Lots of small offspring or fewer larger ones?

Gatto, Casagrandi and De Leo (2002)

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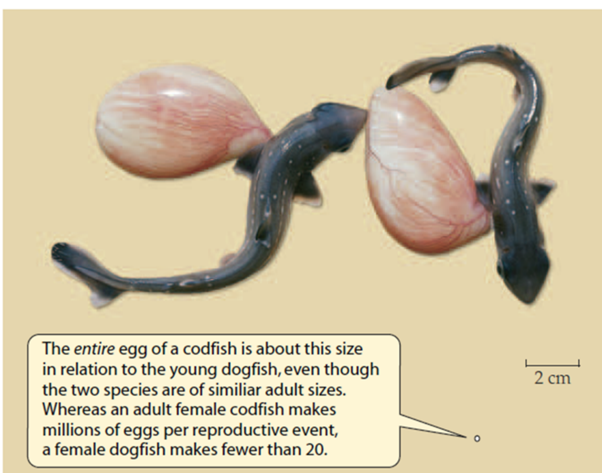
The Problem

A common debate on life history strategies is whether it is better producing many "small" offspring, each with small probability of surviving to the juvenile/adult stage, or fewer "large" offspring, each with more relevant probability of surviving.

Let's try to analyze this problem by using a simple demographic model of a *semelparous*, asexual organism (so we do not have to deal with sex ratio).



Assumptions

We are going to make the following assumptions/definitions:

- δ is the total biomass [grams] invested in reproduction;
- x is the body size (biomass) of each offspring - therefore, the number of offspring produced by an adult individual is: δ/x;
- Offspring with body size x smaller than γ [grams] are too small and die;

- For offspring larger than γ [grams], chance of survival until maturity is an increasing and saturating function of body size x, as described by the following function:

$$\sigma(x) = \alpha \cdot \frac{x - \gamma}{1 + \beta * (x - \gamma)}$$

Let's further assume that natural selection will favor the population with the highest growth rate λ.

Assignment

Assuming that:

- $\delta = 30$ [grams]
- $\alpha = 0.1$ [grams^{-1}]
- $\gamma = 1.00$ [grams]
- $\beta = 0.25$ [grams^{-1}]

compute numerically (and, if you are able, analytically) the optimal body mass of offspring and the corresponding number of offspring

Hint:

- First, draw qualitatively (by hand on paper!) the graph of survival $\sigma(x)$ as a function of offspring size x.
- Then, derive and draw the qualitative graph of the population finite growth rate as a function of body mass x.
- We will then use R to *plot* the graphs of σ and λ as a function of x
- We will find (visually, numerically and analytically) the optimal offspring body weight x_{opt}.
- You will explore which of the 4 parameters (alpha, beta, gamma, delta) has the most influence on x_{opt}.

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Solutions

Qualitative solution

Say N_k the number of adult individuals in generation k.

If x is offspring's mean body size, the total number of offspring generated is equal to:

$$Offspring_k = \frac{\delta}{x} \cdot N_k$$

the number of offspring that survival to become reproductive adult in the generation $k+1$ is this equal to:

$$N_{k+1} = \sigma(x) \cdot Offspring_k$$

Therefore:

$$N_{k+1} = \sigma(x) \cdot \frac{\delta}{x} \cdot N_k$$

and thus, the finite growth rate of the population is equal to:

$$\lambda(x) = \sigma(x) \cdot \frac{\delta}{x}$$

Therefore, the finite groth rate λ is the product of two functions, $\sigma(x)$, which is an increasing and saturating function of body size x, and:

$$\frac{\delta}{x}$$

which is a (hyperbolic) decreasing function of body size x.

Note that λ is equal to zero when $x \leq 1$ and it go to 0 for $x \to \infty$, it is the product of two positive function for $x > 1$. Therefore, λ is an humped function, which increases with x, reaches a maximum and then decreases for larger values of body size x. We thus expect that there is a value of x that maximize the finite growth rate.

Let's find this value, first graphically (by plotting the function λ), then numerically (and, if you want, you can try to find the analytic solution).

