

Deterministic functions for Modelling Biological Data

Michael Noonan

March 22, 2021

Biol 520C: Statistical modelling for biological data

1. Housekeeping
2. The 'Linear' in Linear Regression
3. Finding Out About Functions Numerically and Analytically
4. Deterministic Functions for Modelling Biological Data
5. Fitting Non-Linear Models in R

Housekeeping



- Practical 09 is up and due next week.

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- A reminder that if you want me to review anything in specific, let me know before next week.

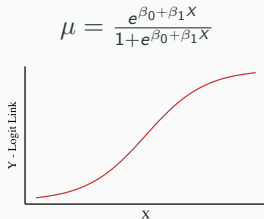
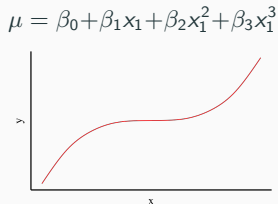
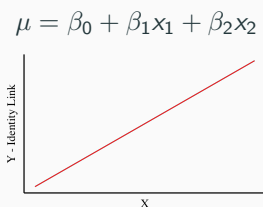
The 'Linear' in Linear Regression



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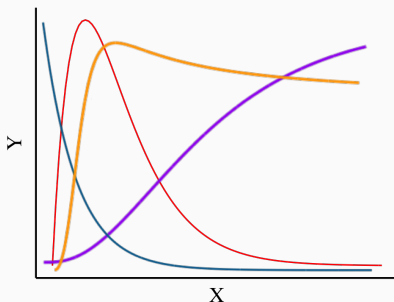
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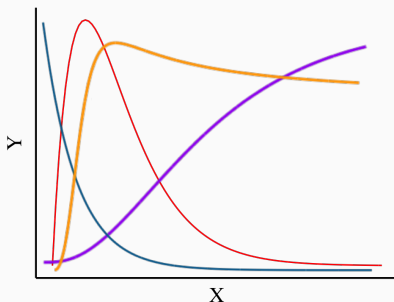
Even if we add polynomial terms, or fit GLMs with link functions the β s still combine linearly.



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Today we will learn about tools that can help you understand new functions, and explore a range of different functions that get used routinely.

Finding Out About Functions Numerically and Analytically



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2. Analytically (evaluate it mathematically using limits, derivatives, etc.)





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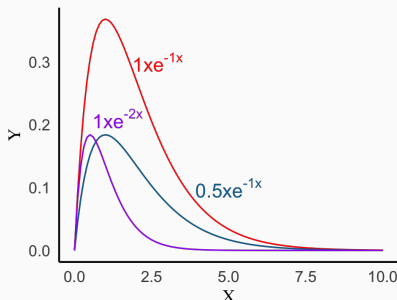
You would then repeat this process for multiple parameter values.

For the Ricker function ($y = axe^{-bx}$), the process would look like this:

```
ricker <- function(x, a = 1, b = 1) {  
  a * x * exp(-b * x)  
}
```

```
x <- seq(0,10, 0.1)
```

```
y <- ricker(x)  
y2 <- ricker(x, a = 0.5)  
y3 <- ricker(x, b = 2)
```







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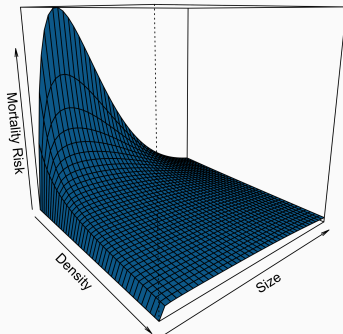
If mortality risk can be modelled as a function of density (N) and size dependent attack rates ($\alpha(s)$) using a Holling Type II functional response ($y = \alpha(s)/(1 + \alpha(s)HN)$) (Vonesh & Bolker, 2005), then:

