

Some guidance on using mathematical notation in biology

Andrew Edwards¹ & Marie Auger-Méthé²



¹Pacific Biological Station & University of Victoria; ²University of British Columbia

Pacific Biological Station Seminar Series

Thursday 21st November, 2019



Fisheries and Oceans
Canada Pêches et Océans
Canada



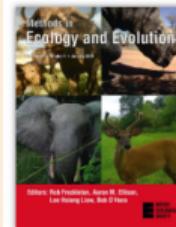
Paper

RESEARCH ARTICLE

Methods in Ecology and Evolution
BRITISH
ECOLOGICAL
SOCIETY

Some guidance on using mathematical notation in ecology

Andrew M. Edwards^{1,2}  | Marie Auger-Méthé^{3,4} 



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Code for building this talk: <https://github.com/andrew-edwards/notation-talk>

Feedback



Brian J. Enquist

@bjenquist

Thank goodness someone published this. Has been on my to wish list to do something similar. 'Some guidance on using mathematical notation in ecology'- "the clarity of mathematical notation varies between papers and can often be inconsistent" <https://t.co/f>

15 Oct 2018



Ryan S. Miller

@RyanSMiller_

As someone that became quantitative later in their career I wish someone had published this long ago! <https://t.co/wsrHtBE9v8>

30 Oct 2018



Kiva Oken

@KivaOken

Bad notation impedes communication of your ideas. Sloppy notation is at *least* as annoying as poor writing. Every ecologist who uses equations should read this! <https://t.co/rZZ5BFKc3P>

03 Apr 2019



Kiva Oken

@KivaOken

Replies to @ericward_ @mark_scheuerell and 2 others

I've already cited this paper in reviews more than once! It needs some sort of shadow citation count...

10:34 AM · Nov 13, 2019 · Twitter Web App

Motivation

We have both reviewed manuscripts in which unclear notation:

- 🎃 made it impossible to understand modelling details
- 🎃 meaning we could not evaluate the results or conclusions
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Guidance is relevant for all technical documents, such as

- 🎃 CSAS working papers
- 🎃 DFO Technical Reports
- 🎃 software manuals

Motivation

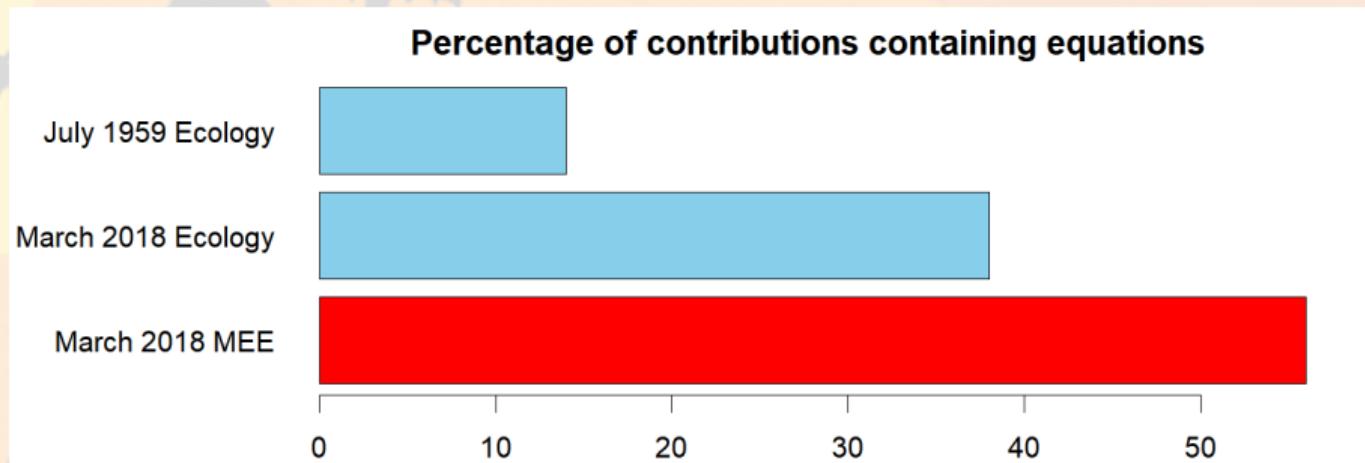
- 🎃 mathematical modelling playing an increasing role in biology
- 🎃 requires communication of details of models
- 🎃 this includes notation
- 🎃 clarity of notation varies between papers

Motivation

- 🎃 mathematical modelling playing an increasing role in biology
- 🎃 requires communication of details of models
- 🎃 this includes notation
- 🎃 clarity of notation varies between papers
- 🎃 poor notation can:
 - 🎃 make models appear more complicated than necessary
 - 🎃 this leads to cluttered equations that impede understanding
 - 🎃 impedes communication of ideas
 - 🎃 can prevent work being properly reviewed – analogous to an incomplete description of the methods of a laboratory experiment

Motivation

Lowry (1959): increase “use of mathematical notation where appropriate in ecological literature”



