# Introduction to Mathematical Modelling

## Lecture 1

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# Mathematical Modelling

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- ▶ models are necessary for extracting information from large, complicated data sets;

- ▶ models that reflect underlying mechanisms can uncover information that could otherwise not be obtained from the data;

- ▶ by turning the raw data into model parameter estimates, the complexity of the data can be reduced in a meaningful way;

- ▶ model can help determine which experiment to do next: choose treatment, points to observation in time and space, etc.;

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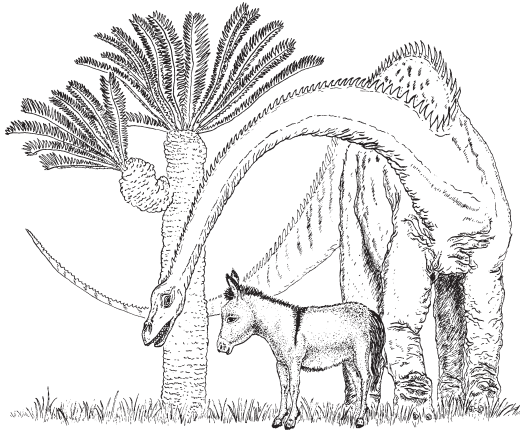
# A story about a donkey and a *Diplodocus*

the *Diplodocus* has tiny head and massive bulk, bizarre proportions as we are more used to herbivores proportioned like the donkey.

why this disparity in proportions?

a little algebra and a clever argument (i.e. a model) can help us answer this question...

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# A story about a donkey and a *Diplodocus*

$$\mathcal{N}\tau = \mathcal{T}Q \quad \text{or} \quad \mathcal{N}/\mathcal{T} = Q/\tau$$

the quantity $\mathcal{N}/\mathcal{T}$ is the average influx of particles, that is, the **ingestion rate** ($\mathcal{I}$) during the time period under consideration, which is also known as the **turnover rate** when the amount in the gut is stable at $Q$.

$$\mathcal{I} = \frac{Q}{\tau} \quad \text{or} \quad \text{turnover} = \frac{\text{standing stock}}{\text{average residence time}}$$

this result explains the mystery of the donkey and the *Diplodocus*!

# A story about a donkey and a *Diplodocus*

their heads are about the same size, and if they both graze all day, their ingestion rates $\mathcal{I}$ must be roughly similar;

according to the previous equation ($Q = \mathcal{I}\tau$), animals with the same $\mathcal{I}$ but different $\tau$ that have larger $Q$ must have larger $\tau$;

the peculiar body shape of *Diplodocus* can thus be understood if its diet of vegetable matter took a long time to digest. This gives us some hints about the potential diet of *Diplodocus*.

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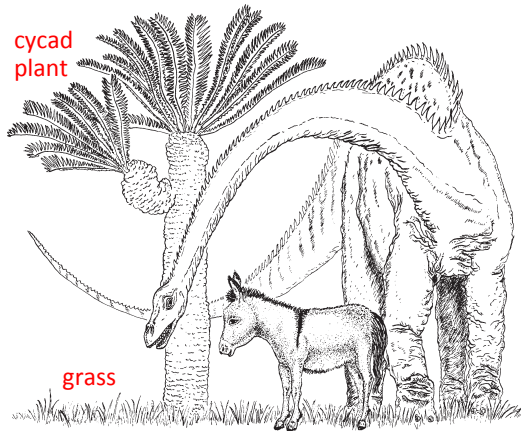


cycad plant

grass

# A story about a donkey and a *Diplodocus*

in fact, a donkey eats grass, whereas *Diplodocus* ate cycad plants, which are much tougher and much harder to digest unless they remain in the digestive system for a long time, allowing microorganisms to degrade the material;

a simple model provides some theoretical predictions about the diet and time of digestions (i.e. cycads are digested very slowly) of an extinct animal!

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NOTE: the general opinion among paleontologists was that cycads have pratically no nutritional value, making a mystery how *Diplodocus* could subsist on cycads; very recent experiments have shown that cycads yield up their nutritional value, but only after long incubation with microbes such as would have been present in the sauropod's digestive tract.

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a **mathematical model** is a description of a phenomenon by means of mathematics, with the view of capturing the salient aspects of the phenomenon at hand.

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# What is a mathematical model?

