

Function	Range	Left end	Right end	Middle
Polynomials				
Line	$\{-\infty, \infty\}$	$y \rightarrow \pm\infty$, constant slope	$y \rightarrow \pm\infty$, constant slope	monotonic
Quadratic	$\{-\infty, \infty\}$	$y \rightarrow \pm\infty$, accelerating	$y \rightarrow \pm\infty$, accelerating	single max/min
Cubic	$\{-\infty, \infty\}$	$y \rightarrow \pm\infty$, accelerating	$y \rightarrow \pm\infty$, accelerating	up to 2 max/min
Piecewise polynomials				
Threshold	$\{-\infty, \infty\}$	flat	flat	breakpoint
Hockey stick	$\{-\infty, \infty\}$	flat or linear	flat or linear	breakpoint
Piecewise linear	$\{-\infty, \infty\}$	linear	linear	breakpoint
Rational				
Hyperbolic	$\{0, \infty\}$	$y \rightarrow \infty$ or finite	$y \rightarrow 0$	decreasing
Michaelis-Menten	$\{0, \infty\}$	$y = 0$, linear	asymptote	saturating
Holling type III	$\{0, \infty\}$	$y = 0$, accelerating	asymptote	sigmoid
Holling type IV ($c < 0$)	$\{0, \infty\}$	$y = 0$, accelerating	asymptote	hump-shaped
Exponential-based				
Neg. exponential	$\{0, \infty\}$	y finite	$y \rightarrow 0$	decreasing
Monomolecular	$\{0, \infty\}$	$y = 0$, linear	$y \rightarrow 0$	saturating
Ricker	$\{0, \infty\}$	$y = 0$, linear	$y \rightarrow 0$	hump-shaped
logistic	$\{0, \infty\}$	y small, accelerating	asymptote	sigmoid
Power-based				
Power law	$\{0, \infty\}$	$y \rightarrow 0$ or $\rightarrow \infty$	$y \rightarrow 0$ or $\rightarrow \infty$	monotonic
von Bertalanffy	like logistic			
Gompertz	ditto			
Shepherd	like Ricker			
Hassell	ditto			
Non-rectangular hyperbola	like Michaelis-Menten			

Table 3.1 Qualitative properties of bestiary functions.

is a good approximation; for y near the asymptote, exponential approach to the asymptote is a good approximation.)

3.5 BESTIARY OF FUNCTIONS

The remainder of the chapter describes different families of functions that are useful in ecological modeling: Table 3.1 gives an overview of their qualitative properties. This section includes little R code, although the formulas should be easy to translate into R. You should skim through this section on the first reading to get an idea of what functions are available. If you begin to feel bogged down you can skip ahead and use the section for reference as needed.

3.5.1 Functions based on polynomials

A polynomial is a function of the form $y = \sum_{i=0}^n a_i x^i$.

Examples

- linear: $f(x) = a + bx$, where a is the intercept (value when $x = 0$) and b is the slope. (You know this, right?)
- quadratic: $f(x) = a + bx + cx^2$. The simplest nonlinear model.
- cubics and higher-order polynomials: $f(x) = \sum_i^n a_i x^i$. The *order* or *degree* of a polynomial is the highest power that appears in it (so e.g. $f(x) = x^5 + 4x^2 + 1$ is 5th-order).

Advantages

Polynomials are easy to understand. They are easy to reduce to simpler functions (*nested* functions) by setting some of the parameters to zero. High-order polynomials can fit arbitrarily complex data.

Disadvantages

On the other hand, polynomials are often hard to justify mechanistically (can you think of a reason an ecological relationship should be a cubic polynomial?). They don't level off as x goes to $\pm\infty$ — they always go to $-\infty$ or ∞ as x gets large. Extrapolating polynomials often leads to nonsensically large or negative values. High-order polynomials can be unstable: following Forsythe et al. (1977) you can show that extrapolating a high-order polynomial from a fit to US census data from 1900–2000 predicts a population crash to zero around 2015!

It is sometimes convenient to parameterize polynomials differently. For example, we could reparameterize the quadratic function $y = a_1 + a_2x + a_3x^2$ as $y = a + c(x - b)^2$ (where $a_1 = a + cb^2$, $a_2 = 2cb$, $a_3 = c$). It's now clear that the curve has its minimum at $x = b$ (because $(x - b)^2$ is zero there and positive everywhere else), that $y = a$ at the minimum, and that c governs how fast the curve increases away from its minimum. Sometimes polynomials can be particularly simple if some of their coefficients are zero: $y = bx$ (a line through the origin, or *direct proportionality*, for example, or $y = cx^2$. Where a polynomial actually represents proportionality or area,

rather than being an arbitrary fit to data, you can often simplify in this way.

