

Mathematical Techniques in Evolution and Ecology

# Functions and approximations

Based on Primer I in Otto and Day (2007)

Spring Quarter 2015  
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## Outline

### Goal

- To revisit some common functional forms
- To learn some guidelines for simplifying and approximating models

### Concepts

- Linear, quadratic, and polynomial functions
- Rational, bell-shaped, and sigmoidal (S-shaped) functions
- Sequences and series
- Linear approximations (1st order Taylor series)
- More general approximations (higher-order Taylor series)

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## Motivation

In practice, we will often want (or have to) make **approximations** or **simplifying assumptions** when constructing and analysing mathematical models. The reasons for this are twofold:

- We want to *abstract only the parts that are important* w.r.t. our question(s)
  - Example: The appropriate scale of a map for a road trip is different from the scale of a map for a hike. So is the amount of detail and type of information you expect on the map.
- Simplification is *often necessary for mathematical analysis*. This is linked to a limited amount of time you have to analyse a model, and to the difficulty of making sense of very complicated and long formulae.
  - Example: To measure the length of a route from A to B on your map, it may be ok to measure the straight line from A to B, as long as the route does not curve too much and there is not too much of a difference in altitude.

Approximation and simplification imply **compromises**. Our goal is to learn how to make these choices in an appropriate way. Throughout the modelling process and when interpreting the results, it is important to be aware of these choices.

## Functions and their forms

### Frame of reference

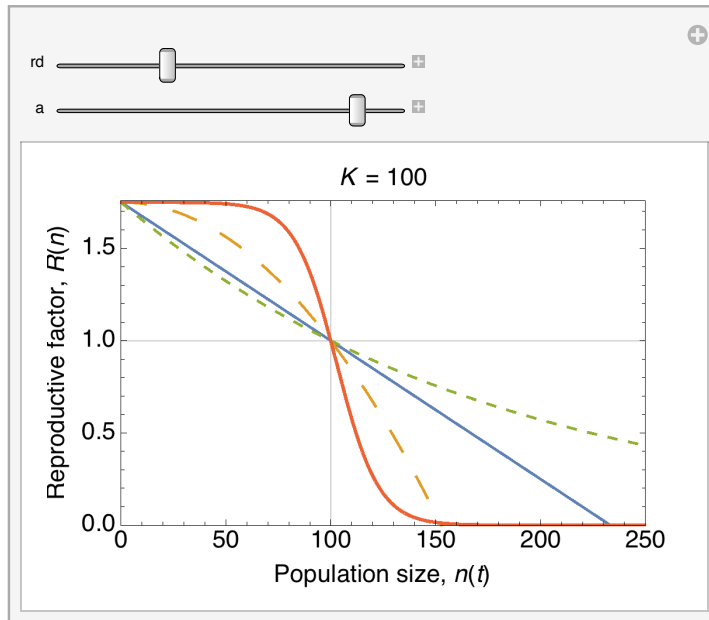
- Model processes *explicitly within a frame of reference* (i.e. a certain level of biological complexity or phenomena)
- Link to *processes/phenomena at other levels implicitly* using functions that behave in a way that is consistent with our understanding of these phenomena
  - Example: In our squirrels example, the frame of reference was the (female) squirrel population on campus, where we modelled birth, death, and immigration. We did not explicitly model the cyclists nor the squirrel population in the Arboretum, which we assumed was the source of immigrants.

- The **phenomenological modelling approach**: a function is used to describe underlying/external biological processes
  - Fewer parameters
  - Often easier to understand
  - Intuition about underlying/external process needed
- The **mechanistic modelling approach**: the details at another level are explicitly tracked
  - More parameters
  - More detailed, potentially more difficult to understand
  - Need more data to estimate the parameters

## The logistic model as an example of the phenomenological approach

- We did not explicitly model the behaviour of individuals during the consumption of resources explicitly, nor the resource
- Instead, we modelled competition implicitly by assuming that the number of surviving offspring per parent,  $R(n)$ , decreases in a certain form as the population size  $n$  increases. We chose this to be a linear decrease, i.e.  $R(n) = 1 + r_d - \frac{r_d}{K} n(t)$ , but alternative choices are possible:

**funcRPlot (\* solid blue: linear, long-dashed orange: quadratic, short-dashed green: exponential, thick red: sigmoidal \*)**



## Some popular functions

A good guiding principle when modelling a process implicitly is to choose a function that is **as simple as possible**, but still has the **desired shape**. The following functions are commonly used in biology; they represent a variety of different shapes.