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2. the slogan *"all models are wrong"* should not obscure the fact that good models do distinguish themselves from bad ones in satisfying the **key requirements of a model**, i.e.:

   a. consistent;

   b. coherent;

   c. efficient (e.g. parsimonious, modular, general);

   d. statistically tractable.

it is not meaningful to ask if a model is *true* or *correct*, and we will refrein from using terms like *valid* or *validation* which might connote such concepts...

# Elements of a mathematical model

*parameter*    a parameter of a model is a quantity that remains constant over time;

*variable*    a variable of a model is a quantity that changes over time;

*function*    a function is a description of a process that is part of the natural phenomenon a model intends to describe, functions are defined with variables and parameters;

*dynamics*    the dynamics of a system is the pattern of change that occurs over time;

*parsimony*    according to the principle of parsimony, a simple explanation (or model) should be preferred over a complex explanation if both are equally compatible with the data.

# The problem of complexity

nature is complex, very complex...

how to deal with such complexity ?

the naïve, brute force approach would be to set up a mathematical model that is a faithful, one-to-one reflection of this complexity;

this would require using hundreds or thousands differential equations, measuring thousands of parameters, solving the equations to get numerical predictions, and then measuring these predictions against nature;

# The problem of complexity

- there are too many parameters to measure, some are vaguely defined or unknown, many would require a lifetime for their measurement;

- the equations are insoluble analytically and exceed the capacity of current best computers;

- even if analytically soluble, the result would be so complicated that it would have no meaning for us.

# The problem of complexity

it is desirable to work with manageable models which maximize **generality**, **realism**, and **precision** toward the goals of *understanding* and *predicting* nature.

but this cannot be achieved!

alternative strategies should be considered...

# Strategies for addressing complexity

1. **sacrifice generality to realism and precision;**
   this is typically the approach of many fishery biologists; this strategy involves reducing parameters to those relevant to the short-term behaviour of the organisms, make fairly accurate measurements, solve numerically on the computer, and conclude with precise, testable predictions applicable to the particular situations investigated;

# Strategies for addressing complexity

2. **sacrifice realism to generality and precision;**

   this is typically the approach of many physicists who enter population biology; this strategy involves setting up quite general equations from which precise results may be obtained; these equations are unrealistic; for example Lotka-Volterra predator-prey systems, which omit time lags, physiological states, the effect of species' population density on its own rate of increase, the environment, etc. it is hoped that natural biological systems behave like frictionless systems or perfect gases; it is expected that small deviations from realism result in small deviations in the conclusions;

# Strategies for addressing complexity

3. **sacrifice precision to realism and generality;**

   this is the approach adopted by those who are interested in qualitative rather than quantitative aspects and results (which are only important in testing hypotheses); such models are typically very flexible, often graphical, and generally assume that functions are increasing or decreasing, convex or concave, greater or less than some values, instead of specifying the mathematical form of an equation; predictions are also expressed as inequalities as between tropical and temperate species, insular *versus* continental fauna, patchy *versus* uniform environments, etc.

# Main point

models are essential for understanding reality but they should not be confused with that reality itself !

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dynamical models can also be distinguished between *discrete time* and *continuous time* models, depending on whether time is repesented in discrete steps or as continuous.

# How to construct a model

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major steps to follow when constructing a model are:

1. formulate the question;
2. determine the basic ingredients;
3. qualitatively describe the relevant system;
4. quantitatively describe the relevant system;
5. analyse the equations;
6. checks and balances;
7. relate the results back to the question.

# How to construct a model

## 1. formulate the question

coming up with a question can be more difficult that it sounds; in most biology or ecology classes, students are told what the questions are and what questions have been found; rarely are students asked to formulate scientific questions; this is unfortunate because, in any scientific research endeavour, the process begin with a question.

for example, consider the following three questions:

   a. how does the number of branches of a tree change over time?

   b. how does a cat change the number of mice in a yard?

   c. how does the number of people with the flu change over the flu season?

these are "toy" questions that we will use to illustrate the steps of modelling.