The advantages and disadvantages listed above all concern the mathematical and phenomenological properties of polynomials. Sometimes linear and quadratic polynomials do actually make sense in ecological settings. For example, a population or resource that accumulates at a constant rate from outside the system will grow linearly with time. The rates of ecological or physiological processes (e.g. metabolic cost or resource availability) that depend on an organism's skin surface or mouth area will be a quadratic function of its size (e.g. snout-to-vent length or height).

3.5.1.1 Piecewise polynomial functions

You can make polynomials (and other functions) more flexible by using them as components of *piecewise* functions. In this case, different functions apply over different ranges of the predictor variable. (See p. 136 for information on using R's `ifelse` function to build piecewise functions.)

Examples

- Threshold models: the simplest piecewise function is a simple threshold model — $y = a_1$ if x is less than some threshold T , and $y = a_2$ if x is greater. Hilborn and Mangel (1997) use a threshold function in an example of the number of eggs a parasitoid lays in a host as a function of how many she has left (her “egg complement”), although the original researchers used a logistic function instead (Rosenheim and Rosen, 1991).
- The *hockey stick* function (Bacon and Watts, 1971, 1974) is a combination of a constant and a linear piece: typically either flat and then increasing linearly, or linear and then suddenly hitting a plateau. Hockey-stick functions have a fairly long history in ecology, at least as far back as the definition of the Holling type I functional response, which is supposed to represent foragers like filter feeders that can continually increase their uptake rate until they suddenly hit a maximum. Hockey-stick models have recently become more popular in fisheries modeling, for modeling stock-recruitment curves (Barrowman and Myers, 2000), and in ecology, for detecting edges in landscapes (Toms and Lesperance, 2003)*. Under the name of *self-excitable threshold autore-*

*It is surely only a coincidence that so much significant work on hockey-stick functions has been done by Canadians.

gressive (SETAR) models, such functions have been used to model density-dependence in population dynamic models of lemmings (Framstad et al., 1997), feral sheep (Grenfell et al., 1998), and moose (Post et al., 2002); in another population dynamic context, Brännström and Sumpter (2005) call them *ramp* functions.

- Threshold functions are flat (i.e., the slope is zero) on both sides of the breakpoint, and hockey sticks are flat on one side. More general piecewise linear functions have non-zero slope on both sides of the breakpoint s_1 :

$$y = a_1 + b_1x$$

for $x < s_1$ and

$$y = (a_1 + b_1s_1) + b_2(x - s_1)$$

for $x > s_1$. (The extra complications in the formula for $x > s_1$ ensure that the function is continuous.)

- *Cubic splines* are a general-purpose tool for fitting curves to data. They are *piecewise cubic* functions that join together smoothly at transition points called *knots*. They are typically used as purely phenomenological curve-fitting tools, when you want to fit a smooth curve to data but don't particularly care about interpreting its ecological meaning Wood (2001, 2006). Splines have many of the useful properties of polynomials (adjustable complexity or smoothness; simple basic components) without their instability.

Advantages

Piecewise functions make sense if you believe there could be a biological switch point. For example, in optimal behavior problems theory often predicts sharp transitions among different behavioral strategies (Hilborn and Mangel, 1997, ch. 4). Organisms might decide to switch from growth to reproduction, or to migrate between locations, when they reach a certain size or when resource supply drops below a threshold. Phenomenologically, using piecewise functions is a simple way to stop functions from dropping below zero or increasing indefinitely when such behavior would be unrealistic.

Disadvantages

Piecewise functions present some special technical challenges for parameter fitting, which probably explains why they have only gained attention more