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```
library(emdbook)

mortrisk <- function(N, size, H = .84) {
  a <- ricker(size)
  a/(1 + a * N * H)
}

curve3d(mortrisk(N = x, size = y),
  to = c(60,6), theta = 50,
  xlab = "Density",
  ylab = "Size",
  zlab = "Mortality Risk")
```





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1. Taking limits
2. Using derivatives



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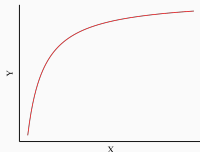
To understand the limiting behaviour of a function we look at what happens when x gets large ($x \rightarrow \infty$), or when x gets small ($x \rightarrow 0$ or $x \rightarrow -\infty$)

As x tends towards these limits terms get dropped and we get a feel for what the tail ends of the function would look like.



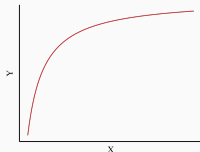
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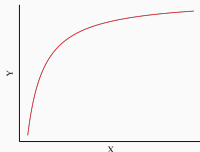


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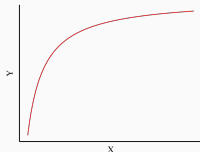


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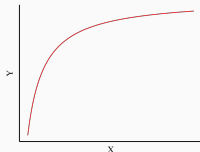


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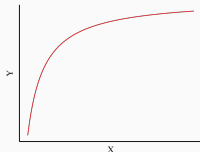


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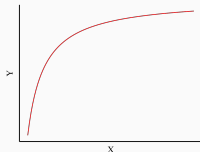
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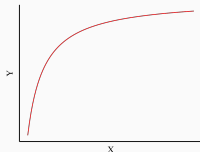
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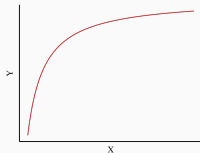
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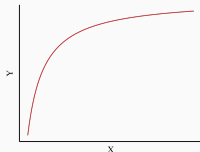
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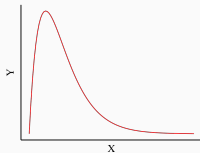
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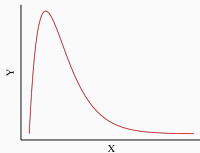


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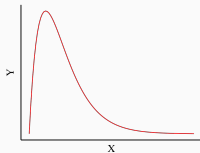


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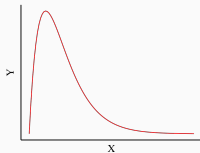
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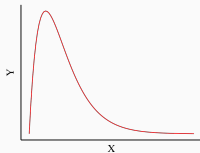
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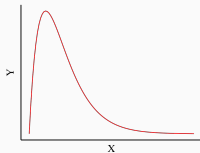
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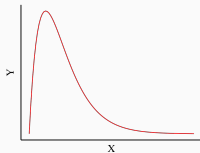


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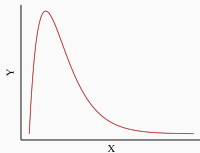


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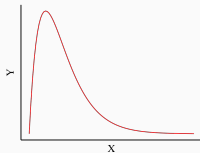


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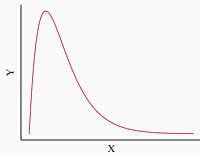
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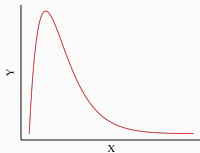
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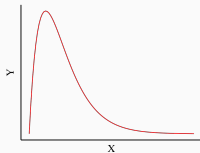
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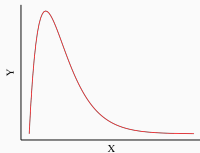
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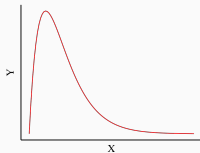
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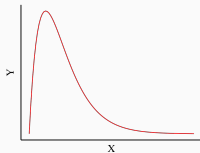
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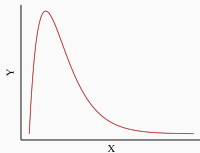
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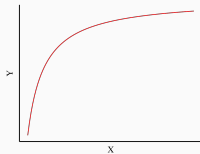
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Usefully, we can work out simple derivatives in R with the `D()` function.



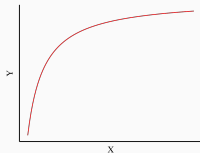
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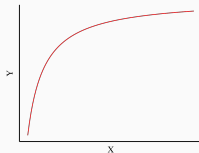
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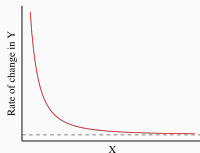
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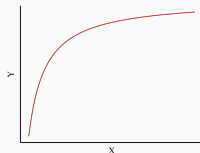
```
michmen = expression(a * x / (b + x))  
D(michmen, "x")
```

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



We know the Michaelis-Menten function limits to 0 and a :

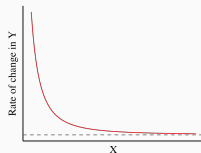
$$y = \frac{ax}{b+x}$$



But how does it approach its limits?