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# How to construct a model

## 2. determine the basic ingredients - variables

once you have a question in mind, think about the entities that may change over time, these are the **variables**; the number of variables depends on the question; for our toy examples we could choose: 1) the number of branches on a tree, $n(t)$, 2) the number of mice in a yard, $n(t)$, 3) the number of people with the flu, $n(t)$, and the number without the flu, $s(t)$; consider the constraints that each variable is subjected to; choose a type of dynamical model (discrete- *versus* continuous-time); choose the time scale over which changes of variables are measured; we will use "day" as the basic unit of time;

# How to construct a model

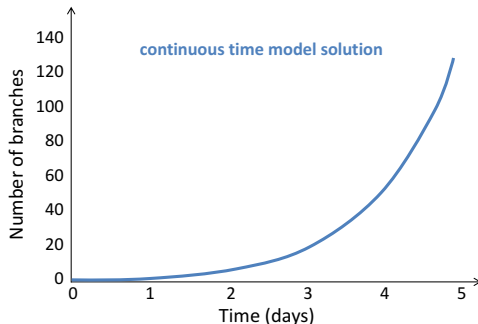## 2. determine the basic ingredients - variables

in **continuous-time** models, equations specify the rate of change of the variables over time:

$$\frac{dn(t)}{dt} = \text{"some function of } n(t) \text{"};$$

this equation is called *differential* equation; a differential equation describes the rate at which a variable changes over time.

# How to construct a model

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tree branching; a hypothetical plot of the number of branches on a tree over time produced using a continuous-time model.

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in the cited examples, the parameters would be: 1) the rate of budding for each old branch, $b$, 2) the rate of consumption of mice, $d$, and the rate of birth per mouse, $b$, 3) the rate of contact between a flu carrier and a susceptible person, $c$, and the probability of transmission of the flu between a carrier and a healthy person per contact, $a$;

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as with variables, one should figure out the constraints imposed on each parameter, including the range of parameter values that are biologically meaningful.

# How to construct a model

### 3. qualitatively describe the biological system - diagrams

before writing the equations down, it is a good idea to organise the model conceptually with aid of a *diagram*; diagrams make it easy to see whether the necessary variables and parameters are included and to write down the equations; we will see three types of diagrams or organisational techniques:

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3. table of events.

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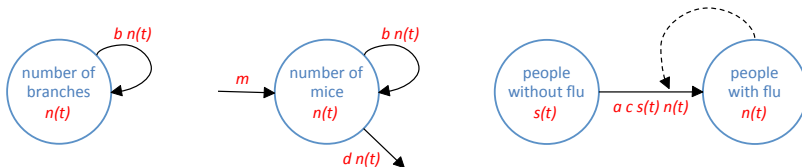
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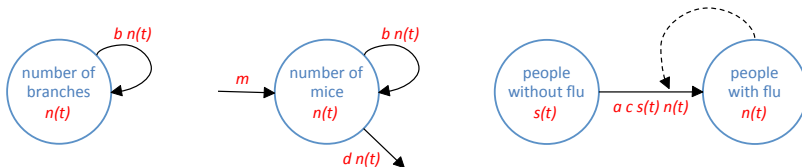


flow diagrams of the three different models considered; a *circle* represents a variable, arrows leading into a circle indicate the process that drives a variable up over time, while arrows exiting a circle indicate the process that drives the variable down over time; returning arrows (those that exit and come back to the same circle) represent variables that can generate more of itself; the arrows represent events (i.e. processes) occuring continuously over time at certain rates; the dashed arrow indicates that a variable influences the flow into another circle but does not represent a decline in the variable from which the arrow begins (e.g. a carrier of the flu does not lose the flu by passing it on).

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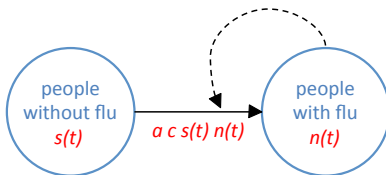


individuals with the flu interact with susceptible individuals at a rate proportional to $n(t)\,s(t)$; specifically, an infected individual has a probability $c$ of contacting any given one of the healthy individuals $s(t)$ per day, giving a total number of contacts per day of $c\,s(t)$ per infected individual; with $n(t)$ infected individuals in the population, we expect a total of $c\,n(t)\,s(t)$ contacts per day; the probability that any contact results in the trasmission of the virus is $a$; therefore, we expect a total of $a\,c\,n(t)\,s(t)$ new cases of flu per day.

# How to construct a model

### 4. quantitatively describe the biological system

at this point we are ready to derive dynamical equations for the model; conceptually, dynamical equations track all of the factors that cause a variable to increase or decrease over time and have the following general form:

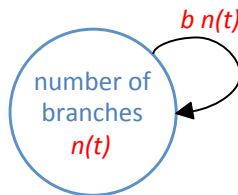$$\frac{dn(t)}{dt} = \text{rate of increase - rate of decrease}$$

the general approach is simple: we sum all the factors causing the variable to increase or decrease without worrying about the order of events within a time step, because the time step is infinitesimally small.

