Calculating Biological Quantities

CSCI 2897

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Lecture 5

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**

- discrete
- continuous

ODE → Recursion

Δt small
more and more
accurate!

Lecture 5 Plan

✓ 1. **Finding the analytical solution to exponential growth.**
✓ 2. **Separation of variables (general)**
✓ 3. "**Separability**"
? 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 n = constant r × current pop.

- **Separation of Variables** (SoV) is a mathematical technique we can use to solve this ODE.

Separation of Variables — Exponential Growth

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

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

① separate

$$dn = r\,n\,dt$$

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

② integrate both sides

Left: = Right

$$\int \frac{1}{n}\,dn \qquad \int r\,dt$$

$$= \ln n + c_1 \qquad = rt + c_2$$

c constant of integration

combined c

③ solve for n

$$\ln n + c_1 = rt + c_2$$

$$\ln n = rt + c \qquad c = c_2 - c_1$$

$e \qquad e$

$$n = e^{rt+c} = e^{rt} \cdot e^{c} \qquad k = e^{c}$$

$$\boxed{n = ke^{rt}}$$

④ solution

Separation of Variables — Exponential Growth

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

$$\frac{dn}{dt} = r\,n \qquad \rightarrow \qquad n(t) = ke^{rt} \qquad \frac{dn}{dt} = ke^{rt}\,r$$

ODE

solution

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

Plug in:

$$\underbrace{ke^{rt}\,r}_{\frac{dn}{dt}} = \underbrace{r}_{r}\,\underbrace{ke^{rt}}_{n}$$

LHS = RHS ✓

Separation of Variables — General I

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

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

RHS is only a function of x

derivative w.r.t. x

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

$$\boxed{y = G(x) + c}$$

$$\int g(x) = G(x) + c$$

antiderivative of g(x)

$g(x) = x$

$G(x) = \frac{x^2}{2}$

$g(x) = \cos(x)$

$G(x) = -\sin(x)$

Separation of Variables — General I

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

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

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

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

LHS

RHS

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

$$\frac{d}{dx}\big(G(x) + c\big) = \frac{d}{dx}\big(G(x)\big) + \cancel{\frac{d}{dx}(c)}^{\,0}$$

$$= g(x)$$

LHS

Separation of Variables — General II

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

$$\frac{dy}{dx} = g(x)\,\overbrace{h(y)}^{\text{new}}$$

$$dy = g(x)\,h(y)\,dx$$

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

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

$$\int p(y)\,dy = \int g(x)\,dx$$

$$\boxed{P(y) = G(x) + c}$$

① If possible, now solve for y.

Explicit solution $\quad y = \text{RHS}$

② Implicit solution $\quad \text{function of } y = \text{RHS}$

$$e^y = y - 1 \qquad y = 1 + e^y$$

Separation of Variables — Recipe

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

Separation of Variables — Example I

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

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

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

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

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

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

$$y = e^{\frac{x^2}{2}} \underbrace{e^{c}}_{k}$$

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

explicit solution

common mistake. $e^{\ln y} = e^{x^2/2} + e^c$

nope!