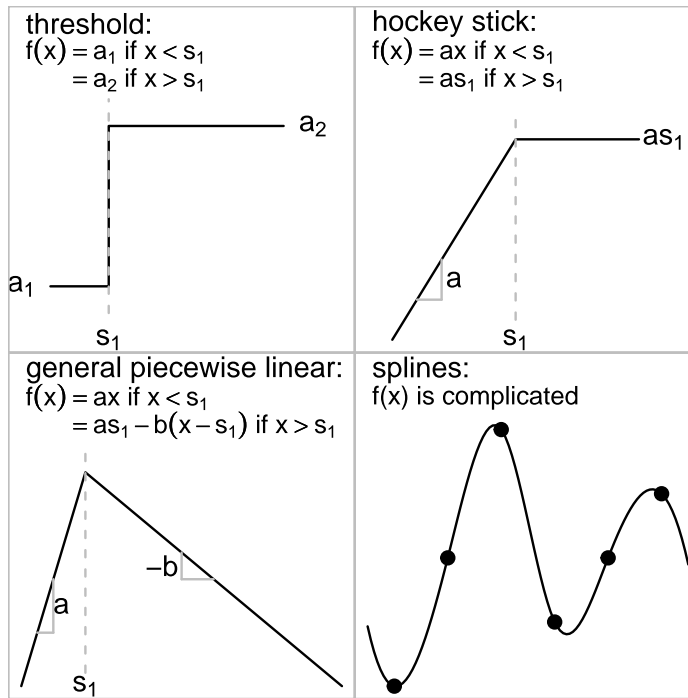


Figure 3.7 Piecewise polynomial functions: the first three (threshold, hockey stick, general piecewise linear) are all piecewise linear. Splines are piecewise cubic; the equations are complicated and usually handled by software (see `?spline` and `?smooth.spline`).

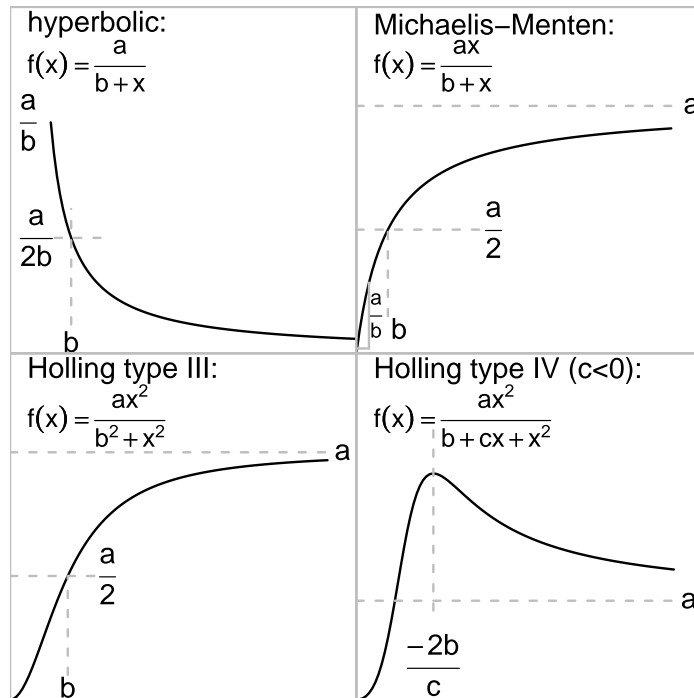


Figure 3.8 Rational functions.

recently. Using a piecewise function means that the rate of change (the derivative) changes suddenly at some point. Such a discontinuous change may make sense, for example, if the last prey refuge in a reef is filled, but transitions in ecological systems usually happen more smoothly. When thresholds are imposed phenomenologically to prevent unrealistic behavior, it may be better to go back to the original biological system and try to understand what properties of the system would actually stop (e.g.) population densities from becoming negative: would they hit zero suddenly, or would a gradual approach to zero (perhaps represented by an exponential function) be more realistic?

3.5.1.2 Rational functions: polynomials in fractions

Rational functions are ratios of polynomials, $(\sum a_i x^i) / (\sum b_j x^j)$.

Examples

- The simplest rational function is the *hyperbolic* function, a/x ; this is often used (e.g.) in models of plant competition, to fit seed production as a function of plant density. A mechanistic explanation might be that if resources per unit area are constant, the area available to a plant for resource exploitation might be proportional to $1/\text{density}$, which would translate (assuming uptake, allocation etc. all stay the same) into a hyperbolically decreasing amount of resource available for seed production. A better-behaved variant of the hyperbolic function is $a/(b+x)$, which doesn't go to infinity when $x=0$ (Pacala and Silander, 1987, 1990).
- The next most complicated, and probably the most famous, rational function is the *Michaelis-Menten* function: $f(x) = ax/(b+x)$. Michaelis and Menten introduced it in the context of enzyme kinetics: it is also known, by other names, in resource competition theory (as the Monod function), predator-prey dynamics (Holling type II functional response), and fisheries biology (Beverton-Holt model). It starts at 0 when $x=0$ and approaches an asymptote at a as x gets large. The only major caveat with this function is that it takes surprisingly long to approach its asymptote: $x/(1+x)$, which is halfway to its asymptote when $x=1$, still reaches 90% of its asymptote when $x=9$. The Michaelis-Menten function can be parameterized in terms of any two of the asymptote, half-maximum, initial slope, or their inverses.

