Analyzing functions: lab 3

September 14, 2005

This lab will be somewhat shorter in terms of "R stuff" than the previous labs, because more of the new material is algebra and calculus than R commands. Try to do a reasonable amount of the work with paper and pencil before resorting to messing around in R.

derivatives ifelse for thresholds

1 Numerical experimentation: plotting curves

Here are the R commands used to generate Figure 1. They just use `curve()`, with `add=FALSE` (the default, which draws a new plot) and `add=TRUE` (adds the curve to an existing plot), particular values of `from` and `to`, and various graphical parameters (`ylim`, `ylab`, `lty`).

```
> curve(2 * exp(-x/2), from = 0, to = 7, ylim = c(0, 2), ylab = "")
> curve(2 * exp(-x), add = TRUE, lty = 4)
> curve(x * exp(-x/2), add = TRUE, lty = 2)
> curve(2 * x * exp(-x/2), add = TRUE, lty = 3)
> text(0.4, 1.9, expression(paste("exponential: ", 2 * e^(-x/2))),
+     adj = 0)
> text(4, 0.7, expression(paste("Ricker: ", x * e^(-x/2))))
> text(4, 0.25, expression(paste("Ricker: ", 2 * x * e^(-x/2))),
+     adj = 0)
> text(2.8, 0, expression(paste("exponential: ", 2 * e^(-x))))
```

The only new thing in this figure is the use of `expression()` to add a mathematical formula to an R graphic. `text(x,y,"x^2")` puts `x^2` on the graph at position (x, y); `text(x,y,expression(x^2))` (no quotation marks) puts x^2 on the graph. See `?plotmath` or `?demo(plotmath)` for (much) more information.

An alternate way of plotting the exponential parts of this curve:

```
> xvec = seq(0, 7, length = 100)
> exp1_vec = 2 * exp(-xvec/2)
> exp2_vec = 2 * exp(-xvec)
> plot(xvec, exp1_vec, type = "l", ylim = c(0, 2), ylab = "")
> lines(xvec, exp2_vec, lty = 4)
```

or, since both exponential vectors are the same length, we could `cbind()` them together and use `matplot()`:

```
> matplot(xvec, cbind(exp1_vec, exp2_vec), type = "l", ylab = "")
```

Finally, if you needed to use `sapply()` you could say:

```
> expfun = function(x, a = 1, b = 1) {
+     a * exp(-b * x)
+ }
> exp1_vec = sapply(xvec, expfun, a = 2, b = 1/2)
> exp2_vec = sapply(xvec, expfun, a = 2, b = 1)
```

The advantage of `curve()` is that you don't have to define any vectors: the advantage of doing things the other way arises when you want to keep the vectors around to do other calculations with them.

Exercise 1.1 *: Construct a curve that has a maximum at ($x = 5$, $y = 1$). Write the equation, draw the curve in R, and explain how you got there.

1.1 A quick digression: `ifelse()` for piecewise functions

The `ifelse()` command in R is useful for constructing piecewise functions. Its basic syntax is `ifelse(condition,value_if_true,value_if_false)`, where `condition` is a logical vector (e.g. `x>0`), `value_if_true` is a vector of alternatives to use if `condition` is `TRUE`, and `value_if_false` is a vector of alternatives to use if `condition` is `FALSE`. If you specify just one value, it will be expanded (*recycled* in R jargon) to be the right length. A simple example:

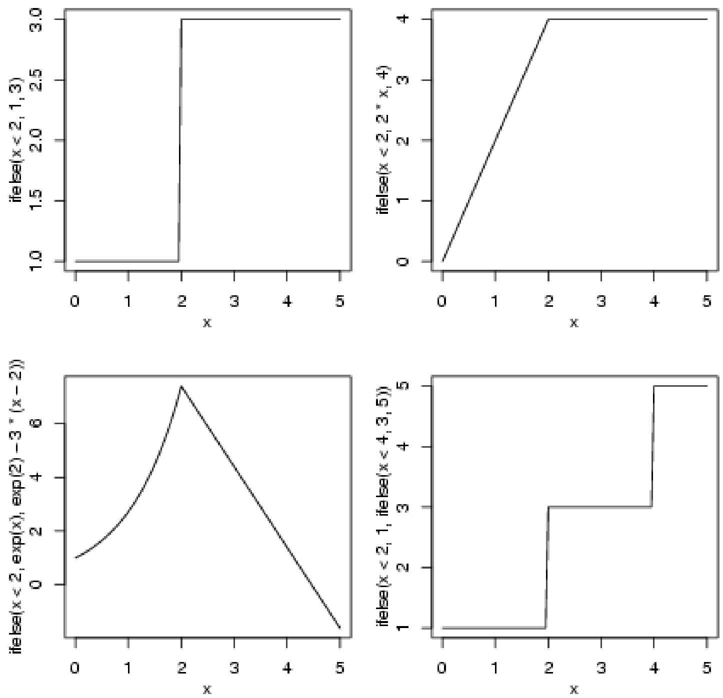
```
> x = c(-25, -16, -9, -4, -1, 0, 1, 4, 9, 16, 25)
> ifelse(x < 0, 0, sqrt(x))
```

```
 [1] 0 0 0 0 0 0 1 2 3 4 5
```

These commands produce a warning message, but it's OK to ignore it since you know you've taken care of the problem (if you said `sqrt(ifelse(x<0,0,x))` instead you wouldn't get a warning: why not?)

Here are some examples of using `ifelse()` to generate (1) a simple threshold; (2) a Holling type I or "hockey stick"; (3) a more complicated piecewise model that grows exponentially and then decreases linearly; (4) a double-threshold model.

```
> op = par(mfrow = c(2, 2), mgp = c(2, 1, 0), mar = c(4.2, 3, 1,
+     1))
> curve(ifelse(x < 2, 1, 3), from = 0, to = 5)
> curve(ifelse(x < 2, 2 * x, 4), from = 0, to = 5)
> curve(ifelse(x < 2, exp(x), exp(2) - 3 * (x - 2)), from = 0,
+     to = 5)
> curve(ifelse(x < 2, 1, ifelse(x < 4, 3, 5)), from = 0, to = 5)
```



The double-threshold example (nested `ifelse()` commands) probably needs more explanation. In words, this command would go "if x is less than 2, set y to 1; otherwise ($x \geq 2$), if x is less than 4 (i.e. $2 \leq x < 4$), set y to 3; otherwise ($x \geq 4$), set y to 5".

2 Evaluating derivatives in R

R can evaluate derivatives, but it is not very good at simplifying them. In order for R to know that you really mean (e.g) `x^2` to be a mathematical expression and not a calculation for R to try to do (and either fill in the current value of `x` or give an error is `x` is undefined), you have to specify it as `expression(x^2)`; you also have to tell R (in quotation marks) what variable you want to differentiate with respect to:

```
> d1 = D(expression(x^2), "x")
> d1

2 * x
```

Use `eval()` to fill in a list of particular values for which you want a numeric answer:

```
> eval(d1, list(x = 2))
```

```
[1] 4
```

Taking the second derivative:

```
> D(d1, "x")
[1] 2
```

(As of version 2.0.1,) R knows how to take the derivatives of expressions including all the basic arithmetic operators; exponentials and logarithms; trigonometric inverse trig, and hyperbolic trig functions; square roots; and normal (Gaussian) density and cumulative density functions; and gamma and log-gamma functions. You're on your own for anything else (consider using a symbolic algebra package like Mathematica or Maple, at least to check your answers, if your problem is very complicated). `deriv()` is a slightly more complicated version of `D()` that is useful for incorporating the results of differentiation into functions: see the help page.