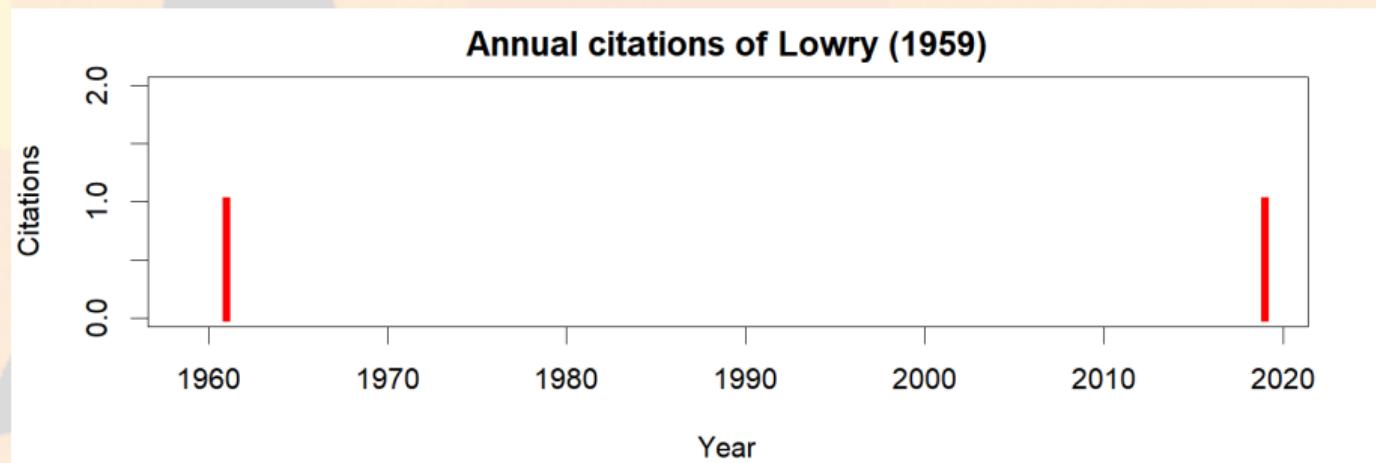
Lowry said advantages include:

- 🎃 precise communication of logical thought (beyond that afforded by the written word)
- 🎃 reproducibility of methods and results

and they “accrue in proportion to **the care used by the author in the use of notation**”.

Motivation

Unusual citation pattern of Lowry (1959):



Motivation

Many skills involved in producing an ecological modelling paper, with books covering:

- 🎃 introductory ecology
- 🎃 general mathematics
- 🎃 ecological modelling
- 🎃 implementing models in R
- 🎃 writing and publishing a paper

Recommendations exist for:

- 🎃 streamlining workflows (tools such as Git and GitHub)
- 🎃 making computer code available and reproducible

But no tips on developing the mathematical notation to use in a model.

Motivation

Improvements have impacts – for Individual Based Models:

- 🎃 previously criticised as generally being so poorly documented that models could not be evaluated or reproduced
- 🎃 motivated development of standardised protocols
- 🎃 led to a more rigorous formulation of models
- 🎃 enhanced understanding

Motivation

Why us?

Similar backgrounds:

- 🎃 all research highly quantitative
- 🎃 lead authors of >20 ecological modelling papers
- 🎃 taught modelling courses to biology students

Differences:

- 🎃 one undergrad in math
- 🎃 **one undergrad in biology**

We have papers with notation that could, in hindsight, be improved.

What is notation?

Notation – we are specifically referring to:

- 🎃 letters used to represent quantities in equations
- 🎃 use of subscripts and superscripts
- 🎃 parentheses etc.
- 🎃 related concepts

Letters can be

- 🎃 Roman – a, b, c, \dots
- 🎃 Greek – $\alpha, \beta, \gamma, \dots$
- 🎃 lower case – $a, b, c, \alpha, \beta, \gamma, \dots$
- 🎃 upper case – $A, B, C, \Gamma, \Delta, \Omega, \dots$

What do journals say?

We reviewed the Author Guidelines for a sample of 14 journals:

- 🎃 *Bulletin of Mathematical Biology*
- 🎃 *Canadian Journal of Fisheries and Aquatic Sciences*
- 🎃 *Ecology*
- 🎃 *Ecology Letters*
- 🎃 *Evolution**
- 🎃 *Functional Ecology*
- 🎃 *Journal of Animal Ecology*
- 🎃 *Journal of the Royal Society Interface**
- 🎃 *Marine Ecology Progress Series*
- 🎃 *Methods in Ecology and Evolution*
- 🎃 *Molecular Biology and Evolution*
- 🎃 *Nature*
- 🎃 *PLOS ONE*
- 🎃 *Science*

*Only two that have no mention of equations.

Minimal guidance in others – almost exclusively restricted to typesetting aspects (such as bold for vectors).

Authors' responsibility

Onus for good notation should be on authors (rather than journals) because:

- 🎃 notation should be decided early on in a study (possibly before deciding on a particular journal)
- 🎃 ideally computer code will match the notation
- 🎃 work may first appear in a technical document such as a thesis before being submitted to a journal
- 🎃 Supporting Information of a paper often contains the full mathematical details of models and is not typeset or edited by publishers – authors are responsible for clarity

Guidelines

- base on those traditionally used in mathematics
- are in a somewhat logical order
- our aim is for them to be useful and adopted
- though we anticipate exceptions for which they are purposefully overlooked
- use examples from common ecological models, our own fields of research and from evolutionary biology

1. Define all terms

Who recognises this equation?

$$E = mc^2$$

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Who recognises this equation?

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Who knows what it means?

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$$E = mc^2$$

Who knows what it means?