The mechanism behind the Michaelis-Menten function in biochemistry and ecology (Holling type II) is similar; as substrate (or prey) become more common, enzymes (or predators) have to take a larger and larger fraction of their time handling rather than searching for new items. In fisheries, the Beverton-Holt stock-recruitment function comes from assuming that over the course of the season the mortality rate of young-of-the-year is a linear function of their density (Quinn and Deriso, 1999).

- We can go one more step, going from a linear to a quadratic function in the denominator, and define a function sometimes known as the *Holling type III* functional response: $f(x) = ax^2/(b^2+x^2)$. This function is *sigmoid*, or S-shaped. The asymptote is at a ; its shape is quadratic near the origin, starting from zero with slope zero and curvature a/b^2 ; and its half-maximum is at $x=b$. It can occur mechanistically in predator-prey systems because of predator switching from rare to common prey, predator aggregation, and spatial and other forms of heterogeneity (Morris, 1997).

- Some ecologists have extended this family still further to the *Holling type IV* functional response: $f(x) = ax^2/(b+cx+x^2)$. Turchin (2003) derives this function (which he calls a “mechanistic sigmoidal functional response”) by assuming that the predator attack rate in the Holling type II functional response is itself an increasing, Michaelis-Menten function of prey density – that is, predators prefer to pursue more abundant prey. In this case, $c > 0$. If $c < 0$, then the Holling type IV function is *unimodal* or “hump-shaped”, with a maximum at intermediate prey density. Ecologists have used this version of the Holling type IV phenomenologically to describe situations where predator interference or induced prey defenses lead to decreased predator success at high predator density (Holt, 1983; Collings, 1997; Wilmshust et al., 1999; Chen, 2004). Whether c is negative or positive, the Holling type IV reaches an asymptote at a as $x \rightarrow \infty$. If $c < 0$, then it has a maximum that occurs at $x = -2b/c$.
- More complicated rational functions are potentially useful but rarely used in ecology. The (unnamed) function $y = (a+bx)/(1+cx)$ has been used to describe species-area curves (Flather, 1996; Tjørve, 2003).

Advantages

Like polynomials, rational functions are very flexible (you can always add more terms in the numerator or denominator) and simple to compute; unlike polynomials, they can reach finite asymptotes at the ends of their range. In many cases, rational functions make mechanistic sense, arising naturally from simple models of biological processes such as competition or predation.

Disadvantages

Rational functions can be complicated to analyze because the quotient rule makes their derivatives complicated. Like the Michaelis-Menten function they approach their asymptotes very slowly, which makes estimating the asymptote difficult — although this problem really says more about the difficulty of getting enough data rather than about the appropriateness of rational functions as models for ecological systems. Section 3.5.3 shows how to make rational functions even more flexible by raising some of their terms to a power, at the cost of making them even harder to analyze.

3.5.2 Functions based on exponential functions

3.5.2.1 Simple exponentials

The simplest examples of functions based on exponentials are the exponential growth (ae^{bx}) or decay (ae^{-bx}) and saturating exponential growth (*monomolecular*, $a(1 - e^{-bx})$). The monomolecular function (so named because it represents the buildup over time of the product of a single-molecule chemical reaction) is also

- the *catalytic curve* in infectious disease epidemiology, where it represents the change over time in the fraction of a cohort that has been exposed to disease (Anderson and May, 1991);
- the simplest form of the *von Bertalanffy* growth curve in organismal biology and fisheries, where it arises from the competing effects of changes in catabolic and metabolic rates with changes in size (Essington et al., 2001);
- the *Skellam model* in population ecology, giving the number of offspring in the next year as a function of the adult population size this year when competition has a particularly simple form (Skellam, 1951; Brännström and Sumpter, 2005).

These functions have two parameters, the multiplier a which expresses the starting or final size depending on the function, and the exponential rate b or “ e -folding time” $1/b$ (the time it takes to reach e times the initial value, or the initial value divided by e , depending whether b is positive or negative). The e -folding time can be expressed as a half-life or doubling time ($\ln(2)/b$) as well. Such exponential functions arise naturally from any compounding process where the population loses or gains a constant proportion per unit time; one example is *Beers’ Law* for the decrease in light availability with depth in a vegetation canopy (Teh, 2006).

The differences in shape between an exponential-based function and its rational-function analogue (e.g. the monomolecular curve and the Michaelis-Menten function) are usually subtle. Unless you have a lot of data you’re unlikely to be able to distinguish from the data which fits better, and will instead have to choose on the basis of which one makes more sense mechanistically, or possibly which is more convenient to compute or analyze (Figure 3.9).