# How to construct a model

### 4. quantitatively describe the biological system

for the tree-branching model:

$$\frac{dn(t)}{dt} = b\,n(t)$$



$dn(t)\,/\,dt = +$ the flow rates along arrows entering the circle - the flow rates along arrows exiting the circle + the flow rates along arrows leaving and returning to the circle.

## 4. quantitatively describe the biological system

for the mouse population model:
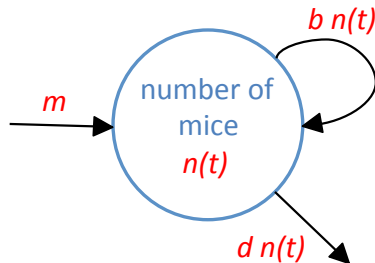
$$\frac{dn(t)}{dt} = b\,n(t) - d\,n(t) + m$$



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for the flu dynamics model:

$$\frac{dn(t)}{dt} = a\,c\,n(t)\,s(t)$$

$$\frac{ds(t)}{dt} = -a\,c\,n(t)\,s(t)$$



people
without flu
*s(t)*

*a c s(t) n(t)*
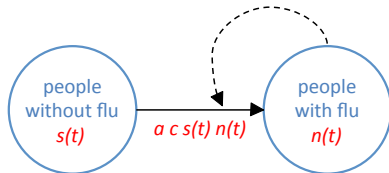
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at this point, the models are said to be *fully specified*; we know the type of model, the variables, the parameters, and the equations for describing the changes in the variables; the next step is to analyse the model;

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there are many different ways of analysing equations, several of which we will discuss in this course; these include:

- ▶ graphical analyses;
- ▶ equilibrium and stability analyses;
- ▶ deriving general solutions;
- ▶ determining long-term or asymptotic behaviours;
- ▶ analysing the model for periodic behaviour.

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another way to check results is to look at special cases where you know what should happen; for example, in the mice model, if predation and immigration are absent (i.e. $d = 0$ and $m = 0$), the equation should describe the same growth process as the tree-branching model;

# How to construct a model

## 6. checks and balances

the process of mathematical modelling is rarely smooth; rarely does the first set of equations that you write down end up being the final set; some suggestions for checking results include:

make sure that your results obey any possible constraint on the variables;

make sure that each equation has the right units or "dimensionality" - for example, if you are modelling the number of individuals in a population, the result should have the dimension of a number, not a number squared; plus the units in the right-hand side of an equation should equal the units of the left-hand side;

another way to check results is to look at special cases where you know what should happen; for example, in the mice model, if predation and immigration are absent (i.e. $d = 0$ and $m = 0$), the equation should describe the same growth process as the tree-branching model;

check if the results make sense; what did you expect to happen? do the results match your expectations?

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carry a detailed sensitivity and uncertainty analyses; the sensitivity analysis investigates how the uncertainty in the output of a mathematical model can be related to different sources of uncertainty in its inputs (e.g. the parameters); the uncertainty analysis has a greater focus on uncertainty quantification and propagation of uncertainty.

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### 7. relate the results back to the question

modelling biological processes is worthwhile only if the mathematical results are related back to biological problems;

theory is closely tied to empirical observations and tests; empirical observations suggest a theoretical model, which in turn generates an empirical test, which suggests that the model needs to be refined in particular ways; this interplay is extremely fruitful and could be driven by asking the following questions:

- ▶ how do the results alter the way scientists should think about a problem?

- ▶ what predictions can be made based on the model?

- ▶ what experiments could test these predictions?

- ▶ are there any data that can be explained or better understood in light of the model results?

# Final summary

- a mathematical model is a description of a natural phenomenon by means of mathematics;

- models are approximation of reality and should not be confused with reality itself;

- relevant components and aspects of mathematical models are parameters, variables, functions, dynamics, and the principle of parsimony;

- models are constructed by following a number of steps, which include (1) defining a question, (2) gathering the main ingredients, (3) formulate the model schematically, (4) translate the conceptual schemes into equations, (5) analyse the equations, (6) perform checks and balances, and (7) relate the results back to the original question.

# Further reading

Hugo van den Berg 2011
*Mathematical Models of Biological Systems*
Oxford University Press

Sarah P. Otto & Troy Day 2007
*A Biologist's Guide to Mathematical Modelling in Ecology and Evolution*
Princeton University Press

Richard Levins
The strategy of model building in population biology
*American Scientist*, 54(4):421–431, 1966