3 Figuring out the logistic curve

The last part of this exercise is an example of figuring out a function — Chapter 3 did this for the exponential, Ricker, and Michaelis-Menten functions The population-dynamics form of the logistic equation is

$$n(t) = \frac{K}{1 + \left(\frac{K}{n(0)} - 1\right)\exp(-rt)} \tag{1}$$

where K is carrying capacity, r is intrinsic population growth rate, and $n(0)$ is initial density.

At $t = 0$, $e^{-rt} = 1$ and this reduces to $n(0)$ (as it had better!)

Finding the derivative with respect to time is pretty ugly, but it will to reduce to something you may already know. Writing the equation as $n(t) = K\cdot(\text{stuff})^{-1}$ and using the chain rule we get $n'(t) = K \cdot (\text{stuff})^{-2} \cdot d(\text{stuff})/dt$ (stuff $= 1 + (K/n(0)-1)\exp(-rt)$). The derivative $d(\text{stuff})/dt$ is $(K/n(0)-1)\cdot -r\exp(-rt)$. At $t = 0$, stuff $= K/n(0)$, and $d(\text{stuff})/dt = -r(K/n(0) - 1)$. So this all comes out to

$$K\cdot(K/n(0))^{-2}\cdot -r(K/(n0)-1) = -rn(0)^2/K\cdot(K/(n0)-1) = rn(0)(1-n(0)/K)$$

which should be reminiscent of intro. ecology: we have rediscovered, by working backwards from the time-dependent solution, that the logistic equation arises from a linearly decreasing *per capita* growth rate.

If $n(0)$ is small we can do better than just getting the intercept and slope.

Exercise 3.1 *: show that if $n(0)$ is very small (and t is not too big), $n(t) \approx n(0)\exp(rt)$. (Start by showing that $K/n(0)e^{-rt}$ dominates all the other terms in the denominator.)

If t is small, this reduces (because $e^{rt} \approx 1 + rt$) to $n(t) \approx n(0) + rn(0)t$, a linear increase with slope $rn(0)$. Convince yourself that this matches the expression we got for the derivative when $n(0)$ is small.

For large t, convince yourself tha the value of the function approaches K and (by revisiting the expressions for the derivative above) that the slope approaches zero.

The half-maximum occurs when the denominator (also known as stuff above) is 2; we can solve stuff = 2 for t (getting to $(K/n(0)-1)\exp(-rt) = 1$ and taking logarithms on both sides) to get $t = \log(K/n(0) - 1)/r$.

We have (roughly) three options:

1. Use `curve()`:

   ```
   > r = 1
   > K = 1
   > n0 = 0.1
   > curve(K/(1 + (K/n0 - 1) * exp(-r * x)), from = 0, to = 10)
   ```

   (note that we have to use `x` and not `t` in the expression for the logistic).

2. Construct the time vector by hand and compute a vector of population values using vectorized operations:

   ```
   > t_vec = seq(0, 10, length = 100)
   > logist_vec = K/(1 + (K/n0 - 1) * exp(-r * t_vec))
   > plot(t_vec, logist_vec, type = "l")
   ```

3. write our own function for the logistic and use `sapply()`:

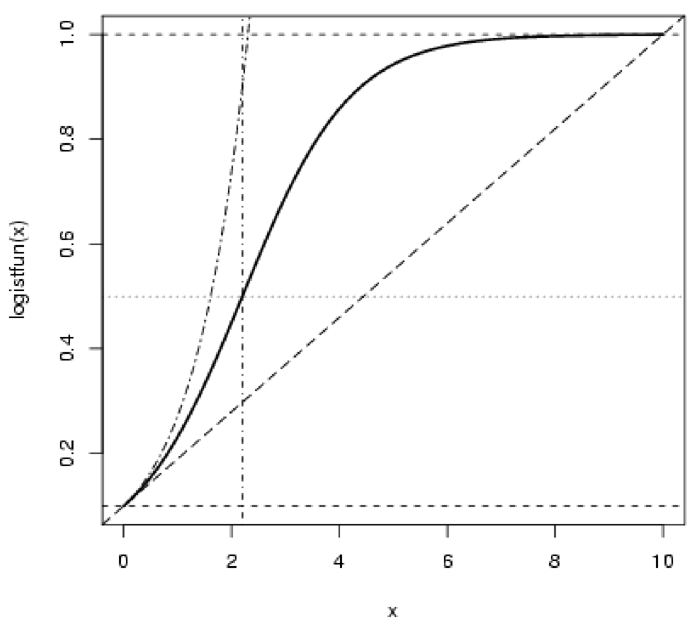
   ```
   > logistfun = function(t, r = 1, n0 = 0.1, K = 1) {
   +     K/(1 + (K/n0 - 1) * exp(-r * t))
   + }
   > logist_vec = sapply(t_vec, logistfun)
   ```