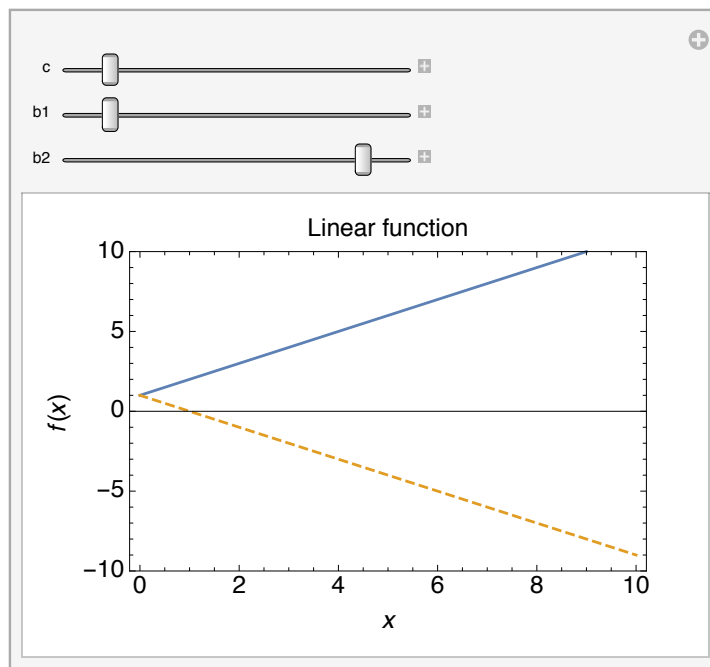
### Linear function

$$f(x) = b x + c \quad (1)$$

- Describes a **straight line** with slope  $b$  and intercept  $c$

In[118]:= `linFuncPlot`

Out[118]=



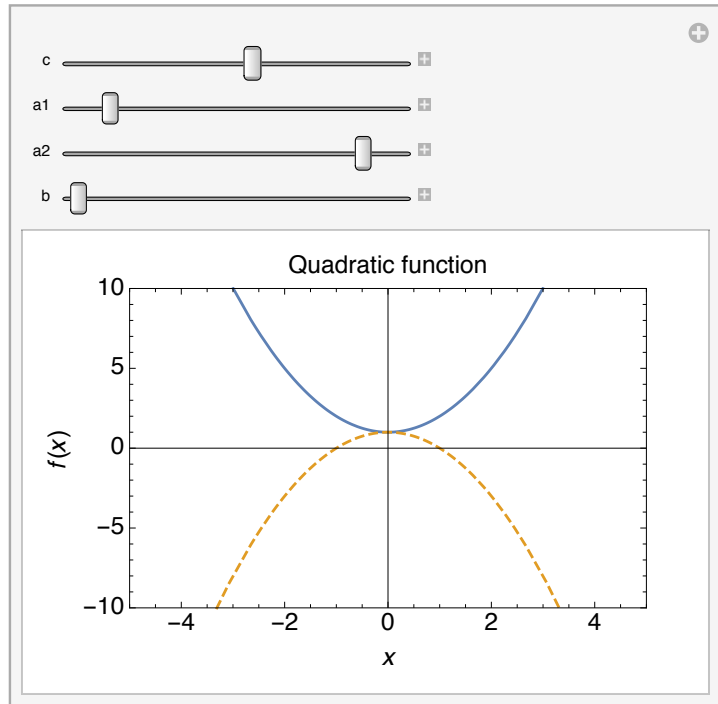
### Quadratic function

$$f(x) = a x^2 + b x + c \quad (2)$$

- Describes a **parabola** that curves up ( $a > 0$ ; convex, solid blue) or down ( $a < 0$ ; concave, dashed orange)
- Where is the maximum (if  $a < 0$ ) / minimum (if  $a > 0$ ) located?