```
michmen = expression(a * x / (b + x))  
D(michmen, "x")
```

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

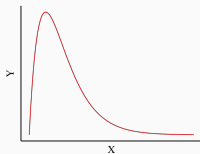


The rate of change in Y is greatest as $X \rightarrow 0$, and limits to 0 as $X \rightarrow \infty$ (called a saturating function)



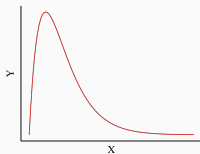
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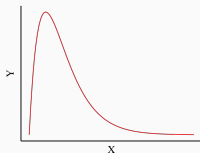
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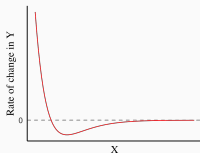
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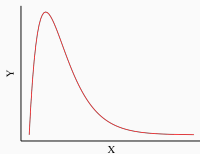
But how does it approach its limits?

```
Ricker = expression(a * x * exp(-b * x))  
Ricker_deriv <- D(f,"x")  
  
a * exp(-b * x) - a * x * (exp(-b * x) * b)
```



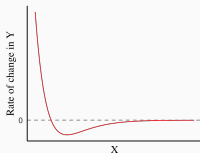
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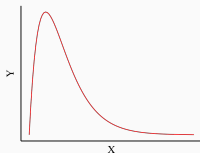
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The rate of change in Y is greatest as $X \rightarrow 0$

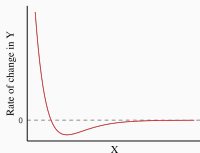
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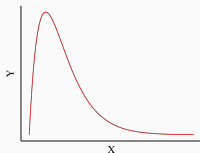
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The rate of change in Y is greatest as $X \rightarrow 0$, it starts off growing but hits an inflection point

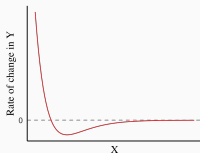
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```



The rate of change in Y is greatest as $X \rightarrow 0$, it starts off growing but hits an inflection point, it then decays and the rate of change limits to 0 as $X \rightarrow \infty$ (saturating)



If you know how to find out about a function's behaviour (numerically or analytically), you can get a better feeling of what each of the parameters are doing.

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You can then change their values, shift or scale the functions, match them to biological parameters (remember they will all have units), etc.

All of this helps you get a better feel for how you can build functions to match the system you're modelling.

Deterministic Functions for Modelling Biological Data

Polynomial functions have the general form $y = \sum_{i=1}^n \beta_i x^i$

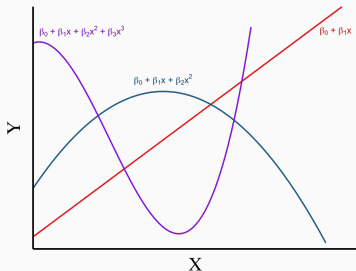
Examples:

Linear: $f(x) = \beta_0 + \beta_1 x$

Quadratic: $f(x) = \beta_0 + \beta_1 x + \beta_2 x^2$

Cubic: $f(x) = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3$

Range: $-\infty, \infty$



Advantages: Easy to understand; easy to reduce; easy to extend to higher orders; can fit arbitrarily complex data.

Disadvantage: Anything beyond 2nd order polynomials are hard to justify mechanistically; they don't level off as $X \rightarrow \infty$ or $-\infty$ (extrapolations are often unrealistic); higher order polynomials can be unstable.

Polynomial functions can be made more flexible by using them as *piecewise* functions where different functions apply over different ranges of your predictor (x).

Examples:

Threshold:

$$f(x) = a_1 \text{ if } x < s_1, \quad a_2 \text{ if } x > s_1$$

Hockey stick:

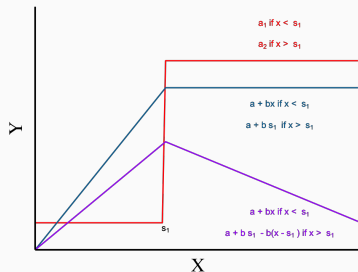
$$f(x) = a + bx \text{ if } x < s_1, \quad a + bs_1 \text{ if } x > s_1$$

Piecewise linear:

$$f(x) = a + bx \text{ if } x < s_1, \quad a + bs_1 + b_2(x - s_1) \text{ if } x > s_1$$

Cubic splines:

$f(x)$ is complicated.



Range: $-\infty, \infty$

Advantages: Make sense and give added flexibility if there is a biological switching point.

Disadvantage: Hard to fit; discontinuous derivatives that may not make biological sense.

Rational functions are ratios of polynomials with the general form: $\frac{\sum a_i x^i}{\sum b_j x^j}$

Examples:

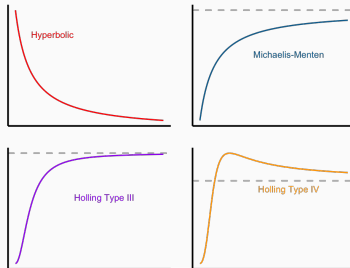
Hyperbolic: $f(x) = \frac{a}{b+x}$

Michaelis-Menten: $f(x) = \frac{ax}{b+x}$

Holling type III: $f(x) = \frac{ax^2}{b^2+x^2}$

Holling type IV (c<0): $f(x) = \frac{ax^2}{b+cx+x^2}$

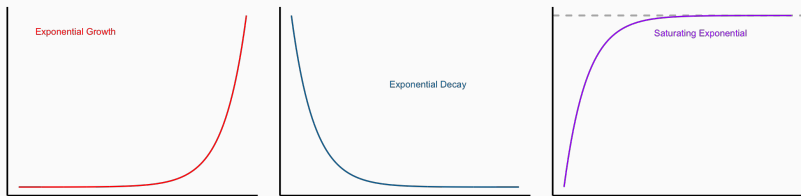
Range: $0, \infty$



Advantages: Very flexible; often make mechanistic sense; simple to estimate parameters; easy to reduce down; reach finite asymptotes so are more stable than polynomials.

Disadvantage: Complicated derivatives; Approach their asymptotes very slowly, which can make these hard to estimate.

Exponential functions are based on exponential growth (ae^{bx}), exponential decay (ae^{-bx}), or saturating exponential functions ($a(1 - e^{-bx})$). Their range is $0, \infty$.



Advantages: Exponential growth/decay occur commonly in nature and these functions make mechanistic sense; can be used to calculate doubling times or half-lives.

Disadvantage: Similar behaviour to rational functions which makes it hard to distinguish between them without a lot of data.

Exponential functions can be combined with other functions to increase their flexibility. Their ranges are $0, \infty$.

Examples:

Ricker: $f(x) = axe^{-bx}$

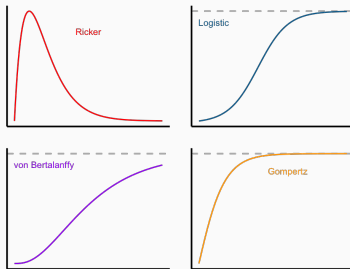
Logistic: $f(x) = \frac{e^{a+bx}}{1+e^{a+bx}}$

von Bertalanffy:

$$f(x) = a(1 - e^{-k(1-d)(x-x_0)})^{\left(\frac{1}{1-d}\right)}$$

Gompertz: $f(x) = e^{-ae^{-bx}}$

Range: $0, \infty$



Advantages: Very flexible; often make mechanistic sense; simple to estimate parameters; easy to reduce down; reach finite asymptotes so are more stable than polynomials.

Disadvantage: Similar behaviour to other functions which makes it hard to distinguish between them without a lot of data.

Fitting Non-Linear Models in R



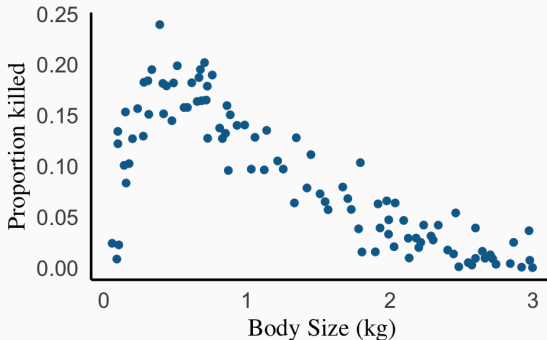
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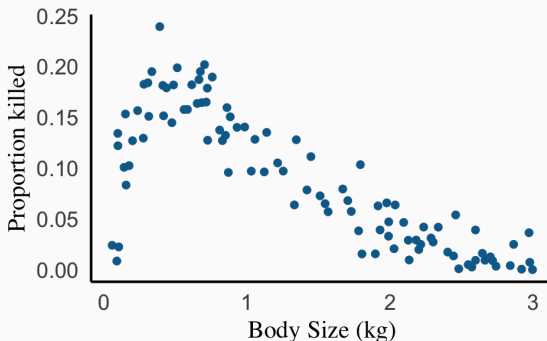
The `nls()` function allows fitting of non-linear relationships between a response variable and one or more explanatory variables using non-linear least squares.



We'll work with a simulated dataset describing size-dependent predation rate.

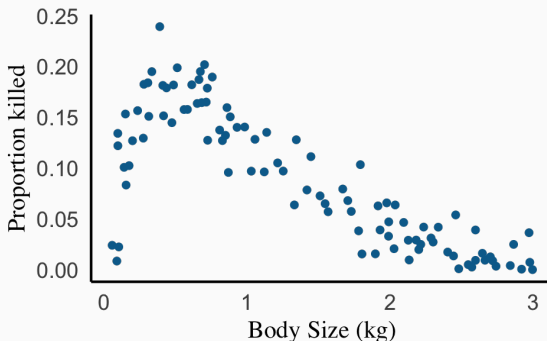


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Does a linear model look like a good option here?

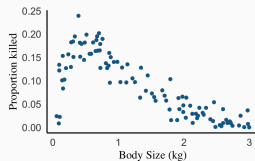
We'll work with a simulated dataset describing size-dependent predation rate.



Does a linear model look like a good option here? What deterministic function do think we should try?

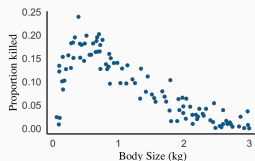


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```
#Need to provide starting values for the parameters
FIT <- nls(prop ~ a * size * exp(-b * size),
          start = list(a = 1,
                      b = 2),
          data = DATA)
```