It does not convey any information, since the **letters are not defined.**

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Common ecological example:

$$S = cA^z$$

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where:

- 🎃 S represents the number of species (of a particular taxonomic category) in area A
- 🎃 constant c is the number of species that would be in one square unit
- 🎃 dimensionless exponent z quantifies the change in species number with area

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So equation represents an increase in species richness with area.

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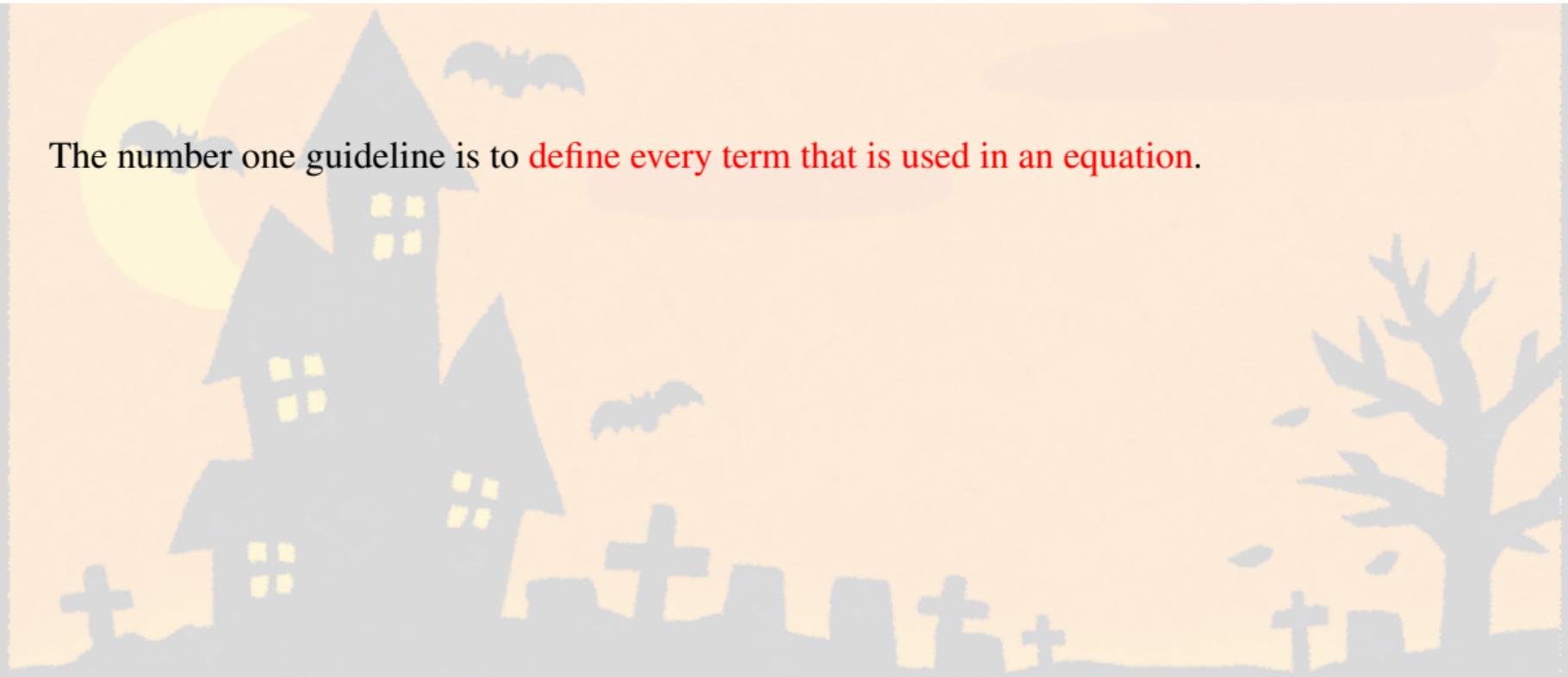
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Immediately after an equation (as part of the same sentence) any previously undefined symbols should be defined using the phrase “where ...”.

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Table of notation helpful for complicated models.

Desirable for tables and figures to be understandable on their own, so any notation in them should be additionally defined in their captions.

1. Define all terms

Recent example had nothing defined:

Table 1. Age-structured operating model

Equation Number	Equations
Unfished Equilibrium States	
(EQ.1)	$m_a = \left(1 + e^{-\log 19 \frac{a - a_{50}^{rec}}{a_{50}^{rec} - a_{10}^{rec}}} \right)^{-1}$
(EQ.2)	$S_{a,p} = e^{-(a-1)\bar{M}_p}$
(EQ.3)	$S_{A,p} = \frac{e^{-(a-1)\bar{M}_p}}{1 - e^{-\bar{M}_p}}$
(EQ.4)	$\phi_p = \sum_a S_{a,p} \cdot \bar{w}_{a,p} \cdot m_a$
(EQ.5)	$R_{0,p} = B_{0,p} / \phi_p$
(EQ.6)	$N_{a,p}^{eq} = R_0 \cdot S_{a,p}$
Catch from discrete fisheries	
(C.1)	$N_{a,p,t+f_j^-} = N_{a,p,t+f_{j-1}^-} \cdot e^{-\frac{1}{2}(t_f - t_{f-1})\bar{M}_t}$
(C.2)	$S_{a,p,f} = \left(1 + e^{-\log 19 \frac{a - a_{f,50}^{rec}}{a_{f,50}^{rec} - a_{f,10}^{rec}}} \right)^{-1}$

2. Use italics, boldface and capitalisation appropriately

By convention, mathematical symbols (except Greek letters) should be *italicised*.
Distinguishes text from mathematical notation:

- 🎃 a large value of *a*
- 🎃 a large value of a

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Vectors and matrices should be Roman script and bold:

- 🎃 \mathbf{a} is a vector
- 🎃 \mathbf{A} is a matrix
- 🎃 element i of \mathbf{a} is often a_i
- 🎃 element in row i and column j of \mathbf{A} is A_{ij} (or sometimes a_{ij})

Generic random variables are usually upper case: X .