In[119]:= **quadFuncPlot**

Out[119]=





## Polynomial function

Linear and quadratic functions are special cases of the **polynomial functions**. The  $n$ th-degree polynomial is a function of the form

$$f(x) = \sum_{i=0}^n a_i x^i. \quad (3)$$

- Polynomials typically have  $n - 1$  extrema (i.e. minima or maxima)
- The behaviour as  $x$  goes to positive or negative infinity is determined by the sign of the term with the highest power,  $a_n x^n$ .

## Exponential function

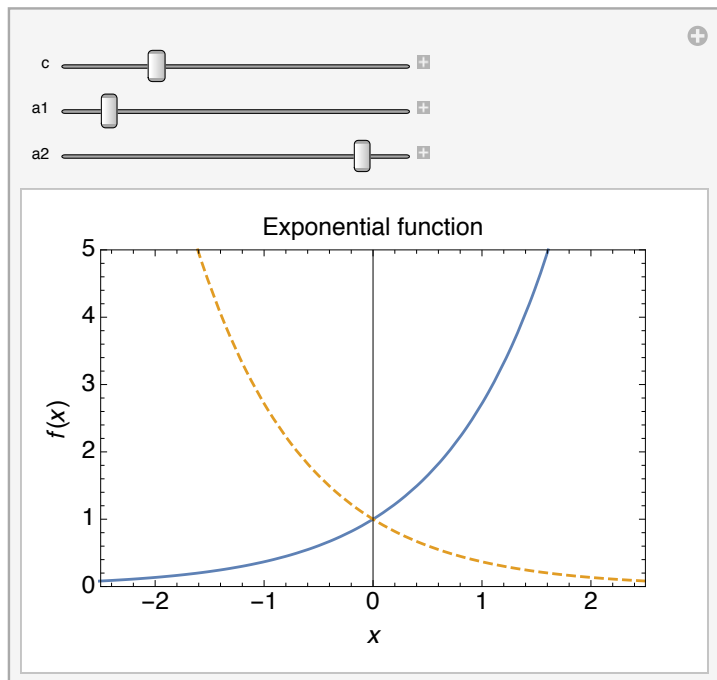
$$f(x) = c e^{a x}$$

(4)

- Describes an exponential rise or fall
- If  $a > 0$ , the function increases exponentially (solid blue)
- If  $a < 0$ , the function decreases exponentially (dashed orange)
- At what value does it cross the y axis (i.e. what is the intercept)?

In[120]:= **expFuncPlot**

Out[120]=



## Rational function

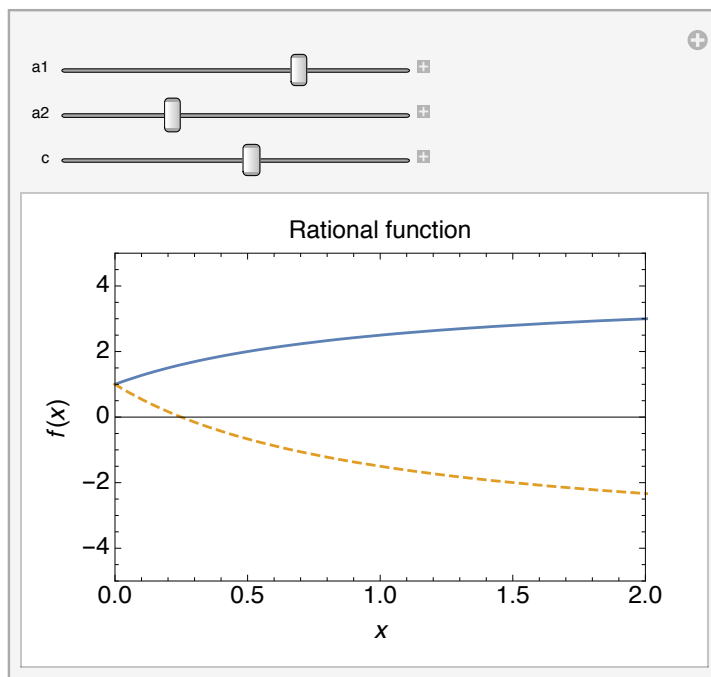
If the desired function is nearly linear for small  $x$ , but reaches a constant value (an **asymptote**) as  $x$  becomes large, one choice is a rational function:

$$f(x) = \frac{ax + c}{bx + d}. \quad (5)$$

- What is the intercept (i.e. the value when  $x = 0$ )
- What is the slope of the increase/decrease when  $x$  is very small?
- What value does  $f(x)$  converge to as  $x$  becomes very large?
- In general, a rational function is any polynomial divided by a polynomial

In[121]:= **ratFuncPlot**

Out[121]=



## Bell-shaped function

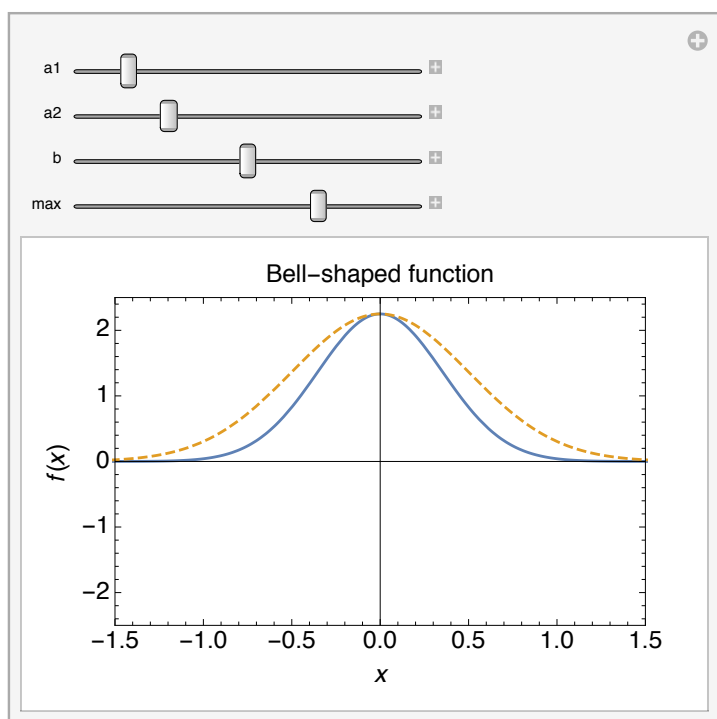
A possible choice for a bell-shaped function is

$$f(x) = m e^{-\frac{(x-b)^2}{a}}. \quad (6)$$

- At what value of  $x$  does it have an extremum? What is  $f(x)$  at this value of  $x$ ?
- Larger values of  $a$  cause the bell to be wider (dashed orange), smaller values of  $a$  make it more narrow (solid blue)
- Note the relation to the **normal distribution**, where  $a = 2\sigma^2$  (twice the *variance*),  $b = \mu$  (the *mean*), and  $m = 1/\sqrt{2\pi\sigma^2}$ .
- In general, a rational function is any polynomial divided by a polynomial

In[122]:= **bellFuncPlot**

Out[122]=



## S-shaped (sigmoidal) function

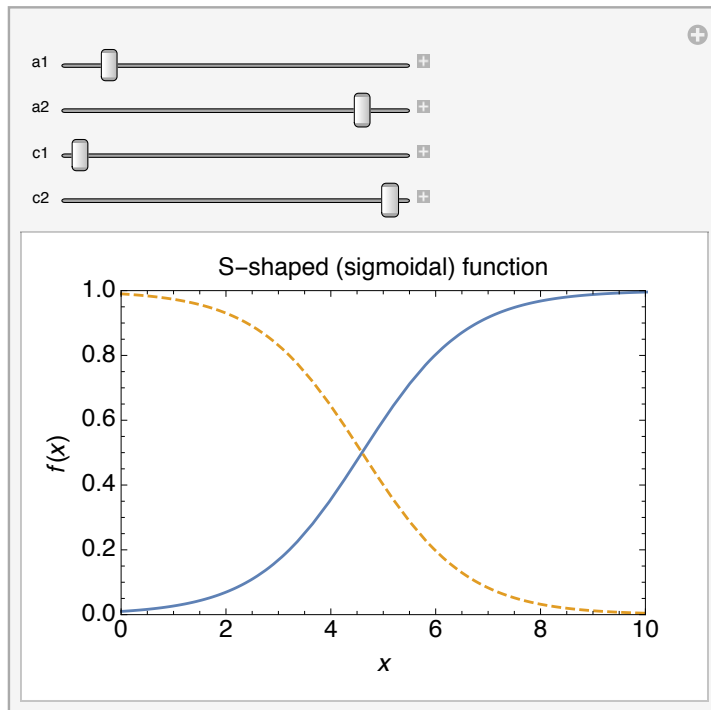
A popular choice for a sigmoidal function is the so-called **logistic function**,