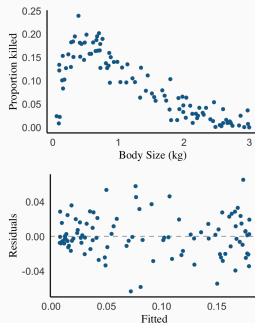
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FIT <- nls(prop ~ a * size * exp(-b * size),
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summary(FIT)

Formula: prop ~ a * size * exp(-b * size)

Parameters:
      Estimate Std. Error t value Pr(>|t|)
a  0.96502    0.04175   23.11  <2e-16 ***
b  1.97821    0.05528   35.79  <2e-16 ***
---
Residual standard error: 0.02352 on 98 degrees of freedom
```



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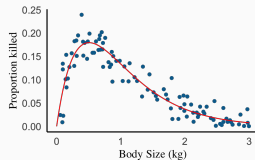
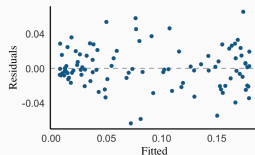
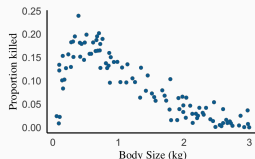
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```

```
#To plot fitted model need to code up the Ricker function
ricker <- function(x) {
  coef(FIT)[1] * x * exp(-coef(FIT)[2] * x)
}
x <- seq(0,3, 0.01)
y <- ricker(x)
```





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Unlike `lm()`, `nls()` requires that the formula includes all of the parameters you want to fit, including an intercept if you want one fitted. E.g., in `lm()` you would write the formula for linear regression as:

$$y \sim x$$

but to fit the same model in `nls()` you would have to write this as:

$$y \sim a + b*x$$



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If you combine these functions with a stochastic model and maximum likelihood estimation you can fit any model you can write down to data (Chapter 8 of Bolker's book).

References

- Vonesh, J.R. & Bolker, B.M. (2005). Compensatory larval responses shift trade-offs associated with predator-induced hatching plasticity. *Ecology*, 86, 1580–1591.
- Bolker, B. M. (2008). Ecological models and data in R. Princeton University Press.