Graphical solution

Let's first set model parameters and their value in R, namely:

```
alpha <- 0.1
gamma <- 1
beta  <- 0.25
delta <- 30
```

We could easily set a value to body size x and compute the fraction σ of offspring of body size x surviving to maturity, for instance:

```
x  <- 4 * gamma; x
```

```
## [1] 4
```

```r
sigma5 <- alpha*((x - gamma)/(1+beta*(x - gamma))); sigma5
```

```
## [1] 0.1714286
```

As the number of offspring is:

```r
delta/x
```

```
## [1] 7.5
```

therefore, the fine growth rate is

```r
(delta/x) * sigma5
```

```
## [1] 1.285714
```

Of course, this is not a really efficient use of R. We can set a range of values of body size x, between, say, 0 and 10 times γ (we could go higher, up to 30 gram, but as we will see, this is more than enough)

```r
size <- seq(gamma/100, 10 * gamma, by = gamma/100) # we do not start from zero
head(size)  # check the last elements of this vector
```

```
## [1] 0.01 0.02 0.03 0.04 0.05 0.06
```

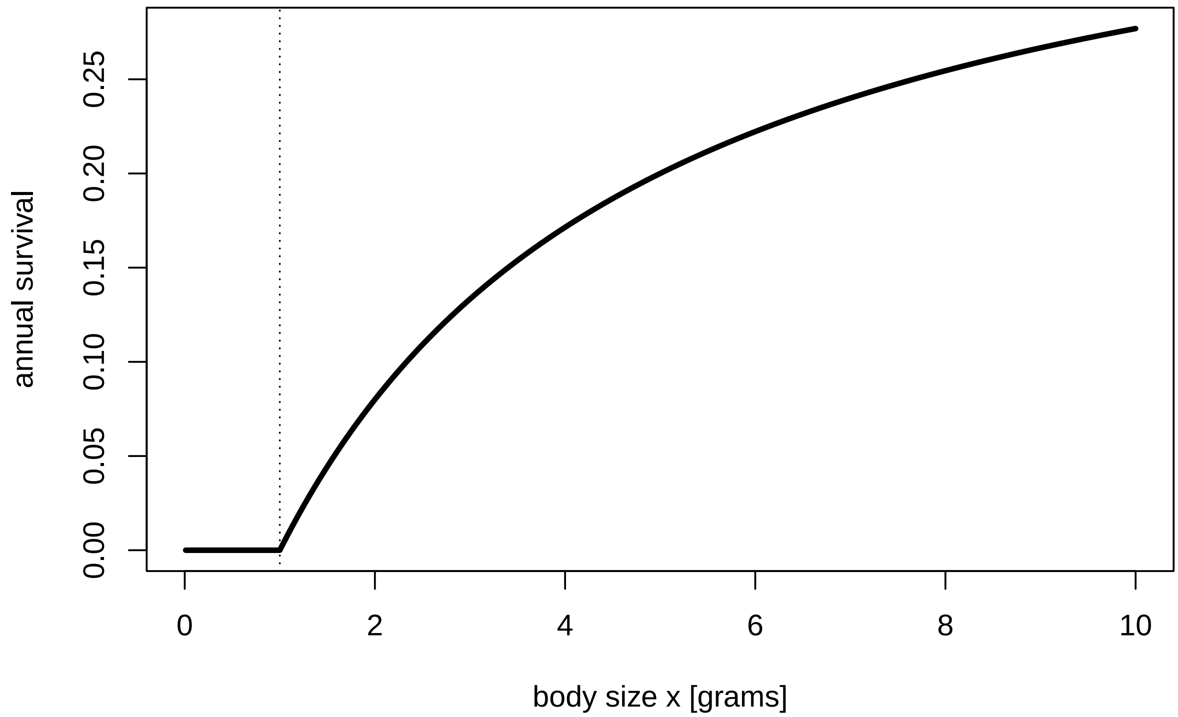
and then we can define a function to compute sigma ($\sigma(x)$) as function of body size x, namely:

```r
f.sigma <-  function(x) {
   ifelse(x<=gamma, 0, alpha*((x-gamma)/(1+beta*(x-gamma))))
}


sigma  <-  f.sigma(size)

tail(sigma)
```

```
## [1] 0.2764479 0.2765432 0.2766384 0.2767334 0.2768283 0.2769231
```

Now, let's plot ($\sigma(x)$) as a functyion body size x:

```r
par(mfrow=c(1,1))
plot(sigma ~ size, type="l", cex=0.5, xlim=c(0,max(size)), xlab = 'body size x [grams]',
                         ylab = 'annual survival', lwd = 3)
abline(v=gamma, lty = 3)
```

