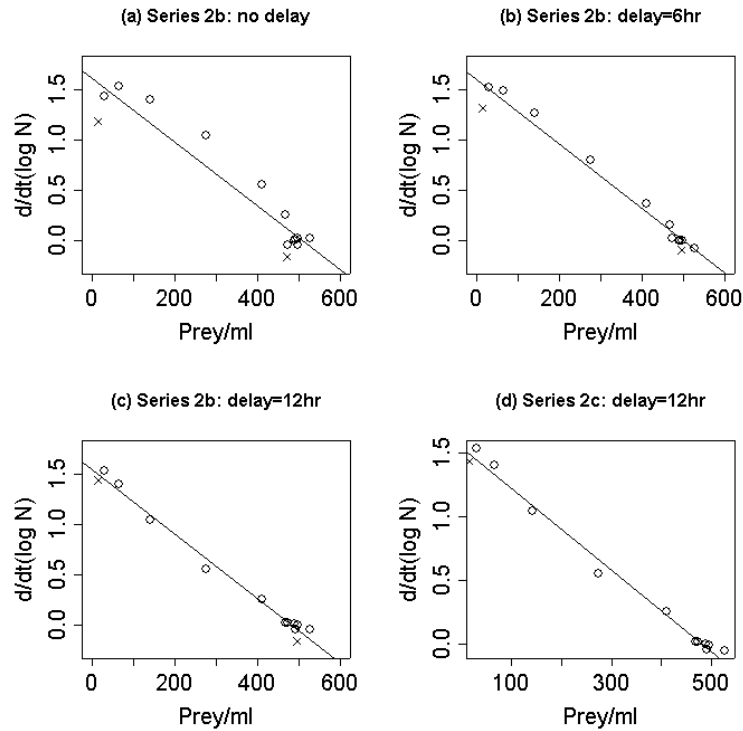


Figure 3.9: Fitting the time-delay logistic $\dot{n}(t) = rn(t)(1 - n(t - \delta)/K)$ by regressing estimated derivative of $\log n$ versus $n(t - \delta)$. Panels a,b,c show fits with 3 values of δ for the data set used above for the logistic without time delay; panel d shows the fit with $\delta = 12h$ for another data set. Points marked with \times are the first and last in the data series, at which the derivative estimates are least accurate. This figure is a re-plot of part of Figure 2 in Jost and Ellner (2000).

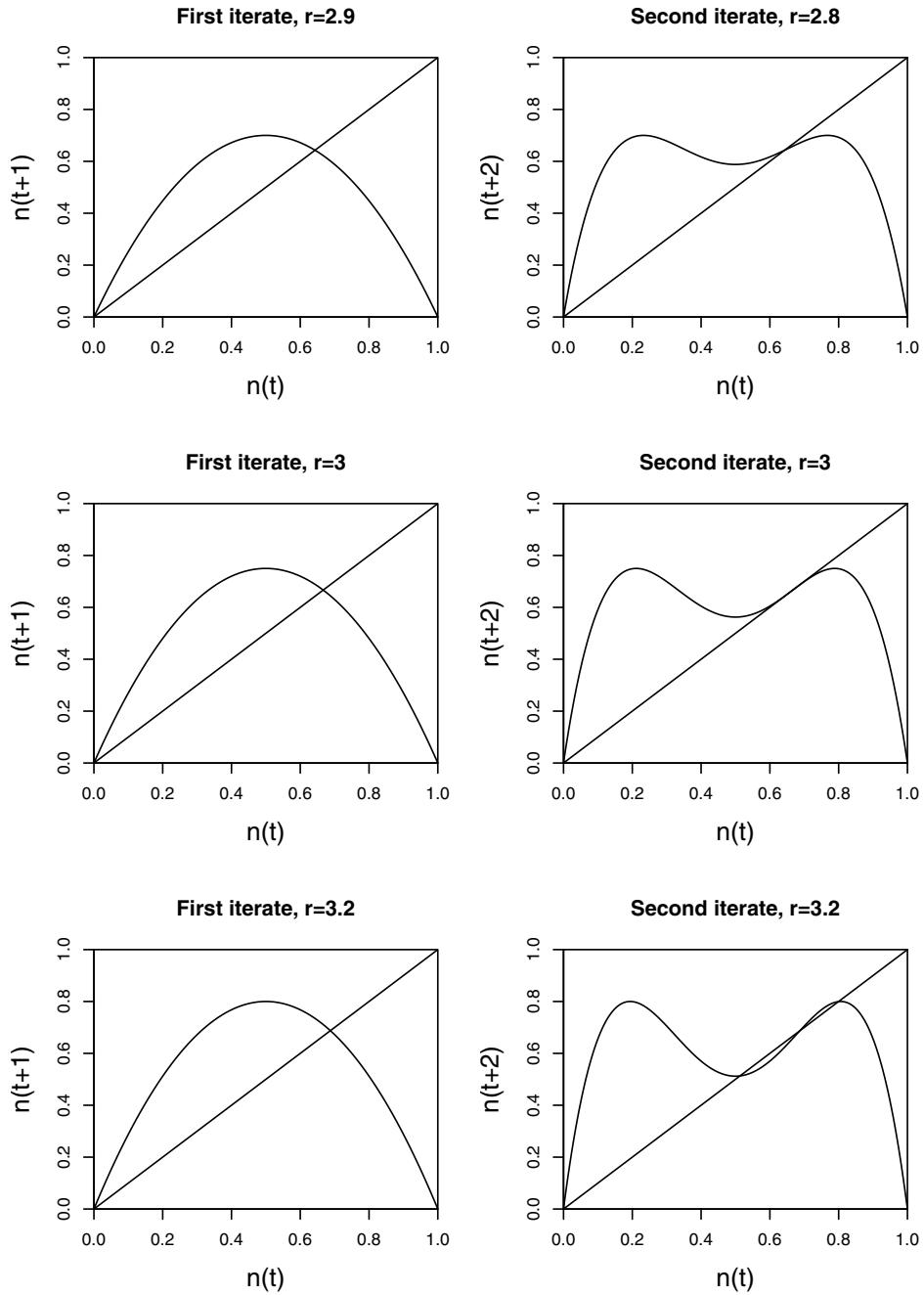


Figure 3.10: The first period-doubling bifurcation in the logistic map, which occurs at $r = 3$. The humped shape of $F(n)$, and the fact that the maximum value of $F(n)$ is > 0.5 , implies that $F_2(n)$ has a double-hump shape.

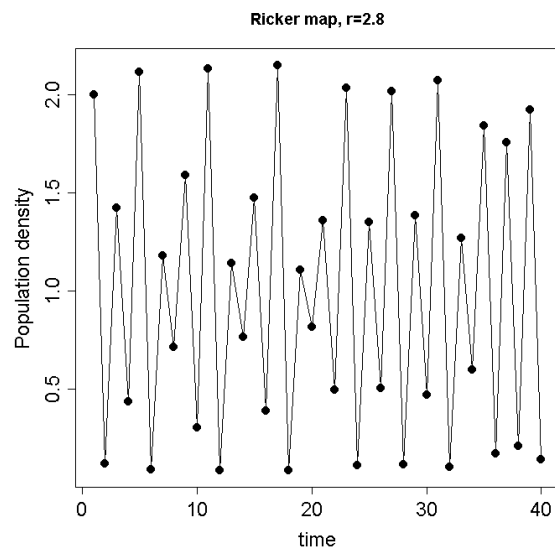


Figure 3.11: Chaotic dynamics in the Ricker map $n_{t+1} = n_t e^{r(1-n_t)}$ for $r = 2.8$