$$f(x) = \frac{c e^{a x}}{c e^{a x} + (1 - c)}. \quad (7)$$

- Here,  $c$  is a fraction ( $0 < c < 1$ ) telling us how far the way up the “S” the function is at  $x = 0$
- If  $a > 0$ , the function rises to 1 as  $x$  increases from 0 (solid blue)
- If  $a < 0$ , the function falls to 0 as  $x$  increases from 0 (reverse S-shape; dashed orange)
- The magnitude of  $a$  determines the sharpness of the rise/fall

In[123]:= **sigmFuncPlot**

Out[123]=



## Rule P1.I: Changing the shape of a function

The following rules can be used to alter a function  $f(x)$  to match a desired shape. This can be very useful in practice!

- To **shift a function to the right or left** by an amount of  $d$ , replace  $x$  by  $(x - d)$  or  $(x + d)$ , respectively
- To **increase or decrease the height of a function** by an amount of  $d$ , replace  $f(x)$  by  $f(x) + d$  or  $f(x) - d$ , respectively
- To **scale a function along the horizontal (x) axis** by a factor of  $d$ , replace  $x$  by  $x/d$ . *Stretching* occurs if  $d > 1$ , *shrinking* occurs if  $d < 1$ .
- To **scale a function along the vertical (y) axis** by a factor of  $d$ , replace  $f(x)$  by  $d f(x)$ . *Stretching* occurs if  $d > 1$ , *shrinking* occurs if  $d < 1$ .
- To **reflect a function across the horizontal (x) axis**, replace  $f(x)$  by  $-f(x)$

### Example

Imagine modelling **the effect of an inhibitor on the level of phosphorus within a cell**. Assume that the level of phosphorus  $P(x)$  declines exponentially at rate  $\alpha$  from an initial level  $P_{\max}$ , as the concentration  $x$  of the inhibitor increases. Assume further that  $P(x)$  asymptotes at some minimum level  $P_{\min}$  as  $x$  becomes very large. How can you modify the exponential function introduced above to model this? In other words, what are the parameters  $c$  and  $a$  in this example?

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## Linear approximations

When analysing models, we often ask: Is it possible to choose a *simpler function* that approximates a complicated function, *at least within a region of interest*? Here, the “region of interest” may refer to

- a *variable lying near a particular point* (e.g. the population size is near 0 or near carrying capacity)
- a *parameter being near a particular value* (e.g. the selection coefficient is near 0)

Knowing how to approximate an equation accurately is a very important technique in modelling!

The most straightforward (and often sufficient!) approximation is based on the idea that **any curve looks roughly like a line if we zoom in close enough**. Hence, given a complicated function  $f(x)$ , we want to approximate it by a function  $\tilde{f}(x)$  of the form

$$\tilde{f}(x) = b x + c$$

such that the approximation is “good” when  $x$  is close to  $a$ , and such that the match is perfect if  $x = a$ , i.e.

$$\tilde{f}(a) = f(a).$$



## Examples

Let us work out two examples:

1. Derive the linear approximation to the example of a phosphorous inhibitor above, assuming that the concentration  $x$  of the inhibitor is low.
2. Derive a linear approximation to the discrete-time recursion equation of the haploid selection model,  $\Delta p = s_d p(t) (1 - p(t)) / (1 + s_d p(t))$ , assuming that selection is weak.