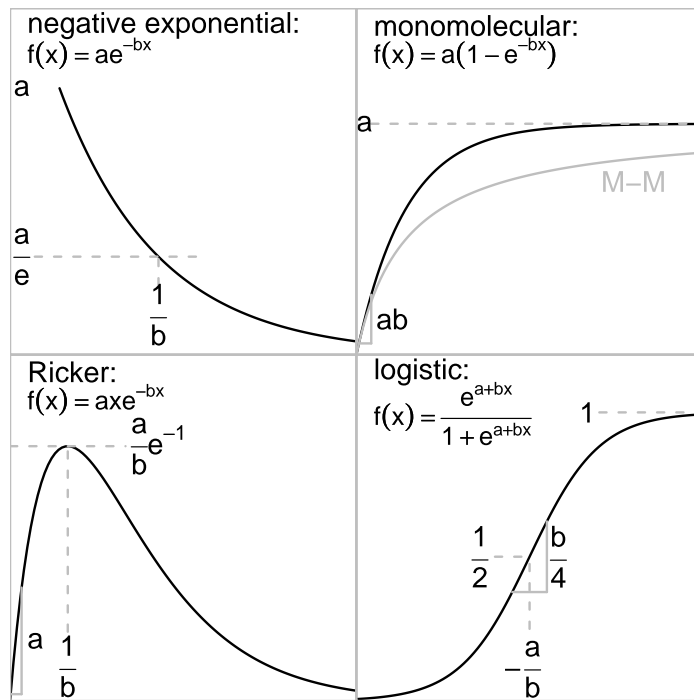


Figure 3.9 Exponential-based functions. “M-M” in the monomolecular figure is the Michaelis-Menten function with the same asymptote and initial slope.

3.5.2.2 Combinations of exponentials with other functions

Ricker function

The Ricker function, $ax \exp(-bx)$, is a common model for density-dependent population growth; if *per capita* fecundity decreases exponentially with density, then overall population growth will follow the Ricker function. It starts off growing linearly with slope a and has its maximum at $x = 1/r$; it's similar in shape to the generalized Michaelis-Menten function ($RN/(1+(aN)^b)$). It is used very widely as a phenomenological model for ecological variables that start at zero, increase to a peak, and decrease gradually back to zero.

Several authors (Hassell, 1975; Royama, 1992; Brännström and Sumpter, 2005) have derived Ricker equations for the dependence of offspring number on density, assuming that adults compete with each other to reduce fecundity; Quinn and Deriso (1999, p. 89) derive the Ricker equation in a fisheries context, assuming that young-of-year compete with each other and increase mortality (e.g. via cannibalism).

Logistic function

There are two widely used parameterizations of the logistic function. The first,

$$y = \frac{e^{a+bx}}{1 + e^{a+bx}} \quad (3.5.1)$$

(or equivalently $y = 1/(1+e^{-(a+bx)})$) comes from a statistical or phenomenological framework. The function goes from 0 at $-\infty$ to 1 at $+\infty$. The location parameter a shifts the curve left or right: the half-maximum ($y = 0.5$), which is also the inflection point, occurs at $x = -a/b$ when the term in the exponent is 0. The scale parameter b controls the steepness of the curve*.

The second parameterization comes from population ecology:

$$n(t) = \frac{K}{1 + \left(\frac{K}{n_0} - 1\right) e^{-rt}} \quad (3.5.2)$$

where K is the carrying capacity, n_0 the value at $t = 0$, and r the initial *per capita* growth rate. (The statistical parameterization is less flexible, with only two parameters: it has $K = 1$, $n_0 = e^a/(1 + e^a)$, and $r = b$.)

*If we reparameterized the function as $\exp(b(x - c))/(1 + \exp(b(x - c)))$, the half-maximum would be at c . Since b is still the steepness parameter, we could then shift and steepen the curve independently.

The logistic is popular because it's a simple sigmoid function (although its rational analogue the Holling type III functional response is also simple) and because it's the solution to one of the simplest population-dynamic models, the *logistic equation*:

$$\frac{dn}{dt} = rn \left(1 - \frac{n}{K}\right), \quad (3.5.3)$$

which says that *per capita* growth rate $((dn/dt)/n)$ decreases linearly from a maximum of r when n is much less than K to zero when $n = K$. Getting from the logistic equation (3.5.3) to the logistic function (3.5.2) involves solving the differential equation by integrating by parts, which is tedious but straightforward (see any calculus book, e.g. Adler (2004)).