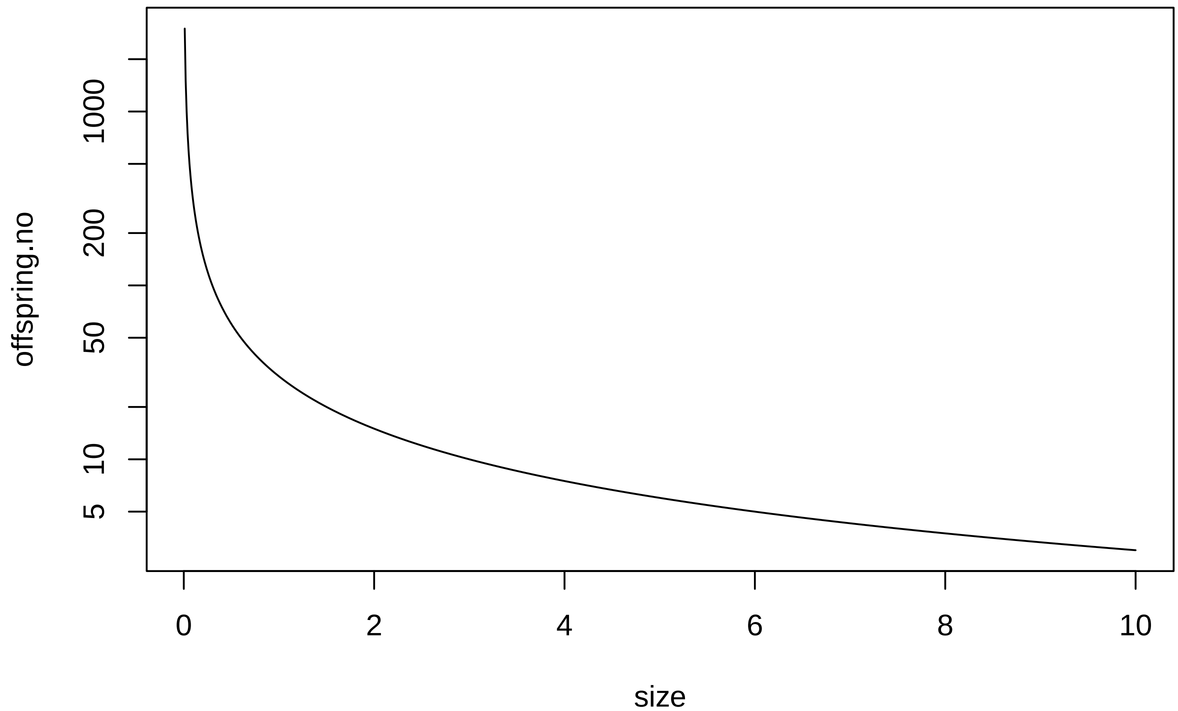


Now, let's compute the average number of offspring with body size x and plot is on semi-log scale:

```
f.offspring.no  <-  function (x) delta/x

offspring.no  <- f.offspring.no(size); head(offspring.no)
```

```
## [1] 3000 1500 1000  750  600  500
```

```
plot(offspring.no ~ size, cex=0.5, type="l", log = 'y')
```



Now, we can finally compute the finite growth rate λ as product of number of offspring on body size x and their survival σ to reproduction, which in r is particularly easy to do, as the multiplication operator "*" multiply the two vectors element by element, that is:

```
lambda <- offspring.no * sigma

head(sigma)
```

```
## [1] 0 0 0 0 0 0
```