### Recipe P1.I: Approximating a function $f(x)$ by a line at $x = a$

For points  $x$  near  $a$ , the function  $f(x)$  can be approximated by the line

$$\tilde{f}(x) = f(a) + \left( \frac{df}{dx} \Big|_{x=a} \right) (x - a).$$

This is also called a **linear Taylor series approximation** (see next subsection).

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## The Taylor series

Linear approximations (previous section) are a special case of a much more general, very powerful technique, the **Taylor series approximation**. The **Taylor series**

- allows us to understand *when* a function can be approximated
- provides a method to obtain approximations to *any order of accuracy*
- is used very often in biological modeling

We start with two definitions.

## Definition P1.8: Sequence

A **sequence** is a *list of mathematical terms*, typically labelled by some index, e.g.  $a_0, a_1, a_2, \dots, a_k$ .

Examples:

- (i) Sequence of squared natural numbers:  $0, 1, 4, 9, \dots, k^2$
- (ii) Geometric progression:  $\frac{1}{2^0}, \frac{1}{2^1}, \frac{1}{2^2}, \frac{1}{2^3}, \dots, \frac{1}{2^k}$

## Definition P1.9: Series

A **series** is a *sum of the terms of a sequence* (e.g.  $a_0 + a_1 + a_2 + \dots + a_k$ ).

Examples:

- (i) Series of squared natural numbers:  $0 + 1 + 4 + 9 + \dots + k^2 = \sum_{a=0}^k a^2$
- (ii) Geometric series:  $\frac{1}{2^0} + \frac{1}{2^1} + \frac{1}{2^2} + \frac{1}{2^3} + \dots + \frac{1}{2^k} = \sum_{i=0}^k \left(\frac{1}{2}\right)^i$

If there are an *infinite number of terms*, we say it is an **infinite series**, and represent it as

$$a_0 + a_1 + a_2 + \dots$$

or

$$\sum_{i=0}^{\infty} a_i \left( \text{more precisely : } \lim_{n \rightarrow \infty} \sum_{i=0}^n a_i \right).$$

## Convergence and divergence

If this sum *approaches a particular value* (other than positive or negative infinity), the infinite series is said to **converge**. If the sum *keeps growing or shrinking* for ever, the infinite series is said to **diverge**.

Decide if the following infinite series are convergent or divergent. If a series is convergent, find out which value it converges to.

- The sum of all integers,  $1 + 2 + 3 + \dots$
- The sum of squared natural numbers,  $0 + 1 + 4 + 9 + \dots = \sum_{a=0}^{\infty} a^2$
- The infinite geometric series,  $\sum_{j=0}^{\infty} a^j$ , if  $a = 1/2$

## Expressing a function as a power series

Most functions can be rewritten as the infinite series

$$f(x) = b_0 + b_1 x + b_2 x^2 + \dots \quad (8)$$

This infinite series is referred to as a **power series**, because it contains *terms that are integer powers* of  $x$ .

Suppose we want to focus on the behaviour of  $f(x)$  around a particular point  $a$ . This corresponds to *shifting the power series along the  $x$  axis* by an amount  $a$ . From Rule P1.1, we therefore have

$$f(x) = b_0 + b_1(x - a) + b_2(x - a)^2 + \dots \quad (9)$$

This is referred to as “a power series in  $x$ , around the point  $x = a$ ”.

All that is left to do is to find the coefficients  $b_j$ . The Taylor series does just that...

### Definition P1.10 The Taylor series of a function $f(x)$

Most functions  $f(x)$  can be represented as a power series around the point  $x = a$  given by

$$f(x) = b_0 + b_1(x - a) + b_2(x - a)^2 + \dots, \quad (10)$$

whose coefficients are given by

$$b_i = \frac{1}{i!} \left. \frac{d^i f}{dx^i} \right|_{x=a}, \quad (11)$$

where  $d^i f / dx^i$  is the  $i$ th derivative of  $f(x)$  w.r.t.  $x$ . The coefficients  $b_i$  are evaluated at  $x = a$  and do not depend on  $x$ . This is called the **Taylor series** of the function.

