

Calculating Biological Quantities

CSCI 2897

Prof. Daniel Larremore

2021, Lecture 5

daniel.larremore@colorado.edu

[@danlarremore](https://twitter.com/danlarremore)

Last time on CSCI 2897..

1. How to verify that a function is a solution of an ODE. ✓
2. Solving an ODE initial value problem *numerically* by stepping along the solution. ✓
3. Logistic & Exponential Growth ✓

- ↓
- vector fields
 - long term behavior

Lecture 5 Plan

1. Finding the analytical solution to exponential growth.
2. Separation of variables (general) ✓
3. Separability (idea)
4. Finding the analytical solution to logistic growth

Exponential Growth in Continuous Time

- Let $n(t)$ be the population at time t
- Let r be the growth rate of the population
- Then our ODE is $\frac{dn}{dt} = r n$
rate of change of pop. = (const x current pop.) "is proportional to current population."
- **Separation of Variables** (SoV) is a mathematical technique we can use to solve this ODE.

$$\frac{dn}{dt} = \text{ratio of a little change in } n \text{ } dn \text{ and a little change in } t \text{ } dt$$

Separation of Variables — Exponential Growth

Goal: get all the n terms on the LHS and all the t terms on the RHS.

$$\ln n + c_3 = rt + c_2$$

$$\ln n = rt + c_4$$

$$(\ln n) = (rt + c) \leftarrow \text{rel'ship btwn } n, t$$

$$n = e^{rt+c}$$

↓ mks of exp.

$$n = e^{rt} e^c$$

$$\boxed{n = k e^{rt}}$$

$$e^{a+b} = e^a e^b$$

$$k = e^c \text{ (also a constant)}$$

$$\frac{dn}{dt} = r n$$

$$\int \frac{dn}{n} = \int r dt$$

↓

$$= \int n^{-1} dn$$

$$= \ln n + c_3$$

$$= r \int dt = r(t + c_1)$$

$$= rt + rc_1$$

$$= rt + c_2$$

Separation of Variables — Exponential Growth

Goal: get all the n terms on the LHS and all the t terms on the RHS.

$$\frac{dn}{dt} = r n \quad \rightarrow \quad n(t) = k e^{rt}$$

Followup: Verify that what we found is indeed a solution to the ODE.

$$\begin{aligned} \textcircled{1} \quad \frac{dn}{dt} &= \frac{d}{dt} n(t) = \frac{d}{dt} k e^{rt} \\ &= k \frac{d}{dt} e^{rt} \\ &= k e^{rt} r \end{aligned}$$

$$\begin{aligned} \textcircled{2} \quad \frac{dn}{dt} &= r n \\ \underline{k} \underline{e}^{rt} \underline{r} &= \underline{r} \underline{k} \underline{e}^{rt} \quad \checkmark \end{aligned}$$

Separation of Variables — General I

General Goal: get all the n terms on the LHS and all the t terms on the RHS.

$\frac{dy}{dx} = g(x)$ $\xrightarrow{\hspace{2cm}}$ $dy = g(x) dx$

\uparrow derivative

\nwarrow RHS only a function of x .

$\int dy = \int g(x) dx$

$y + c_1 = G(x) + c_2$

$y = G(x) + c$

$G(x) = \text{antideriv. of } g(x)$

Antiderivative:

$\frac{d}{dx} G(x) = g(x)$

Separation of Variables — General I

General Goal: get all the n terms on the LHS and all the t terms on the RHS.

$$\frac{dy}{dx} = g(x) \quad \rightarrow \quad y(x) = \int g(x) dx = G(x) + c$$

where $G(x)$ is the antiderivative of $g(x)$.