In R you can write out the logistic function yourself, using the `exp` function, as `exp(x)/(1+exp(x))`, or you can also use the `plogis` function. The *hyperbolic tangent* (`tanh`) function is another form of the logistic. Its range extends from -1 as $x \rightarrow -\infty$ to 1 as $x \rightarrow \infty$ instead of from 0 to 1.

Gompertz function

The *Gompertz* function, $f(x) = e^{-ae^{-bx}}$, is an alternative to the logistic function. Similar to the logistic, it is accelerating at $x = 0$ and exponentially approaches 1 as x gets large, but it is asymmetric — the inflection point or change in curvature occurs $1/e \approx 1/3$ of the way up to the asymptote, rather than halfway up. In this parameterization the inflection point occurs at $x = 0$; you may want to shift the curve c units to the right by using $f(x) = e^{-ae^{b(x-c)}}$. If we derive the curves from models of organismal or population growth, the logistic assumes that growth decreases linearly with size or density while the Gompertz assumes that growth decreases exponentially.

3.5.3 Functions involving power laws

So far the polynomials involved in our rational functions have been simple linear or quadratic functions. Ecological modelers sometimes introduce an arbitrary (fractional) power as a parameter (x^b) instead of having all powers as fixed integer values (e.g. x , x^2 , x^3); using power laws in this way is often a phenomenological way to vary the shape of a curve, although these functions can also be derived mechanistically.

Here are some categories of power-law functions.

- Simple power laws $f(x) = ax^b$ (for non-integer b ; otherwise the func-

tion is just a polynomial: Figure 3.10a) often describe allometric growth (e.g. reproductive biomass as a function of diameter at breast height (Niklas, 1993), or mass as a function of tarsus length in birds); or quantities related to metabolic rates (Etienne et al., 2006a); or properties of landscapes with fractal geometry (Halley et al., 2004); or species-area curves (Tjørve, 2003).

- The generalized form of the von Bertalanffy growth curve, $f(x) = a(1 - \exp(-k(a-d)t))^{1/(1-d)}$, (Figure 3.10b) allows for energy assimilation to change as a function of mass (assimilation = mass^d). The parameter d is often taken to be $2/3$, assuming that energy assimilation is proportional to length^2 and mass is proportional to length^3 (Quinn and Deriso, 1999).
- A generalized form of the Michaelis-Menten function, $f(x) = ax/(b+x^c)$ (Figure 3.10c), describes ecological competition (Maynard-Smith and Slatkin, 1973; Brännström and Sumpter, 2005). This model reduces to the standard Michaelis-Menten curve when $c = 1$; $0 < c < 1$ corresponds to “contest” (undercompensating) competition, while $c > 1$ corresponds to “scramble” (overcompensating) competition (the function has an intermediate maximum for finite densities if $c > 1$). In fisheries, this model is called the *Shepherd function*. Quinn and Deriso (1999) show how the Shepherd function emerges as a generalization of the Beverton-Holt function when the density-dependent mortality coefficient is related to the initial size of the cohort.
- A related function, $f(x) = ax/(b+x)^c$, is known in ecology as the *Hassell* competition function (Hassell, 1975; Brännström and Sumpter, 2005); it is similar to the Shepherd/Maynard-Smith/Slatkin model in allowing Michaelis-Menten ($c = 1$), undercompensating ($c < 1$) or overcompensating ($c > 1$) dynamics.
- Persson et al. (1998) used a generalized Ricker equation, $y = A(\frac{x}{x_0} \exp(1 - \frac{x}{x_0}))^\alpha$, to describe the dependence of attack rate y on predator body mass x (Figure 3.1 shows the same curve, but as a function of *prey* body mass). In fisheries, Ludwig and Walters proposed this function as a stock-recruitment curve (Quinn and Deriso, 1999). Bellows (1981) suggested a slightly different form of the generalized Ricker, $y = x \exp(r(1 - (a/x)^\alpha))$ (note the power is inside the exponent instead of outside), to model density-dependent population growth.
- Emlen (1996) used a generalized form of the logistic, $y = a + b/(1 + c \exp(-dx^e))$ extended both to allow a non-zero intercept (via the a parameter, discussed above under “Scaling and shifting”) and also to allow more flexibility in the shape of the curve via the power exponent e .