For this to work, all derivatives  $d^i f / dx^i$  must be finite. This restriction determines which functions can and cannot be represented by a Taylor series.



**Remark:** Because  $0! = 1$  (by definition) and the 0th derivative of a function is the function itself, the first three terms in a Taylor series are

1.  $b_0 = \frac{1}{0!} \frac{d^0 f}{dx^0} \Big|_{x=a} = f(a)$

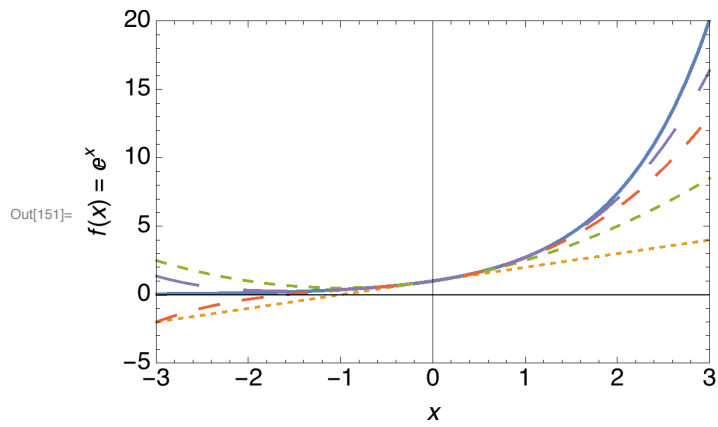
2.  $b_1 = \frac{1}{1!} \frac{d^1 f}{dx^1} \Big|_{x=a} = \frac{df}{dx} \Big|_{x=a}$

3.  $b_2 = \frac{1}{2!} \frac{d^2 f}{dx^2} \Big|_{x=a} = \frac{1}{2} \frac{d^2 f}{dx^2} \Big|_{x=a}$

**Example 1:  $f(x) = e^x$** 

- Derive the Taylor series of the exponential function  $f(x) = e^x$  around the point  $x = a = 0$ .
- Does the series converge?
- Repeat this for the more general version  $f(x) = c e^{ax}$ .

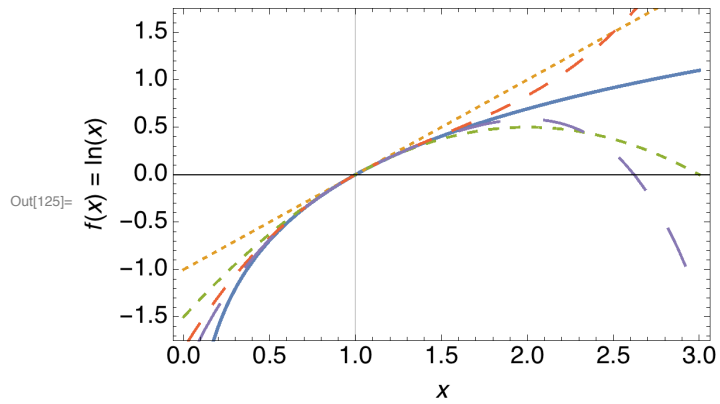
```
In[151]:= plotSeriesExp (* Thick blue: f(x); dashed curves: linear, quadratic,
cubic, and quartic approximation with increasing amount of dashing. *)
```



**Example 2:  $f(x) = \ln(x)$** 

- Derive the Taylor series of the logarithmic function  $f(x) = \ln(x)$  around the point  $x = a = 1$ .
- Does the series converge?

```
In[125]:= plotSeriesLog (* Thick blue: f(x); dashed curves: linear, quadratic,
cubic, and quartic approximation with increasing amount of dashing. *)
```



## Recipe P1.2 Obtaining the Taylor series approximation of a function $f(x)$

Most functions  $f(x)$  can be approximated around the point  $x = a$  by truncating the Taylor series to the degree of accuracy desired and ignoring remaining terms. If the terms that are ignored are on the order of  $(x - a)^i$ , we write these terms as  $O(x - a)^i$ . Doing so clarifies the degree of accuracy of the approximation.

