Lab 3: solutions

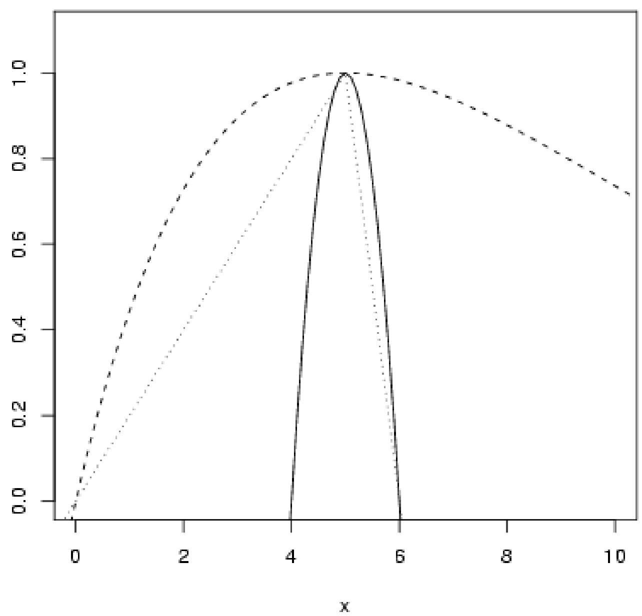
©2005 Ben Bolker

September 14, 2005

Exercise 0.1 *:

- Quadratic: easiest to construct in the form ($y = -(x-a)^2 + b$), where a is the location of the maximum and b is the height. (Negative sign in front of the quadratic term to make it curve downward.) Thus $a = 5$, $b = 1$.
- Ricker: if $y = axe^{-bx}$, then (as discussed in the chapter) the location of the maximum is at $x = 1/b$ and the height is at $a/(be)$. Thus $b = 0.2$, $a = 0.2 * e$.
- Triangle: let's say for example that the first segment is a line with intercept zero and slope 1/5, and the second segment has equation $-1 * (x - 5) + 1$.

```
> curve(-(x - 5)^2 + 1, from = 0, to = 10, ylim = c(0, 1.1), ylab = "")
> curve(0.2 * exp(1) * x * exp(-0.2 * x), add = TRUE, lty = 2)
> curve(ifelse(x < 5, x/5, -(x - 5) + 1), add = TRUE, lty = 3)
```



What else did you try? (Sinusoid, Gaussian ($\exp(-x^2)$), ?)

Exercise 0.2 *:

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

Since $n(0) \ll 1$ (close to zero, or much less than 1), $K/n(0) - 1 \approx K/n(0)$. So:

$$n(t) \approx \frac{K}{1 + \frac{K}{n(0)}\exp(-rt)}$$

Provided t isn't too big, $K/n(0)\exp(-rt)$ is also a lot larger than 1, so

$$n(t) \approx \frac{K}{\frac{K}{n(0)}\exp(-rt)}$$

Now multiply top and bottom by $n(0)/K\exp(rt)$ to get the answer.

Exercise 0.3 *: When $b = 1$, the Shepherd function reduces to $RN/(1 + aN)$, which is a form of the M-M. You should try not to be confused by the fact that earlier in class we used the form $ax/(b + x)$ (asymptote=a, half-maximum=b); this is just a different *parameterization* of the function. To be formal about it, we could multiply the numerator and denominator of $RN/(1+aN)$

by $1/a$ to get our equation in the form $(R/a)N/((1/a)+N)$, which matches what we had before with $a = R/a$, $b = 1/a$.

Near 0: we can do this either by evaluating the derivative $S'(N)$ at $N = 0$ (which gives R — see below) or by taking the limit of the whole function $S(N)$ as $N \to 0$, which gives RN (because the aN term in the denominator becomes small relative to 1), which is a line through the origin with slope R.

For large N: if $b = 1$, we know already that this is Michaelis-Menten, and in this parameterization the asymptote is R/a (in the limit, the 1 in the denominator becomes irrelevant and the function becomes approximately $\frac{RN}{aN} = \frac{R}{a}$). If b is not 1 (we'll assume it's greater than 0) we can start the same way $(1+aN \approx aN)$, but now we have $RN/(aN)^b$. Write this as $\frac{R}{a^b}N^(1-b)$. If $b > 1$, N is raised to a negative power and the function goes to zero as $N \to \infty$. If $b < 1$, N is raised to a positive power and $R(N)$ approaches infinity as $N \to \infty$ (it never levels off).