Possible numeric values represented by the corresponding lower-case letter: x .

2. Use italics, boldface and capitalisation appropriately

Roman letters for standard mathematical functions:

🎃 $\sin x, \cos x, \log x, \ln x, e^x$

and for other words such as:

$$X \sim \text{Normal}(\mu, \sigma^2)$$

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Also use a Roman d for derivative and integral of variable X with respect to time t :

$$\frac{dX}{dt} \quad \text{and} \quad \int f(x)dx$$

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Units should be given in Roman type to distinguish them from mathematical variables:

- 🎃 the speed of the polar bear was 1 km h⁻¹
- 🎃 let the speed be x km h⁻¹

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Subscripts represent different values of a quantity.

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Because:

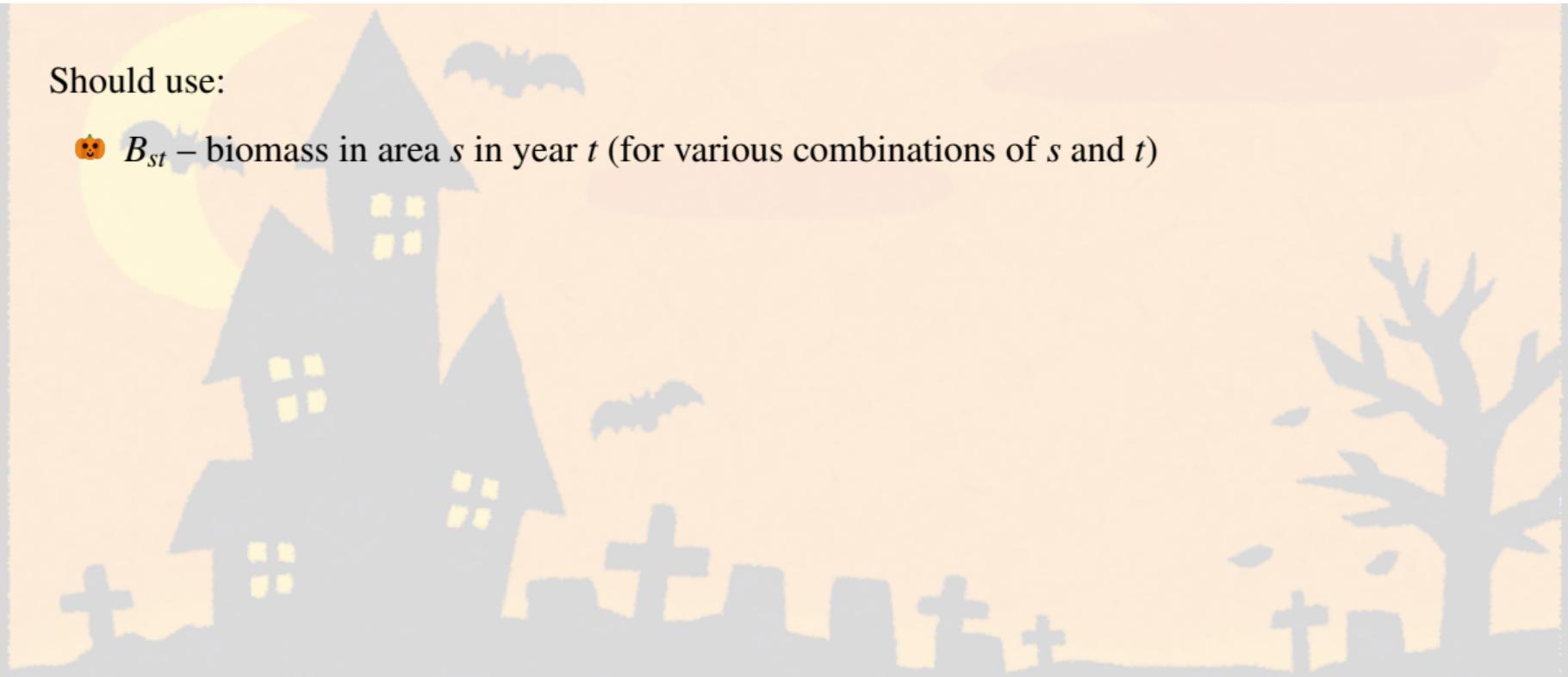
- 🎃 $t = 1$ gives B_1 as the biomass in year 1
- 🎃 $s = 1$ gives B_1 as the biomass in spatial area 1

Obvious confusion.

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Should use:

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Extending this, for data from fish trawl surveys:

- 🎃 B_{ijkmn} – biomass caught per hour (g h^{-1}) of:

- 🎃 taxonomic group i
- 🎃 length class j
- 🎃 haul k
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Succinctly describes detailed structure of the data, and made subsequent calculations unambiguous.