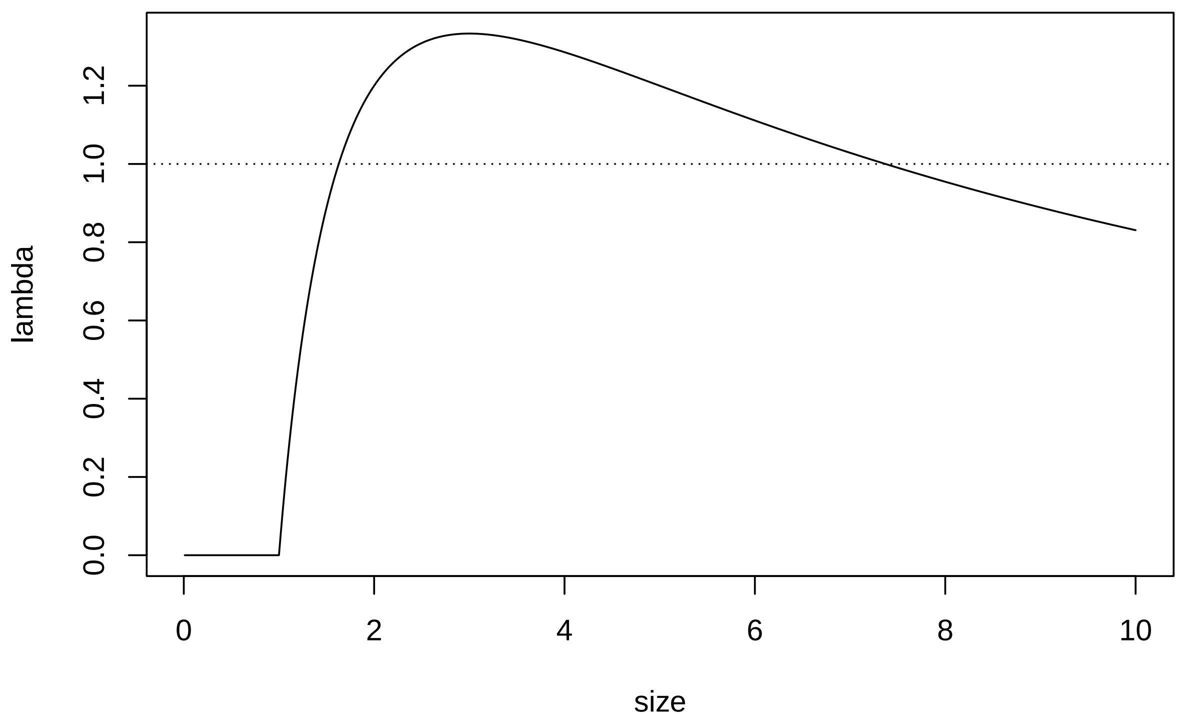
```
head(offspring.no)
```

```
## [1] 3000 1500 1000  750  600  500
```

```
head(lambda)
```

```
## [1] 0 0 0 0 0 0
```

```
plot(lambda ~ size, cex=0.5, type="l")
abline(h=1, lty = 3) # add a horizontal line for lambda=1 (by the way, why lambda=1?)
```



Therefore, we can see that λ is indeed an unimodal function of body size x with a maximum for a body size between 2.5 and 3.5

We can find numerically the value of x that maximizes λ as follows:

```
size[which(lambda == max(lambda))]
```

```
## [1] 3
```

Analytic solution

Note that this value is probably the right one (as we designed the exercise so that λ is maximum for $x = 3$). Yet, this result depends upon how finely we set the vector *size* of body sizes with R's *seq()* function

We can derive analytically the optimal body size by noting that when λ reaches its maximum value, there its first derivative is equal to zero by definition.

Therefore, we should find the value of x for which:

$$\frac{d\lambda(x)}{dx} \equiv 0$$

As $\lambda(x) = \sigma(x) \cdot Offspring(x)$ (actually, let's rename $G(x) \equiv Offspring(x)$, this means:

$$\frac{d\lambda(x)}{dx} = \frac{d\sigma(x) \cdot G(x)}{dx} = \frac{d\sigma(x)}{dx} \cdot G(x) + \sigma(x) \cdot \frac{dG(x)}{dx} \equiv 0$$

or also:

$$\alpha\frac{1+\beta(x-\gamma)-(x-\gamma)\beta}{(1+\beta(x-\gamma))^2}\cdot\frac{\delta}{x}+\alpha\frac{x-\gamma}{1+\beta*(x-\gamma)}\cdot\left(-\frac{\delta}{x^2}\right)\equiv 0$$

which can be simplified to:

$$\beta(x-\gamma)^2=\gamma$$

and, thus, the optimal body size is:

$$x_0=\gamma+\sqrt{\frac{\gamma}{\beta}}$$

Therefore,

```
x.opt = gamma + sqrt(gamma/beta); x.opt
```

```
## [1] 3
```

some minor (but cool) addition

Using R for symbolic calculation

In case you might not remember all the derivative rules, R can help you by doing symbolic calculation, and here below we will show you how.

Specifically, we will make R to compute the derivative of lambda with respect to body size and then use *uniroot()* to find where the derivative is equal to zero.