Followup: Verify that what we found is indeed a solution to the ODE.

$$\begin{aligned} y(x) &= G(x) + c \\ \frac{dy}{dx} &= \frac{d}{dx} (G(x) + c) \\ &= g(x) + 0 \end{aligned}$$

$\frac{dy}{dx} = g(x)$

$g(x) = g(x) \checkmark$

Separation of Variables — General II

General Goal: get all the ^y~~h~~ terms on the LHS and all the ^x~~t~~ terms on the RHS.

$$\frac{dy}{dx} = g(x) \underbrace{h(y)}_{\text{new}}$$

$$\frac{dy}{h(y)} = g(x) dx$$

$$\int \frac{1}{h(y)} dy = \int g(x) dx$$

$$\text{let } p(y) = \frac{1}{h(y)}$$

$$\int p(y) dy = G(x) + c$$

$$P(y) = G(x) + c$$

if possible, solve for y .
→ explicit solution $y = \text{RHS}$

else, implicit solution
function of $y = \text{RHS}$

Separation of Variables — Recipe

1. Get your equation into this form: $\frac{dy}{dx} = g(x) h(y)$
2. Identify $g(x)$ and $h(y)$.
3. Divide both sides by $h(y)$, *bring dx to RHS.*
4. Integrate both sides—don't forget your constant!
5. Solve for $y(x)$ if possible.