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Commas: can use B_{st} or $B_{s,t}$, but always use them to avoid ambiguity: $B_{3,17}$ rather than B_{317} .

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Abbreviations as (non-italicised) subscripts to indicate related definitions.

For example, when modelling DNA records from sediments:

- 🎃 P_{fp} – probability of **false positives**
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Please please please avoid using acronyms such as *MSY* to represent a variable.

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$$y_t = 2x_i + 3.$$

Can lead to confusion:

- 🎃 $i = 1, x_1 = 3$ gives $y_t = 9$
- 🎃 $i = 2, x_2 = 5$ gives $y_t = 13$

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An expression such as

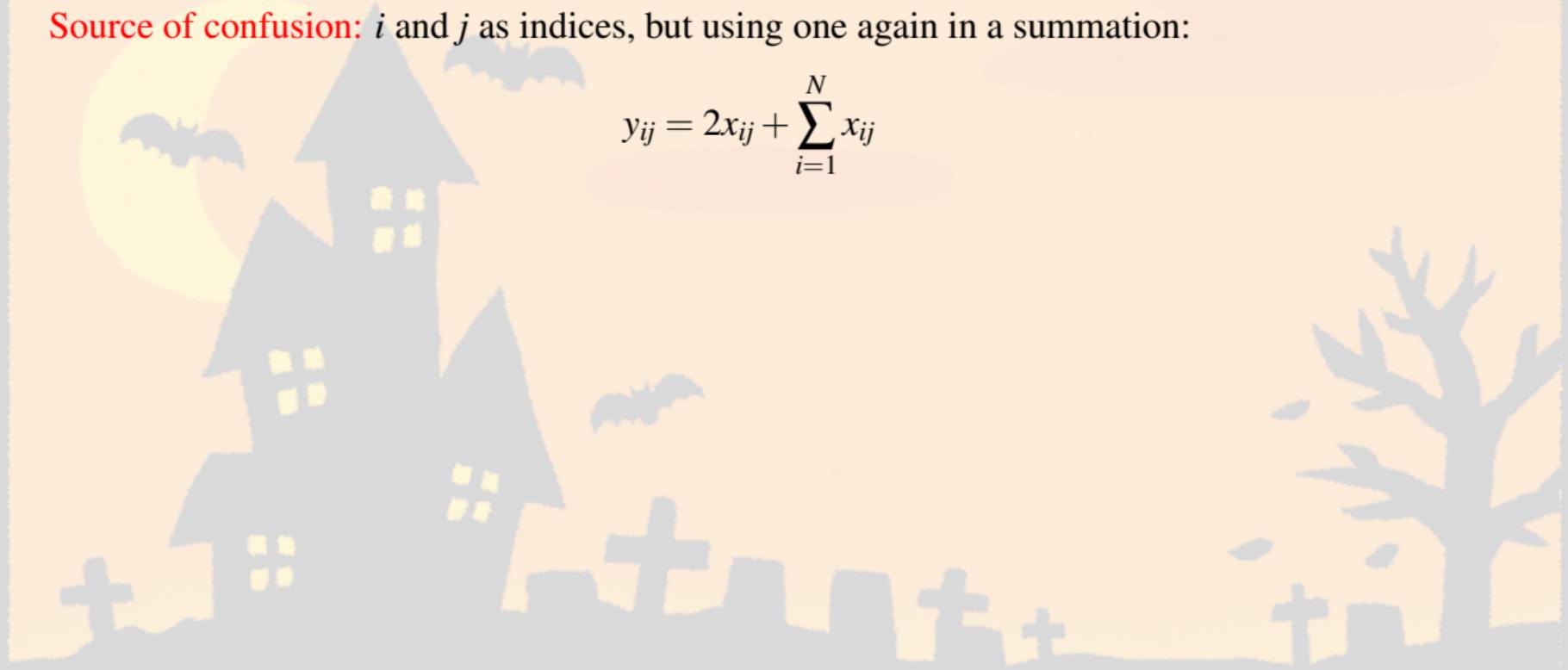
$$y_{ij} = 2x_i + 3$$

is valid.

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$$y_{ij} = 2x_{ij} + \sum_{i=1}^N x_{ij}$$



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Another way to understand:

$$\sum_{k=1}^N x_{kj} = \sum_{l=1}^N x_{lj} = \sum_{m=1}^N x_{mj}$$

since k , l and m are just dummy indices.

4. Be careful with superscripts

Superscripts can distinguish related variables:

- 🎃 X
- 🎃 X'

Though be careful – single quotes sometimes used for derivatives of functions:

- 🎃 $f'(x)$

or transpose of vectors and matrices:

- 🎃 \mathbf{X}'

but transpose can also be

- 🎃 \mathbf{X}^t
- 🎃 \mathbf{X}^T

Asterisks traditionally represent the steady state of a dynamic variable:

- 🎃 X^*

4. Be careful with superscripts

Please please please **do not use** a number or a letter (as an index) as a superscript:

🎃 B^t – biomass in year t

but this looks like B raised to the power t .

Setting $t = 2$ gives

🎃 B^2

which is interpreted as $B \times B$, not the desired biomass in year 2.

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Even worse example:

🎃 u_{at}^{sg} – exploitation rate of fish of:

🎃 sex s

🎃 age a

🎃 caught by fishing gear g

🎃 in year t

Just use subscripts and go with

🎃 u_{atsg}

like the earlier example of B_{ijkmn} .