First we transform the function to compute λ to a "text expression" in R, namely:

```
lambda.expr <- expression(alpha*((x-gamma)/(1+beta*(x-gamma)))*delta/x)
lambda.expr
```

```
## expression(alpha * ((x - gamma)/(1 + beta * (x - gamma))) * delta/x)
```

Then, we simply ask R to compute the derivative for us:

```
lambda.der <- D(lambda.expr, "x")

lambda.der
```

```
## alpha * (1/(1 + beta * (x - gamma)) - (x - gamma) * beta/(1 +
##     beta * (x - gamma))^2) * delta/x - alpha * ((x - gamma)/(1 +
##     beta * (x - gamma))) * delta/x^2
```

The result is a text expression as well, so we need to tell R to *evaluate* it for any value of model parameters and for the specific value of body size, namely:

```
f.lambda.der = function(x) eval(lambda.der)
f.lambda.der
```

```
## function(x) eval(lambda.der)
```

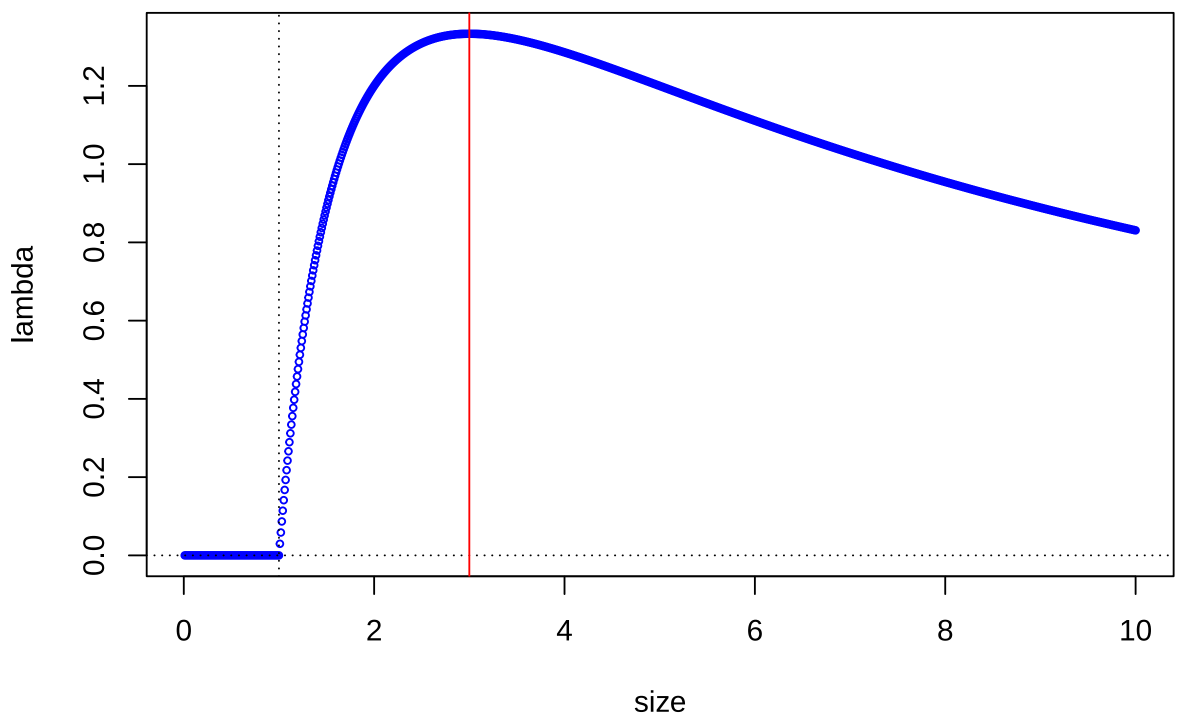
Let's see whether the numerical derivative is indeed quite close to zero:

```
f.lambda.der(x.opt)
```

```
## [1] 5.551115e-17
```

Let's compute and then plot the derivative of λ as a function of body size x

```
lambda.der.v = sapply(size, f.lambda.der)
plot(lambda ~ size, cex=0.5, col="blue")
abline(v=c(gamma, 20*gamma), h=0, lty = 3)
abline(v=x.opt, col="red")
```