Separation of Variables — Example I

$$\frac{dy}{dx} = xy$$

① $\frac{dy}{dx} = g(x)h(y)$

② $g(x) = x$
 $h(y) = y$

③ $\xleftarrow{\text{LHS}} y = x \xrightarrow{\text{RHS}}$

$$\int \frac{dy}{y} = \int x dx$$

④ $\int = \int$

$$\ln y = \frac{x^2}{2} + c$$

⑤ solve for y

$$y = e^{x^2/2 + c}$$
$$= e^{x^2/2} e^c$$

$$y = k e^{x^2/2}$$

$$\int x^n dx = \frac{x^{n+1}}{n+1} + c$$

unless $n = -1$

$$\text{If } n = -1 \quad \int x^{-1} dx = \ln x + c$$

Separation of Variables — Example II

$$\frac{dy}{dx} = -\frac{x}{y}$$

$$\int y \, dy = -\int x \, dx$$

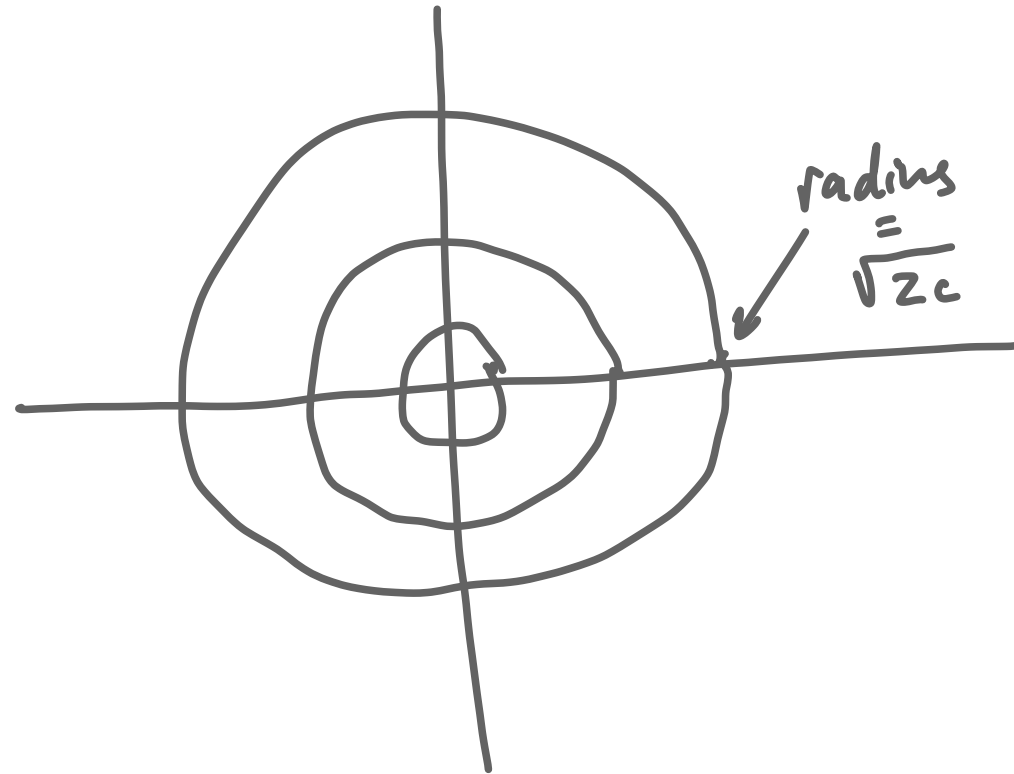
$$\frac{y^2}{2} = -\frac{x^2}{2} + c$$

$$y^2 = -x^2 + 2c$$

$$y = \pm \sqrt{2c - x^2} \quad \text{explicit sol'n.}$$

new branch

$$y^2 + x^2 = 2c \quad \leftarrow \text{circle!}$$



$$\text{let } k^2 = 2c \quad k = \sqrt{2c}$$

$$x^2 + y^2 = k^2$$

$$x^2 + y^2 = \text{radius}^2$$

centered at the origin.

$$r^2 = 2c$$
$$r = \sqrt{2c}$$

Separation of Variables — Example III

$$\frac{dy}{dx} = \sin 5x$$

$$\int dy = \int \sin 5x \, dx$$

$$y = \frac{1}{5}(-\cos 5x) + c$$

$$y = -\frac{\cos 5x}{5} + c$$

should we get $\frac{\cos 5x}{5}$ or

$$\frac{-\cos 5x}{5} ?$$

$$\frac{d}{dx} \cos 5x = -\sin 5x \cdot 5$$

(General Form 1)

Separation of Variables — Example IV

$$\frac{dy}{dx} = x + y$$

I cannot algebra this!

$$dy = (x + y) dx$$

$$\frac{dy}{dx} - y = x$$

$$\frac{dy}{y} = \frac{(x + y) dx}{y}$$

$$dy - y dx = x dx$$

damn!

$$\frac{dy}{y} = \left(1 + \frac{x}{y}\right) dx$$

damn!

Cannot separate!

Separability

$$\frac{dy}{dx} = x + y \quad \text{nope!}$$

When we can write a first-order ODE in the form $\frac{dy}{dx} = g(x) h(y)$,

we call that equation **separable**, or say that it has **separable variables**.

Q: Why do we care?

A: We can solve separable equations using SoV. But if we cannot separate the variables, well... we can't use separation of variables to solve!

Real World Examples: Separability

Suppose that you are collecting data on avian malaria among the local Chickadee population, here in nests around Boulder.

Real World Examples: Separability

Suppose that you are collecting data on avian malaria among the local Chickadee population, here in nests around Boulder. **Suddenly**, a *crazy comp bio professor* leaps out from behind a tree and *shouts at you*:

Real World Examples: Separability

$$\frac{dy}{dx} = g(x) h(y)$$

Suppose that you are collecting data on avian malaria among the local Chickadee population, here in nests around Boulder. **Suddenly**, a *crazy comp bio professor* leaps out from behind a tree and *shouts at you*: Which ODEs are separable?!???

1. $\frac{dy}{dx} = (x+1)^2$

Separable: no y on RHS. $dy = (x+1)^2 dx$ $h(y) = 1$

~~2. $\frac{dy}{dx} = (x+y)^2$~~

not separable: x and y added. $\frac{dy}{dx} = x^2 + xy + y^2 \dots$ can't write as $g(x) h(y)$

3. $\frac{dy}{dx} = y^2 e^x \ln x^y$

$$\begin{aligned} \frac{dy}{dx} &= y^2 \cdot e^x \cdot \ln x^y = y^2 \cdot e^x \cdot y \ln x \\ &= \underbrace{y^3} \cdot \underbrace{e^x \ln x} \quad \checkmark \end{aligned}$$

4. $\frac{dy}{dx} = e^{3x+2y}$

$$= e^{3x} e^{2y}$$

$g(x) \quad h(y)$

log rule!

$$a \log b = \log b^a$$

$$\log c + \log d = \log cd$$

$$\log c - \log d = \log \frac{c}{d}$$

Revisiting Logistic Growth

Recall our Logistic Growth Equation:

$$\frac{dn}{dt} = rn \left(1 - \frac{n}{K} \right)$$

Is this equation separable? *yes!*
no t on RHS!