4. Be careful with superscripts

Subscripts and superscripts should always come after the variable. Not:

🎃 jv_t

Otherwise, if θ multiplied by jv_t gives

🎃 $\theta_j v_t$

but ambiguous: is first component θ_j or θ ?

5. Helpful to distinguish variables from parameters

Example – Ricker model:

$$R = \alpha S e^{-\beta S}$$

where

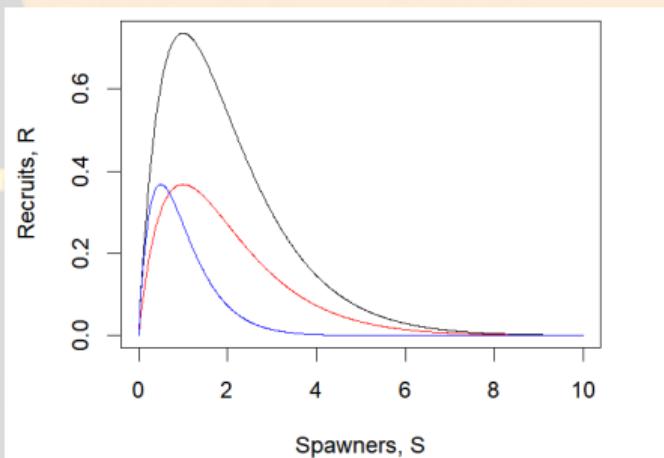
- 🎃 R – the recruitment of new fish (dependent variable on the left-hand side)
- 🎃 S – the spawning stock biomass (independent variable on the right-hand side)
- 🎃 α – maximum number of recruits produced by each unit of spawning stock biomass (parameter)
- 🎃 β – scales the intensity of density dependence (parameter).

5. Helpful to distinguish variables from parameters

$$R = \alpha S e^{-\beta S}$$

The model says how the variables R and S relate to each other.

Using particular parameter values of α and β distinguishes one realisation of the model from another:



5. Helpful to distinguish variables from parameters

Useful, if possible:

- 🎃 variables – upper case
- 🎃 parameter and constants (like gravitational constant g) – lower case and Greek letters

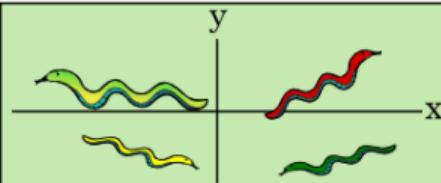
However, stick with established convention when this is not followed, or for simple equations such as

$$y = 3x + 7$$

with variables x and y (often the first choice to represent variables).

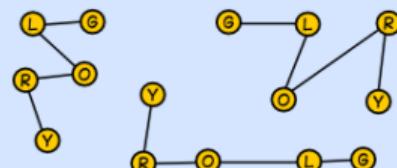
Quiz time

CAN YOU FIGURE OUT THESE MOVIE TITLES?



$$P(\text{Monday} \cap \text{Tuesday}) \\ = P(\text{Monday})P(\text{Tuesday})$$

$$\frac{1}{n} \sum_{i=1}^n \text{girl}_i$$



12.874752 km

$$\begin{bmatrix} \cos \theta & -\sin \theta \\ \sin \theta & \cos \theta \end{bmatrix}$$

6. Avoid multi-letter variable names

Use only **one letter** (rather than two or more) to represent a quantity.

Common abbreviation: SSB for spawning stock biomass.

Fine as an **acronym in a sentence**, but problematic when *SSB* used as a mathematical quantity in an equation:

- 🎃 SSB_t – spawning stock biomass in year t
- 🎃 S – selectivity (proportion of biomass caught by fishing)
- 🎃 B_t – total (spawning plus non-spawning) biomass in year t

But this breeds ambiguity:

$$\frac{SB_t}{SSB_t}$$

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But this breeds ambiguity:

$$\frac{SB_t}{SSB_t} = \frac{\$B_t}{\$SB_t} = \frac{SB_t'}{SSB_t'} \quad ?$$

Solution: pick, say, B_t and T_t for, respectively, the spawning and total biomasses at time t .

6. Avoid multi-letter variable names

Occasionally may be okay to use an acronym or word as a variable name.
Often used in simple statistical models:

$$e^{\beta_1 + \beta_2 \times \text{MeanDepth}_i}$$

which intuitively represents an exponential effect of a linear function of mean depth (β_1 and β_2 are parameters).

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Just ensure:

- 🎃 no potential for confusion (can be hard to guarantee when first defining notation)
- 🎃 equations don't become cumbersome and hard to understand

6. Avoid multi-letter variable names

One solution is to simultaneously give equations in word and notation form:

$$\frac{dN}{dt} = -\text{uptake} + \text{respiration} + Z \text{ excretion} + Z \text{ predation excretion} + \text{mixing}$$

$$\frac{dP}{dt} = \text{uptake} - \text{respiration} - \text{grazing by } Z - \text{sinking} - \text{mixing}$$

$$\frac{dZ}{dt} = \text{growth} - \text{higher predation}$$

The specific functional forms used (discussed in Section 3) are:

$$\frac{dN}{dt} = -\frac{N}{e+N} \frac{a}{b+cP} P + rP + \frac{\beta\lambda P^2}{\mu^2+P^2} Z + \gamma dZ^2 + k(N_0 - N) \quad (1)$$

$$\frac{dP}{dt} = \frac{N}{e+N} \frac{a}{b+cP} P - rP - \frac{\lambda P^2}{\mu^2+P^2} Z - (s+k)P \quad (2)$$

$$\frac{dZ}{dt} = \frac{\alpha\lambda P^2}{\mu^2+P^2} Z - dZ^2 \quad (3)$$

7. Fully define probability distributions

🎃 **Discrete** random variable – takes discrete values (e.g. 1, 2, 3, ...)