If $b = 0$ then the function is just a straight line (no asymptote), with slope $R/2$.

We don't really need to calculate the slope (we can figure out logically that it must be negative but decreasing in magnitude for large N and $b > 1$; positive and decreasing to 0 when $b = 1$; and positive and decreasing, but never reaching 0, when $b > 1$. Nevertheless, for thoroughness (writing this as a product and using the product, power, and chain rules):

$$\begin{aligned} \left(RN(1+aN)^{-b}\right)' &= R(1+aN)^{-b} + RN \cdot -b(1+aN)^{(-b-1)}a && (1) \\ &= R(1+aN)^{-b} - abRN(1+aN)^{(-b-1)} && (2) \\ &= R(1+aN)^{-b-1}((1+aN) - abN) && (3) \\ &= R(1+aN)^{-b-1}(1+aN(1-b)) && (4) \end{aligned}$$

You could also do this by the quotient rule. The derivative of the numerator is R (easy); the derivative of the denominator is $b \cdot (1+aN)^{b-1} \cdot a = ab(1+aN)^{b-1}$ (power rule/chain rule).

$$\begin{aligned} S(N)' &= \frac{g(N)f'(N) - f(N)g'(N)}{(g(N))^2} && (5) \\ &= \frac{R(1+aN)^b - RN\left(ab(1+aN)^{b-1}\right)}{(1+aN)^{2b}} && (6) \\ &= \frac{R(1+aN)^{b-1}(1+aN-abN)}{(1+aN)^{2b}} && (7) \end{aligned}$$

You can also do this with R (using `D()`), but it won't simplify the expression for you:

```
> dS = D(expression(R * N/(1 + a * N)^b), "N")
> dS
```

```
R/(1 + a * N)^b - R * N * ((1 + a * N)^(b - 1) * (b * a))/((1 +
    a * N)^b)^2
```

If you want to know the value for a particular N, and parameter values, use `eval()` to **eval**uate the expression:

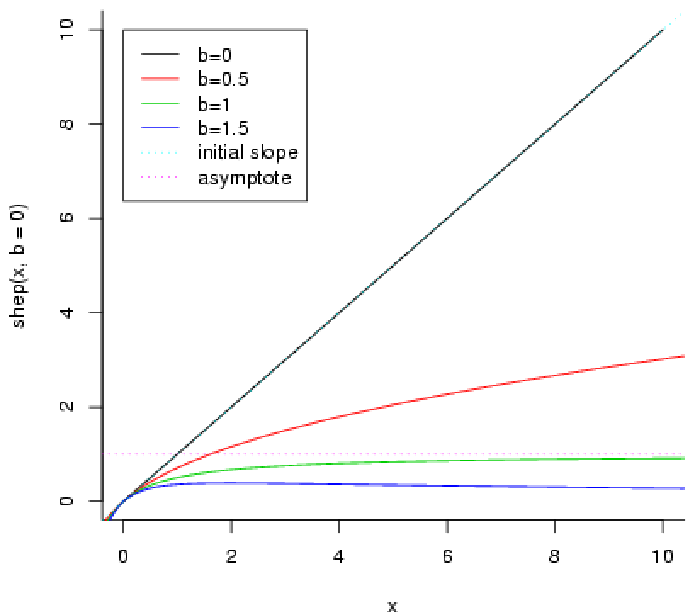
```
> eval(dS, list(a = 1, b = 2, R = 2, N = 2.5))

[1] -0.06997085
```

A function to evaluate the Shepherd (with default values $R = 1$, $a = 1$, $b = 1$):

```
> shep = function(x, R = 1, a = 1, b = 1) {
+     R * x/(1 + a * x)^b
+ }
```

Plotting:

```
> curve(shep(x, b = 0), xlim = c(0, 10), bty = "l")
> curve(shep(x, b = 0.5), add = TRUE, col = 2)
> curve(shep(x, b = 1), add = TRUE, col = 3)
> curve(shep(x, b = 1.5), add = TRUE, col = 4)
> abline(a = 0, b = 1, lty = 3, col = 5)
> abline(h = 1, col = 6, lty = 3)
> legend(0, 10, c("b=0", "b=0.5", "b=1", "b=1.5", "initial slope",
+     "asymptote"), lty = rep(c(1, 3), c(4, 2)), col = 1:6)
```