Revisiting Logistic Growth

Partial fractions $\frac{1}{n(1-\frac{n}{K})} = \frac{1}{n} + \frac{1/K}{1-\frac{n}{K}}$

$$\frac{dn}{dt} = rn \left(1 - \frac{n}{K} \right)$$

$$\frac{dn}{n \left(1 - \frac{n}{K} \right)} = r dt$$

$$\left(\frac{1}{n} + \frac{\frac{1}{K}}{1 - \frac{n}{K}} \right) dn = r dt$$

$$\underbrace{\int \frac{1}{n} dn}_{(1)} + \underbrace{\int \frac{1/K}{1 - \frac{n}{K}} dn}_{(2)} = \underbrace{\int r dt}_{(3)}$$

$$(1) \int \frac{1}{n} dn = \ln n + c$$

$$(3) \int r dt = r \int dt = rt + c$$

$$(2) \frac{1}{K} \int \frac{1}{1 - \frac{n}{K}} dn = \int \frac{1}{K - n} dn$$

$$\begin{aligned} u &= K - n \\ du &= -dn \\ -du &= dn \\ &= -\int \frac{1}{u} du \rightarrow -\ln u + c \\ &= -\ln(K - n) + c \end{aligned}$$

Revisiting Logistic Growth

$$\frac{dn}{dt} = rn \left(1 - \frac{n}{K} \right)$$

①

②

③

$$\ln n - \ln (K - n) = rt + c$$

$$\ln \frac{n}{K - n} = rt + c$$

$$\frac{n}{K - n} = e^{rt + c}$$

$$\frac{n}{K - n} = \alpha e^{rt}$$

$$\alpha = e^c \text{ const.}$$

$$\beta = \frac{1}{\alpha} \text{ const.}$$

$$n = (K - n) \alpha e^{rt}$$

$$n = K \alpha e^{rt} - \underline{n \alpha e^{rt}}$$

$$n + n \alpha e^{rt} = K \alpha e^{rt}$$

$$n (1 + \alpha e^{rt}) = K \alpha e^{rt}$$

$$n = \frac{K \alpha e^{rt}}{1 + \alpha e^{rt}} = \frac{K}{\frac{1}{\alpha e^{rt}} + 1}$$