$f(x)$ – *probability mass function* of a **discrete** variable X :

$$f(x) = \text{P}(X = x)$$

where

🎃 $\text{P}(\cdot)$ – probability of occurrence of the event in parentheses (X takes the value x)

For example, Poisson distribution for count data:

$$f(x) = \frac{\lambda^x e^{-\lambda}}{x!}, \quad x = 0, 1, 2, \dots$$

where x are the possible values and there is just one parameter $\lambda > 0$.

7. Fully define probability distributions

🎃 **Continuous** random variable – can take any value within a specified range (e.g. between 0 and 10).

$f(x)$ – **continuous** probability density function, for example:

$$f(x) = \frac{1}{\sqrt{2\pi}\sigma} e^{-(\log x - \mu)^2/2\sigma^2}, \quad x > 0$$

for parameters μ and σ , and \log is **natural logarithm**.

Worth defining ‘ \log ’ and using \log_{10} for base-10 logarithm (realising \ln is also used for the natural logarithm).

7. Fully define probability distributions

Note in both examples the **domain** is specified:

$$f(x) = \frac{\lambda^x e^{-\lambda}}{x!}, \quad x = 0, 1, 2, \dots$$

$$f(x) = \frac{1}{\sqrt{2\pi}\sigma x} e^{-(\log x - \mu)^2/2\sigma^2}, \quad x > 0$$

This also helps confirm the distribution is appropriate for the question at hand.

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Normal distribution – generally no need to explicitly specify that $-\infty < x < \infty$.

7. Fully define probability distributions

For **discrete** and **continuous** distributions, can define

- 🎃 $F(x)$ – cumulative probability distribution:

discrete $F(x) = P(X \leq x) = \sum_{i=0}^x f(i)$

continuous $F(x) = P(X \leq x) = \int_{-\infty}^x f(u)du$

7. Fully define probability distributions

For a second random variable, Y , possible options are:

- 🎃 $g(y)$
- 🎃 $f_Y(y)$, and use $f_X(x)$ for X
- 🎃 $f(y)$ – does **not** work as **not distinguishable** from $f(x)$

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- 🎃 $f(y)$ – does **not** work as **not distinguishable** from $f(x)$

Some distributions have a conventional shorthand, e.g.:

- 🎃 $X \sim N(\mu, \sigma^2)$ – variable X is normally distributed with mean μ and standard deviation σ
- 🎃 $X \sim N(0, 2)$ – here specify whether the 2 is the standard deviation or the variance to avoid ambiguity
- 🎃 $X \sim \text{Gamma}(a, b)$ – Gamma distribution, but define parameters as can be parameterised using shape and either rate, scale or mean

8. Give equations of a model rather than just computer code

One reason that acronyms or words get used to identify variables may be that this is how they are written in computer code.

Words in code can make code easier to read and avoid typographical errors.

But words in equations are not recommended. Solutions:

- 🎃 write equations first and then have a comment in the corresponding code that links the words used in the code to the corresponding mathematical notation
- 🎃 **modern simpler alternative is the R package knitr**
- 🎃 knitr interweaves text and computer code in a single file, easily enabling the same succinct notation to be used throughout
- 🎃 **R**markdown now allows easy interweaving math, code, write up, references, figures etc.

8. Give equations of a model rather than just computer code

- 🎃 Writing equations may seem a necessary prerequisite to writing code
- 🎃 Some people are proficient programmers but are sometimes unable to translate the code into mathematical notation

For example, for a numeric vector x in R, the command

```
y <- cumsum(x)
```

is defined as creating a vector y where each element is the cumulative sum of the elements of x .
Equivalent math: for a vector \mathbf{x} of length n ,

$$y_i = \sum_{j=1}^i x_j, \quad i = 1, 2, 3, \dots, n.$$

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$$y_i = \sum_{j=1}^i x_j, \quad i = 1, 2, 3, \dots, n.$$

However, the verbal description is ambiguous, unlike the equation.

8. Give equations of a model rather than just computer code

The `cumsum(x)` example is usually just for book-keeping.

But for more complex code (e.g. log-likelihood functions), give the equation not the code, since:

- 🎃 code relies on reader having knowledge of that particular language
- 🎃 languages evolve and fall out of favour
- 🎃 properly documented equations will stand the test of time

Though still very useful to supply code as Supporting Information or as a package.