   When we use this function, it will no longer matter how `r`, `n0` and `K` are defined in the workspace: the values that `R` uses in `logistfun()` are those that we define in the call to the function.

   ```
   > r = 17
   > logistfun(1, r = 2)

   [1] 0.4508531

   > r = 0
   > logistfun(1, r = 2)

   [1] 0.4508531
   ```

We can do more with this plot: let's see if our conjectures are right. Using `abline()` and `curve()` to add horizontal lines to a plot to test our estimates of starting value and ending value, vertical and horizontal lines that intersect at the half-maximum, a line with the intercept and initial linear slope, and a curve corresponding to the initial exponential increase:

```
> curve(logistfun(x), from = 0, to = 10, lwd = 2)
> abline(h = n0, lty = 2)
> abline(h = K, lty = 2)
> abline(h = K/2, lty = 3)
> abline(v = -log(n0/(K - n0))/r, lty = 4)
> r = 1
> abline(a = n0, b = r * n0 * (1 - n0/K), lty = 5)
> curve(n0 * exp(r * x), from = 0, lty = 6, add = TRUE)
```



Exercise 3.2 *: Plot and analyze the function $G(N) = \frac{RN}{(1+aN)^b}$, (the Shepherd function), which is a generalization of the Michaelis-Menten function. What are the effects of the R and a parameters on the curve? For what parameter values does this function become equivalent to the Michaelis-Menten function? What is the behavior (value, initial slope) at $N = 0$? What is the behavior (asymptote [if any], slope) for large N, for $b = 0$, $0 < b < 1$, $b = 1$, $b > 1$? Define an R function for the Shepherd function (call it `shep`). Draw a plot or plots showing the behavior for the ranges above, including lines that

show the initial slope. Extra credit: when does the function have a maximum between 0 and ∞? What is the height of the maximum when it occurs? (Hint: when you're figuring out whether a fraction is zero or not, you don't have to think about the denominator at all.) The calculus isn't that hard, but you may also use the `D()` function in R. Draw horizontal and vertical lines onto the graph to test your answer.

Exercise 3.3 *: Reparameterize the Holling type III functional response ($f(x) = ax^2/(1 + bx^2)$) in terms of its asymptote and half-maximum.

Exercise 3.4 *: Figure out the correspondence between the population-dynamic parameterization of the logistic function (eq. 1: parameters r, $n(0)$, K) and the statistical parameterization ($f(x) = \exp(a + bx)/(1 + \exp(a + bx))$: parameters a, b). Convince yourself you got the right answer by plotting the logistic with $a = -5$, $b = 2$ (with lines), figuring out the equivalent values of K, r, and $n(0)$, and then plotting the curve with both equations to make sure it overlaps. Plot the statistical version with lines (`plot(...,type="l")` or `curve(...)` and then add the population-dynamic version with points (`points()` or `curve(...,type="p",add=TRUE)`).

Small hint: the population-dynamic version has an extra parameter, so one of r, $n(0)$, and K will be set to a constant when you translate to the statistical version.

Big hint: Multiply the numerator and denominator of the statistical form by $\exp(-a)$ and the numerator and denominator of the population-dynamic form by $\exp(rt)$, then compare the forms of the equations.