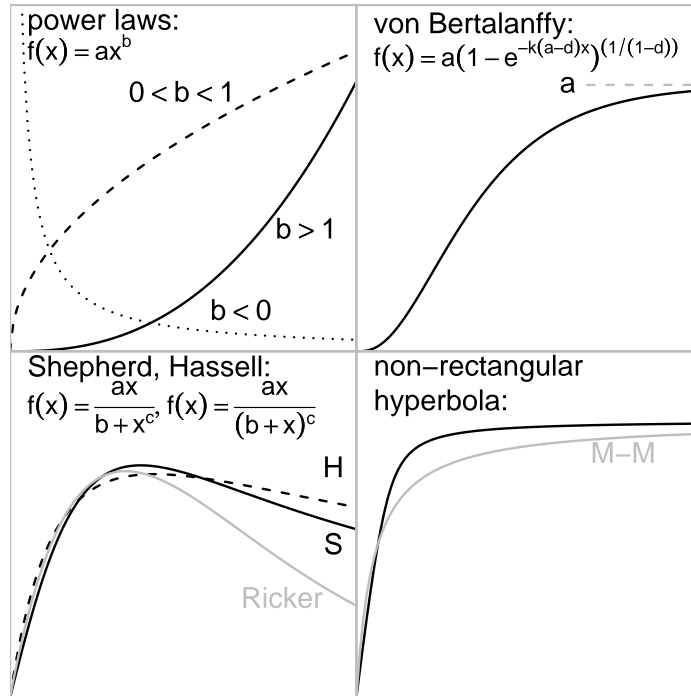


Figure 3.10 Power-based functions. The lower left panel shows the Ricker function for comparison with the Shepherd and Hassell functions. The lower right shows the Michaelis-Menten function for comparison with the non-rectangular hyperbola.

- The *non-rectangular hyperbola* (Figure 3.10, lower right), based on first principles of plant physiology, describes the photosynthetic rate P as a function of light availability I :

$$P(I) = \frac{1}{2\theta} \left(\alpha I + p_{\max} - \sqrt{(\alpha I + p_{\max})^2 - 4\theta\alpha I p_{\max}} \right),$$

where α is photosynthetic efficiency (and initial slope); p_{\max} is the maximum photosynthetic rate (asymptote); and θ is a sharpness parameter. In the limit as $\theta \rightarrow 0$, the function becomes a Michaelis-Menten function: in the limit as $\theta \rightarrow 1$, it becomes piecewise linear (a hockey stick: Thornley, 2002).

Advantages

Functions incorporating power laws are flexible, especially since the power parameter is usually added to an existing model that already allows for changes in location, scale, and curvature. In many mechanistically derived power-law functions the value of the exponent comes from intrinsic geometric or allometric properties of the system and hence does not have to be estimated from data.

Disadvantages

Many different mechanisms can lead to power-law behavior (Mitzenmacher, 2003). It can be tempting but is often misguided to reason backward from an observed pattern to infer something about the meaning of a particular estimated parameter.

Despite the apparent simplicity of the formulas, estimating exponents from data can be numerically challenging — leading to poorly constrained or unstable estimates. The exponent of the non-rectangular hyperbola, for example, is notoriously difficult to estimate from reasonable-size data sets (Thornley, 2002). (We will see another example when we try to fit the Shepherd model to data in Chapter 5.)

3.5.4 Other possibilities

Of course, there is no way I can enumerate all the functions used even within traditional population ecology, let alone fisheries, forestry, ecosystem, and physiological ecology. Haefner (1996, pp. 90-96) gives an alternative list of function types, focusing on functions used in physiological and ecosystem ecology, while Turchin (2003, Table 4.1, p. 81) presents a variety of predator functional response models. Some other occasionally useful categories are:

- *curves based on other simple mathematical functions*: for example, trigonometric functions like sines and cosines (useful for fitting diurnal or seasonal patterns), and functions based on logarithms.
- *generalized or “portmanteau” functions*: these are complex, highly flexible functions that reduce to various simpler functions for particular parameter values. For example, the four-parameter Richards growth

model

$$y = \frac{k_1}{\left(1 + \left(\frac{k_1}{k_2} - 1\right) e^{-k_3 k_4 x}\right)^{1/k_4}} \quad (3.5.4)$$

includes the monomolecular, Gompertz, von Bertalanffy, and logistic equation as special cases (Haefner, 1996; Damgaard et al., 2002). Schnute (1981) defines a still more generalized growth model.