9. Abide by conventions (but still define everything)

Common mathematical usage of particular letters and symbols

Letter/symbol	Common usage
e	usually avoided to prevent confusion with non-italicised e (=2.718...)
f, g	function, e.g. $f(x) = x^3 + 7$
i, j, k	index, e.g. the i th element of vector \mathbf{x} is x_i
n, N	sample size
o, O	usually avoided to prevent confusion with number 0
t	time
u, v, w	speeds
x, y, z	variables, or co-ordinates in space
$P(\cdot)$	probability of occurrence of the event in parentheses
X, Y, Z	variables

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Common mathematical usage of particular letters and symbols

Letter/symbol	Common usage
$\alpha, \beta, \gamma, \theta$	parameters
δ, Δ	difference or change in a variable, ΔX , or a parameter
ε	a small value, or random noise term
μ	mean
π	the value 3.141...
\prod	product of the proceeding values
σ	standard deviation
\sum	summation of the proceeding values
X^*	steady-state value of X
\dot{X}	derivative of X
$f'(x)$	derivative of $f(x)$ with respect to x
$\partial f / \partial x$	partial derivative of $f(x, y)$ with respect to x
$\hat{\theta}$	an estimate of θ

9. Abide by conventions (but still define everything)

Compare:

1. The population size is given by

$$t_\varepsilon = g t_{\varepsilon-1} (1 - t_{\varepsilon-1}) + f_\varepsilon$$

where

- 🎃 t_ε – population in year ε ($\varepsilon = 1, 2, 3, \dots, \Gamma$)
- 🎃 g – intrinsic growth rate at low population size
- 🎃 f_ε – normally distributed random noise with mean σ and variance μ^2

9. Abide by conventions (but still define everything)

With:

2. The population size is given by

$$X_t = rX_{t-1}(1 - X_{t-1}) + \varepsilon_t$$

where

- 🎃 X_t – population in year t ($t = 1, 2, 3, \dots, T$)
- 🎃 r – intrinsic growth rate at low population size
- 🎃 ε_t – normally distributed random noise with mean μ and variance σ^2 .

9. Abide by conventions (but still define everything)

Within some fields, certain notation may be standard.

But still clearly define notation, in particular because of the multidisciplinary nature of ecology.

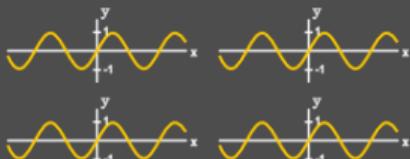
Established conventions:

- 🎃 may be best to try to retain
- 🎃 but maybe not if conventional notation was not well thought-out
- 🎃 can help when learning a new area
- 🎃 multidisciplinary work – can be hard to retain all conventions (and appease everyone)

Quiz time

CAN YOU FIGURE OUT THESE MOVIE TITLES?

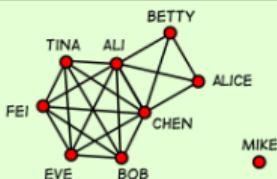
$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix}$$



$$B_{\text{fire}}(p) = \{x \in M \mid d(x, p) < \text{fire}\}$$



Fe \times Fe



10. Use parentheses and brackets only as necessary

Parentheses ()

- 🎃 around the arguments of a function, e.g. $f(x)$
- 🎃 denote which calculations in an equation need to be done first, e.g. $3(x + 5)$

To avoid too many slightly-different sized parentheses also use:

- 🎃 square brackets []
- 🎃 braces { }

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To avoid too many slightly-different sized parentheses also use:

- square brackets []
- braces { }

But don't overuse parentheses:

$$f(x) = \frac{(\lambda^x)(e^{-\lambda})}{x!}, \quad x = 0, 1, 2, \dots$$

makes the equation appear more complicated than it is.

This often happens in practice – but extra clutter can impede comprehension.

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Almost always no need to use a symbol such as \times or \cdot for multiplication, unless

- 🎃 using words as variable names
- 🎃 breaking up long equations for readability

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Parentheses also used:

- 🎃 $x \in (0, 1)$ means $0 < x < 1$
- 🎃 $x \in [0, 1]$ means $0 \leq x \leq 1$
- 🎃 $x \in [0, 1)$ means $0 \leq x < 1$

11. Equations should be part of sentences

Sometimes require punctuation:

- 🎃 maybe a comma when in middle of sentence
- 🎃 a period when completing a sentence

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Single terms in equations (or very simple equations) appear within text and not on their own line.

Fractions within such lines should be a/b not $\frac{a}{b}$.

12. Revise notation early on if necessary

- 🎃 Think about notation before defining a model
- 🎃 Can be useful to revisit notation *early on* in a project once some details are fleshed out
- 🎃 But hard to change notation once proceeded far enough, such as:
 - 🎃 two papers already published
 - 🎃 thousands of lines of computer code shared with others
 - 🎃 potentially confusing to switch notation in related works

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Similar to functionalising computer code – taking a pause and rewriting code in a more user-friendly way tends to pay off in future.

12. Revise notation early on if necessary

Related point – PROOFREAD.

Different publishers have different minor typesetting rules (that may or may not impact comprehension).

Letters should have unique definition in single piece of work.

Example of confusing notation

Highlights several problems:

$$\sigma_a^{s^2} = \left(\frac{sd_a^S}{L_a^S} \right)^2$$

where:

- 🎃 sd_a^S – standard deviation of the length of a fish of age a and sex S
- 🎃 σ_a^s – standard deviation of the distribution of $\log(\text{length})$ at age a for sex s
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- 🎃 s – sex, $s = 1$ for females and $s = 2$ for males

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Closing remarks

Hope these guidelines:

- 🎃 are useful
- 🎃 help improve future comprehension of biological models
- 🎃 help improve reproducibility

Re-iterate: these are **guidelines** but **not rules**, and should be overlooked when appropriate.

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