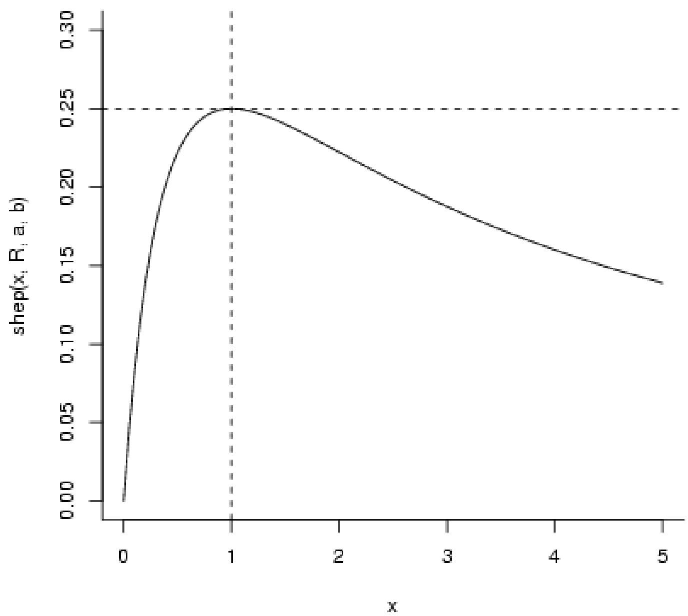


extra credit: use the expression above for the derivative, and look just at the numerator. When does $(1 + aN - abN) = (1 + a(1 - b)N) = 0$? If $b \leq 1$ the whole expression must always be positive ($a \geq 0$, $N \geq 0$). If $b > 1$ then we can solve for N:

$$1 + a(1 - b)N = 0 \quad (8)$$
$$a(b - 1)N = 1 \quad (9)$$
$$N = 1/(a(b - 1)) \quad (10)$$

When $N = 1/(a(b-1))$, the value of the function is $R/(a\cdot(b-1)\cdot(1+1/(b-1))^b)$ (for $b = 2$ this simplifies to $R/(4a)$).

```
> a = 1
> b = 2
> R = 1
> curve(shep(x, R, a, b), bty = "l", ylim = c(0, 0.3), from = 0,
+     to = 5)
> abline(v = 1/(a * (b - 1)), lty = 2)
> abline(h = R/(a * (b - 1) * (1 + 1/(b - 1))^b), lty = 2)
```



There's actually another answer that we've missed by focusing on the numerator. As $N \to \infty$, the limit of the derivative is

$$\frac{R(aN)^{b-1}(a(1-b)N)}{(aN)^{2b}} = \frac{R(1-b)}{(aN)^b};$$

$R > 0$, $(1-b) < 0$ for $b > 1$, $aN > 0$, so the whole thing is negative and decreasing in magnitude toward zero.

Exercise 0.4 *: Holling type III functional response, standard parameterization: $f(x) = ax^2/(1+bx^2)$.

Asymptote: as $x \to \infty$, $bx^2 + 1 \approx bx^2$ and the function approaches a/b.

Half-maximum:

$$\begin{aligned} ax^2/(1+bx^2) &= (a/b)/2 \\ ax^2 &= (a/b)/2(1+bx^2) \\ ax^2 &= (a/b)/2(1+bx^2) \\ (a-a/2)x^2 &= (a/b)/2 \\ x^2 &= (2/a)(a/b)/2 = 1/b \\ x &= \sqrt{1/b} \end{aligned}$$

So, if we have asymptote $A = a/b$ and half-max $H = \sqrt{1/b}$, then $b = 1/H^2$ and $a = Ab = A/H^2$.