$$n = \frac{K}{\frac{1}{\alpha e^{rt}} + 1}$$

$$n(t) = \frac{K}{1 + \beta e^{-rt}}$$

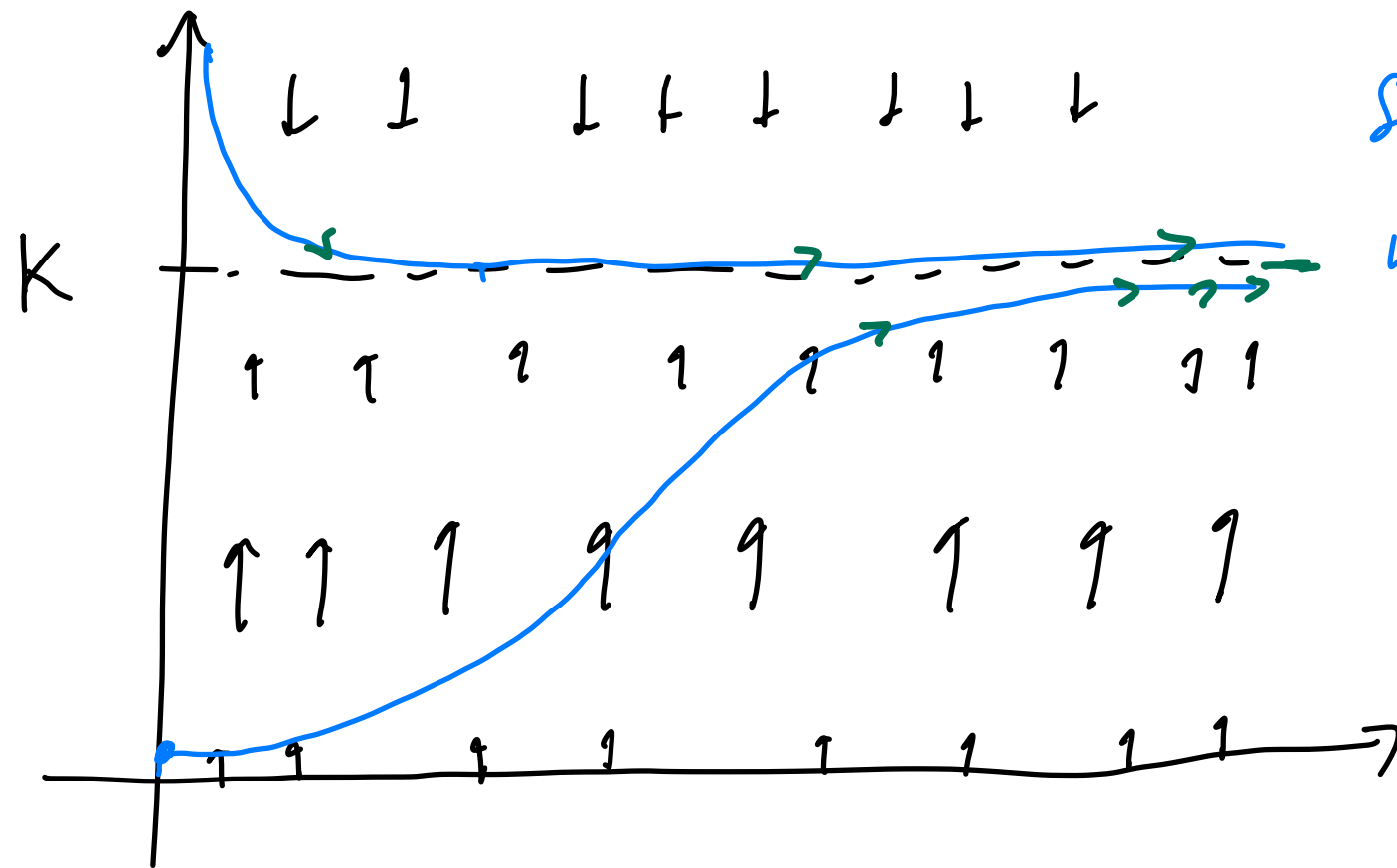
Revisiting Logistic Growth

$$\frac{dn}{dt} = r \overset{\downarrow}{n} \left(1 - \overset{\downarrow}{\frac{n}{K}} \right)$$

leads to a solution

$$n(t) = \frac{K}{1 + CKe^{-rt}} \quad n > 0$$

$$n(t) = 0 \quad \text{for } n = 0$$



see python notebook.

Revisiting Logistic Growth

$$\frac{dn}{dt} = rn \left(1 - \frac{n}{K} \right)$$

→

$$n(t) = \frac{K}{1 + CKe^{-rt}}$$

$$n(t) = \frac{K}{1 + \frac{K-n_0}{n_0} e^{-rt}}$$

K is a parameter.
"carrying capacity"

What happens when $t = 0$?

$$n(0) = \frac{K}{1 + CK \boxed{e^{-r \cdot 0}}} = \frac{K}{1 + CK}$$

$$e^0 = 1$$

constant from integration.

What happens when $t \rightarrow \infty$?

$$\lim_{t \rightarrow \infty} \frac{K}{1 + CKe^{-rt}} = \frac{K}{1 + CK \cdot 0} = K$$

$$e^{-rt} \rightarrow 0 \text{ as } t \rightarrow \infty$$

at $t=0$, we have
an initial condition of n_0

$$\Rightarrow n_0 = \frac{K}{1 + CK}$$

$$n_0 + n_0 CK = K$$

$$n_0 CK = K - n_0$$

$$C = \frac{K - n_0}{n_0 K}$$

Examples of logistic growth

- Mable & Otto (2001) — cultivated both haploid & diploid *S. cerevisiae* (yeast) in two separate flasks.
- Diploid yeast cells are *bigger* and thus take up more resources.