- *Functions not in closed form*: sometimes it's possible to define the dynamics of a population, but not to find an analytical formula (what mathematicians would call a “closed-form solution”) that describes the resulting population density.
 - The *theta-logistic* or *generalized logistic* model (Nelder, 1961; Richards, 1959; Thomas et al., 1980; Sibly et al., 2005) generalizes the logistic equation by adding a power (θ) to the logistic growth equation given above (3.5.3):

$$\frac{dn}{dt} = rn \left(1 - \left(\frac{n}{K}\right)^\theta\right). \quad (3.5.5)$$

When $\theta = 1$ this equation reduces to the logistic equation, but when $\theta \neq 1$ there is no closed-form solution for $n(t)$ — i.e., no solution we can write down in mathematical notation. You can use the `odesolve` library in R to solve the differential equation numerically and get a value for a particular set of parameters.

- the *Rogers random-predator equation* (Rogers, 1972; Juliano, 1993) describes the numbers of prey eaten by predators, or the numbers of prey remaining after a certain amount of time in situations where the prey population becomes depleted. Like the theta-logistic, the Rogers equation has no closed-form solution, but it can be written in terms of a mathematical function called the *Lambert W function* (Corless et al., 1996). (See `?lambertW` in the `emdbook` package.)

3.6 CONCLUSION

The first part of this chapter has shown you (or reminded you of) some basic tools for understanding the mathematical functions used in ecological modeling — slopes, critical points, derivatives, and limits — and how to use them to figure out the basic properties of functions you come across in your work. The second part of the chapter briefly reviewed some common functions. You will certainly run across others, but the tools from the first part should help you figure out how they work.

3.7 R SUPPLEMENT

3.7.1 Plotting functions in various ways

Using `curve`:

Plot a Michaelis-Menten curve:

```
> curve(2 * x/(1 + x))
```

You do need to specify the parameters: if you haven't defined `a` and `b` previously `curve(a*x/(b+x))` will give you an error. But if you're going to use a function a lot it can be helpful to define a function:

```
> micmen <- function(x, a = 2, b = 1) {
+   a * x/(b + x)
+ }
```

Now plot several curves (being more specific about the desired x and y ranges; changing colors; and adding a horizontal line (`abline(h=...)`) to show the asymptote).

```
> curve(micmen(x), from = 0, to = 8, ylim = c(0, 10))
> curve(micmen(x, b = 3), add = TRUE, col = 2)
> curve(micmen(x, a = 8), add = TRUE, col = 3)
> abline(h = 8)
```

Sometimes you may want to do things more manually. Use `seq` to define x values:

```
> xvec <- seq(0, 10, by = 0.1)
```

Then use vectorization (`yvec=micmen(xvec)`) or `sapply` (`yvec=sapply(xvec,micmen)`) or a `for` loop (`for i in (1:length(xvec)) { yvec[i]=micmen(xvec[i])}`) to calculate the y values. Use `plot(xvec,yvec,...)`, `lines(xvec,yvec,...)`, etc. (with options you learned Chapter 2) to produce the graphics.

3.7.2 Piecewise functions using `ifelse`

The `ifelse` function picks one of two numbers (or values from one of two vectors) depending on a logical condition. For example, a simple threshold function:

```
> curve(ifelse(x < 5, 1, 2), from = 0, to = 10)
```

or a piecewise linear function:

```
> curve(ifelse(x < 5, 1 + x, 6 - 3 * (x - 5)), from = 0,
+       to = 10)
```

You can also nest `ifelse` functions to get more than one switching point:

```
> curve(ifelse(x < 5, 1 + x, ifelse(x < 8, 6 - 3 *
+   (x - 5), -3 + 2 * (x - 8))), from = 0, to = 10)
```

3.7.3 Derivatives

You can use `D` or `deriv` to calculate derivatives (although R will not simplify the results at all): `D` gives you a relatively simple answer, while `deriv` gives you a function that will compute the function and its derivative for specified values of x (you need to use `attr(..., "grad")` to retrieve the derivative — see below). To use either of these functions, you need to use `expression` to stop R from trying to interpret the formula.

```
> D(expression(log(x)), "x")
```

```
1/x
```

```
> D(expression(x^2), "x")
```

```
2 * x
```

```
> logist <- expression(exp(x)/(1 + exp(x)))
> dfun <- deriv(logist, "x", function.arg = TRUE)
```

```
> xvec <- seq(-4, 4, length = 40)
> y <- dfun(xvec)
> plot(xvec, y)
> lines(xvec, attr(y, "grad"))
```

Use `eval` to fill in parameter values:

```
> d1 <- D(expression(a * x/(b + x)), "x")
> d1
```

$$a/(b + x) - a * x/(b + x)^2$$

```
> eval(d1, list(a = 2, b = 1, x = 3))
```

```
[1] 0.125
```