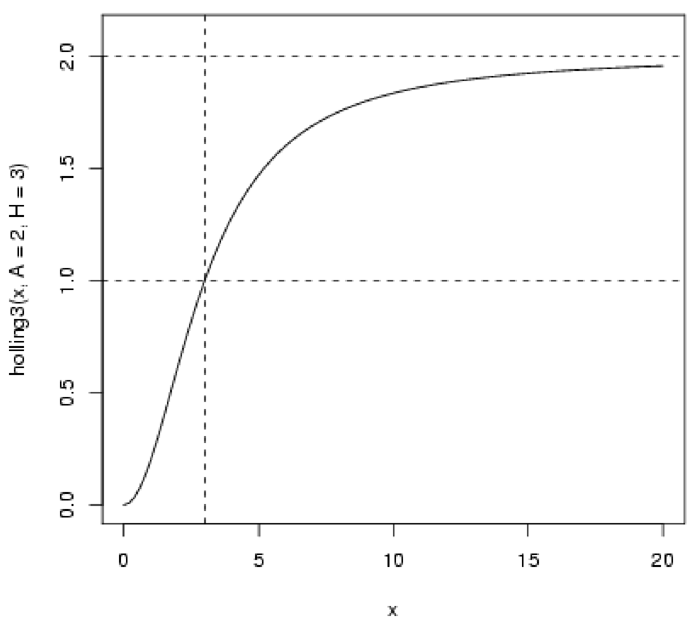
So

$$f(x) = \frac{(A/H^2)x^2}{1 + x^2/H^2}$$

which might be more simply written as $A(x/H)^2/(1 + (x/H)^2)$.

Check with a plot:

```
> holling3 = function(x, A = 1, H = 1) {
+     A * (x/H)^2/(1 + (x/H)^2)
+ }
> curve(holling3(x, A = 2, H = 3), from = 0, to = 20, ylim = c(0,
+     2.1))
> abline(h = c(1, 2), lty = 2)
> abline(v = 3, lty = 2)
```



Exercise 0.5 *:
Population-dynamic:

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

Asymptote K, initial exponential slope r, value at $t = 0$ $n(0)$, derivative at $t = 0$ $rn(0)(1 - n(0)/K)$.

Statistical:

$$f(x) = \frac{e^{a+bx}}{1 + e^{a+bx}}$$

Asymptote 1, value at $x = 0$ $\exp(a)/(1 + \exp(a))$.

The easiest way to figure this out is first to set $K = 1$ and multiply the population-dynamic version by $\exp(rt)/\exp(rt)$:

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

and multiply the statistical version by $\exp(-a)/\exp(-a)$:

$$f(x) = \frac{\exp(bx)}{\exp(-a) + \exp(bx)}$$

This manipulation makes it clear (I hope) that $b = r$, $x = t$, and $(1/n(0) - 1) = \exp(-a)$, or $a = -\log(1/n(0) - 1)$, or $n(0) = 1/(1 + \exp(-a))$.

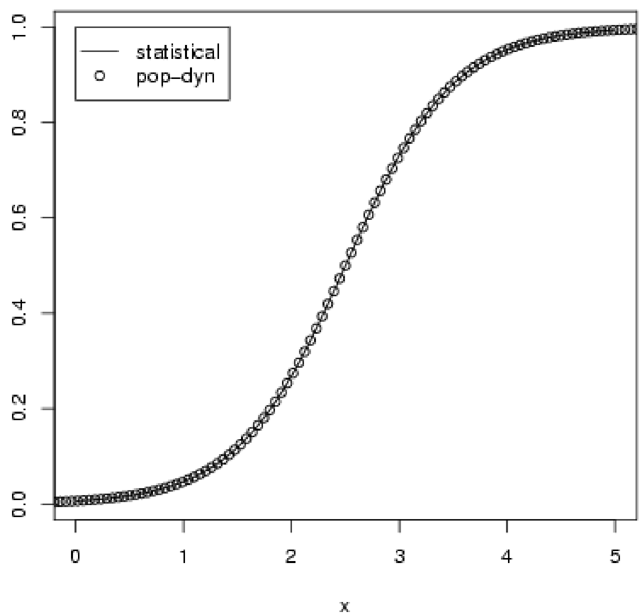
Set up parameters and equivalents:

```
> a = -5
> b = 2
> n0 = 1/(1 + exp(-a))
> n0

[1] 0.006692851
```

```
> K = 1
> r = b
```

Draw the curves:

```
> curve(exp(a + b * x)/(1 + exp(a + b * x)), from = 0, to = 5,
+     ylab = "")
> curve(K/(1 + (K/n0 - 1) * exp(-r * x)), add = TRUE, type = "p")
> legend(0, 1, c("statistical", "pop-dyn"), pch = c(NA, 1), lty = c(1,
+     NA), merge = TRUE)
```



The merge=TRUE statement in the legend() command makes R plot the point and line types in a single column.