The crudest approximation is the **constant approximation**:

$$f(x) = f(a) + O(x - a).$$

It is correct only at  $x = a$  and provides no information about what happens as we move  $x$  even just a little away from  $a$ .

A more accurate approximation is the line, i.e. a **linear approximation**:

$$f(x) = f(a) + \left( \frac{df}{dx} \Big|_{x=a} \right) (x - a) + O(x - a)^2.$$

The term  $df/dx \Big|_{x=a}$  is the slope and determines whether the function increases or decreases as we move  $x$  away from  $a$ .

Including the next order gives a **quadratic approximation**:

$$f(x) = f(a) + \left( \frac{df}{dx} \Big|_{x=a} \right) (x-a) + \frac{1}{2} \left( \frac{d^2f}{dx^2} \Big|_{x=a} \right) (x-a)^2 + O(x-a)^3.$$

The approximation implies that the function curves upward around  $x = a$  when  $d^2f/dx^2 \Big|_{x=a}$  is positive (convex), but downward if it is negative (concave).

In practice, we often ignore the  $O()$  terms, but replace the “equals” sign by an “approximately equals” sign, i.e.

$$f(x) = f(a) + \left( \frac{df}{dx} \Big|_{x=a} \right) (x-a) + O(x-a)^2$$

can be written as

$$f(x) \approx f(a) + \left( \frac{df}{dx} \Big|_{x=a} \right) (x-a),$$

which is shorter, but it may not be immediately clear of what order the approximation is.

## Some remarks on the Taylor series approximation

1. If a Taylor series does *not converge* in the region of interest, it is *of little help*. Even if a Taylor series does not converge for all values of  $x$ , it *may still do so for the interval of interest*. To **get a feeling of whether a series will converge**, consider the terms  $d^i f / dx^i |_{x=a} (x-a)^i / i!$ . As  $i$  increases, the subterms  $(x-a)^i / i!$  eventually go to zero, because the factorial function in the denominator rises faster than the power in the numerator. Consequentially, as long as the derivative terms  $d^i f / dx^i |_{x=a}$  do not increase too dramatically as  $i$  increases, the series will converge at least for values of  $x$  near  $a$ .
2. In practice, we can therefore “almost always” approximate a function  $f(x)$  near the point  $x = a$  using the first few terms of the Taylor series.
3. In most cases, **the more terms** are included in Taylor series approximation, **the more accurate** the approximation tends to be. We must be careful if the series does not converge over the full range of  $x$ , though.



4. We only expect a Taylor series approximation to be accurate near the point  $a$  around which it is taken. If convergence is an issue, the Taylor series can give a completely wrong answer for  $x$  that are not close to  $a$ . Technically, the **radius of convergence** defines the boundary.
5. The Taylor series **can fail completely** for functions if their *derivatives do not exist* at certain points and/or *if higher-order derivatives are too large to ignore*. Such functions tend to be jagged, with discontinuities ("kinks"), or have points where the function goes off to plus or minus infinity ("poles").
6. It is a good idea to **plot the original function and along with its approximation** to spot potential issues.

## Problem assignment

1. Determine the functions  $R(n)$  for the reproductive factor in the logistic growth model, such that the shape of the functions is consistent with the first figure above. In each case, choose the parameters such that the intercept is  $R(0) = 1 + r$ , and the value when  $N = K$  is  $R(K) = 1$ . Specifically, derive
  - (a) A function that declines exponentially to zero.
  - (b) A quadratic function with a maximum at  $n = 0$ .
  - (c) A reverse-S-shaped function that declines from  $1 + r$  to zero. Keep  $a$  arbitrary, and use Rule P1.1 above to increase the intercept to  $1 + r$ .
2. Use Recipe P1.1 to confirm the following linear approximations:
  - (a)  $e^r \approx 1 + r$                       assuming  $r$  is small
  - (b)  $\frac{1}{1+s} \approx 1 - s$                       assuming  $s$  is small
  - (c)  $\ln(t) \approx t - 1$                       assuming  $t$  is near 1
  - (d)  $\frac{1}{x} \approx \frac{1}{a} - \frac{1}{a^2} (x - a)$                       assuming  $x$  is near  $a$