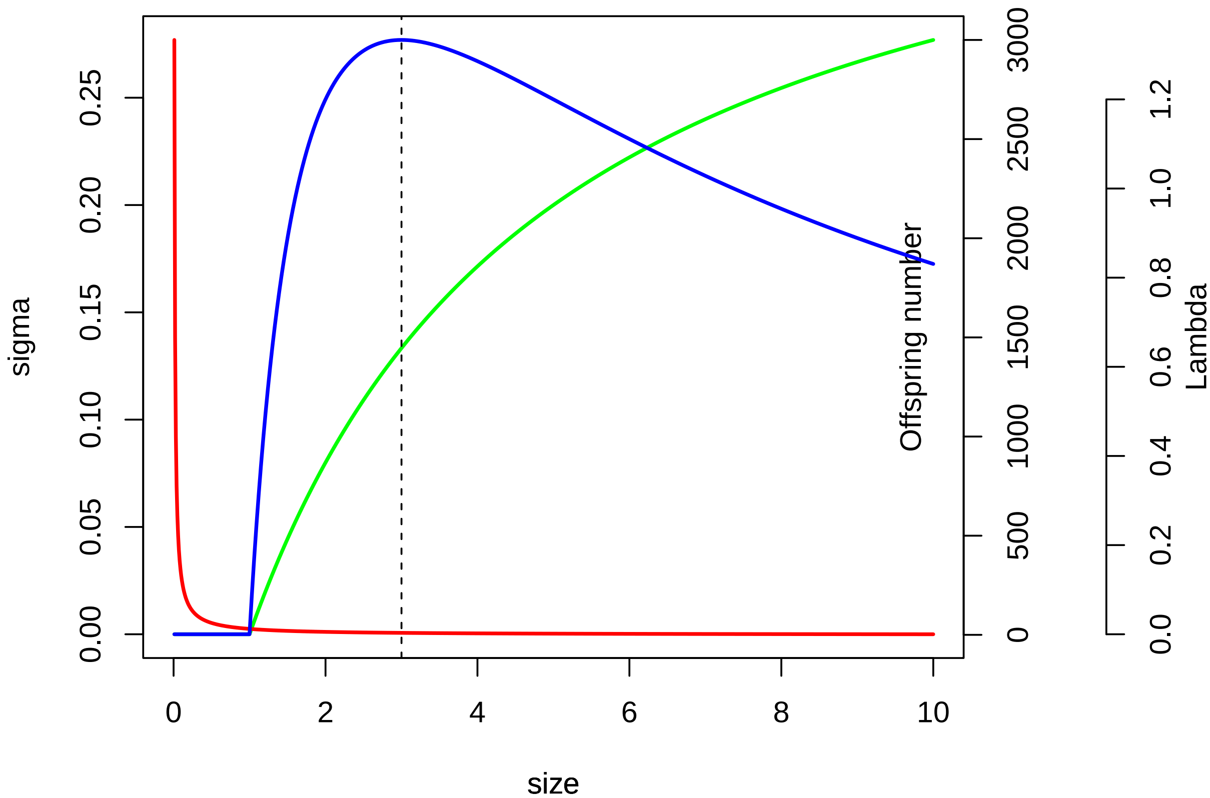


Plot all three graphs on the same plot

plot several function each with its scale on the same panel par(mfrow =c(1,1), mar=c(6,4,1,8)) set margin size to accomodate two y axes on right

```
par(mfrow =c(1,1), mar=c(6,4,1,8)) # set margin size to accomodate two y axes on right
plot(sigma ~ size, type="l", cex=0.5, col="green", lwd=2, xlim=c(0,10*gamma))
leg.txt <- c("Sigma", "Offspring number", "Lambda")
legend(0.0004, 0.000004, leg.txt, col=c("green", "red", "blue"), lty=1,
       lwd=2, bty="n")
```

```
par(new=T)  #par adds new data to prior plot without overwriting it
plot(offspring.no ~ size, axes = F, cex=0.5, col="red", ylab="", lwd=2,
     type="l", xlim=c(0,10*gamma))

axis(4)  #position 4 is the right side of the quartz window
mtext("Offspring number", side = 4, line=-2) # 'line' adjusts position of axis label

par(new=T)  #par adds new data to prior plot without overwriting it
plot(lambda ~ size, axes = F, cex=0.5, col="blue", type = 'l', ylab="", lwd=2,
     xlim=c(0,10*gamma))

axis(4, line=4)  #position 4 is the right side of the quartz window
mtext("Lambda", side = 4, line=6)

abline(v=x.opt, col="black", lty=2)
```



Find optimal body size by using R's uniroot() function

Lastly, I just want to note that in case we were unable to derive the analytic solution, we could still find the solution numerically by using R's *uniroot()* function to find the value of x for which the derivative of λ is equal to zero, namely:

```r
obs <- uniroot(f.lambda.der, c(gamma, 10*gamma), tol = 10^-12)
opt.body.size = obs[1];opt.body.size
```

```
## $root
## [1] 3
```

Asssignment

- Discuss the relationship between optimal body size x_{opt} and γ and β.
- In terms of life history traits, what is the meaning/your interpretation of these relationships?