Separation of Variables — Example II

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

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

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

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

$$y = \pm\sqrt{2c - x^2}$$

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

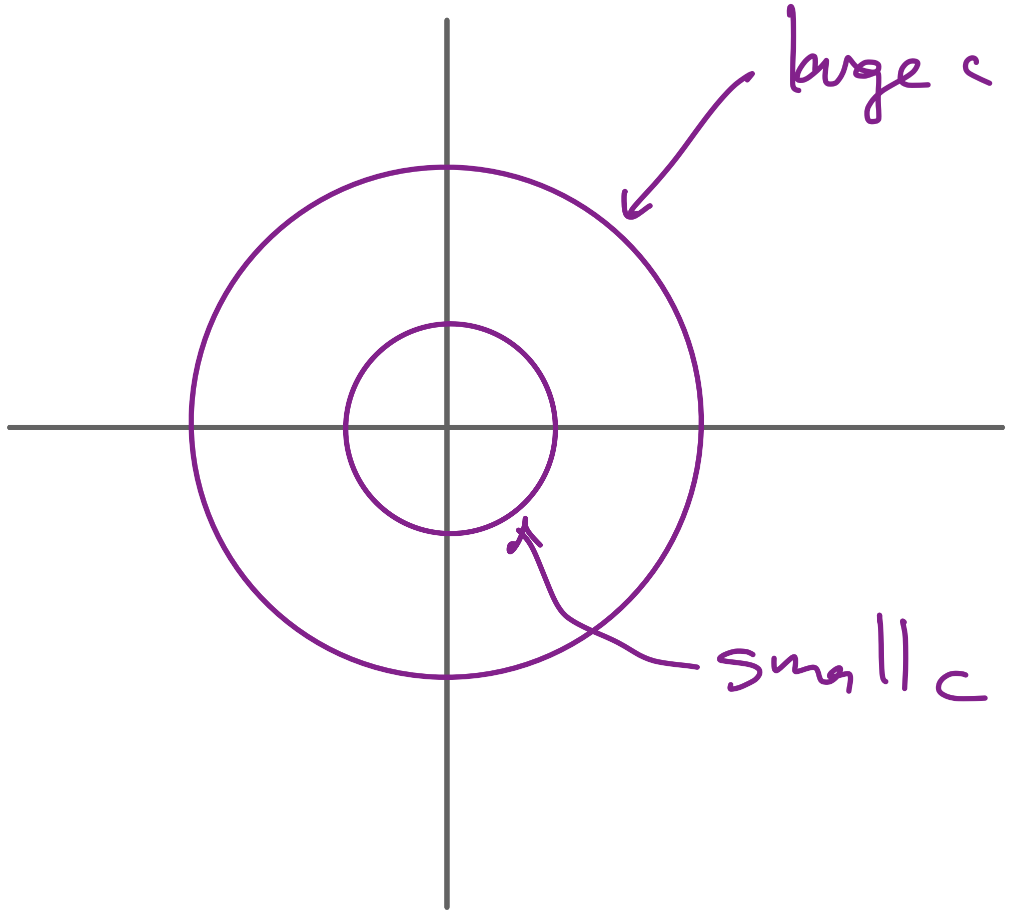
$$x^2 + y^2 = 2c$$

$$x^2 + y^2 = (\sqrt{2c})^2$$

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

$$x^2 + y^2 = r^2$$

implicit



Separation of Variables — Example III

$\cos(0) = 1$

initial value.

$$\frac{dy}{dx} = \sin 5x, \quad y(0) = 2021$$

① solve ODE by itself

② plug in initial value.

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

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

- explicit solution
- family

$y(0) = 2021$

$y = 2021$ when $x = 0$

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

$$2021 = \frac{-\cos(5 \cdot 0)}{5} + c$$

$$2021 = \frac{-1}{5} + c$$

$$c = 2021\tfrac{1}{5} = 2021.2$$

$$\boxed{y = \frac{-\cos 5x}{5} + 2021.2}$$

particular solution

Separation of Variables — Example IV

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

$dy = dx(x+y)$

$dy = x\,dx + y\,dx$

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

hmmm...

Cannot separate!

$\frac{dy}{dx} = g(x)h(y)$ does not apply

to

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

Separability

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

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.

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

$$dy = (x+1)^2\,dx$$

✗ 2. $\dfrac{dy}{dx} = (x+y)^2$

$$\frac{dy}{dx} = x^2 + 2xy + y^2$$

show can't separate

show that this isn't $g(x)\cdot h(y)$

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

$$\frac{dy}{y^2} = e^x\,dx \ln x^y = e^x\,dx \quad y\cdot\ln x$$

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

✓ 4. $\dfrac{dy}{dx} = e^{3x+2y}$

$$\frac{dy}{dx} = e^{3x}e^{2y} \quad e^{-2y}dy = \frac{dy}{e^{2y}} = e^{3x}dx$$

Revisiting Logistic Growth

Recall our Logistic Growth Equation:

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

no functions of t!

Is this equation separable? yes!

$$\frac{dn}{dt} = g(n)h(t)$$

$g(n)$: $rn\left(1-\frac{n}{K}\right)$ $\quad$ $h(t)$: 1

$g(n)$: $n\left(1-\frac{n}{K}\right)$ $\quad$ $h(t)$: r

Revisiting Logistic Growth

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

Partial Fractions

$$\frac{1}{n\left(1-\frac{n}{K}\right)} = \frac{1}{n} + \frac{1/K}{1-\frac{n}{K}}$$

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

$$\int \frac{1}{n}\,dn + \int \frac{1/K}{1-n/K}\,dn = r\int dt \quad (3) \rightarrow rt + c$$

(1) $\rightarrow \ln n$

(2)

$$\left.\begin{aligned} u &= 1 - n/K \\ du &= -\frac{1}{K}\,dn \\ -K\,du &= dn \end{aligned}\right\} \rightarrow \int \frac{1/K}{u}(-K\,du) = -\int \frac{1}{u}\,du = -\ln u = -\ln\left(1-\frac{n}{K}\right)$$

$$\boxed{\ln n - \ln\left(1-\frac{n}{K}\right) = rt + c}$$

Revisiting Logistic Growth

① $\ln a - \ln b = \ln \frac{a}{b} = -\ln \frac{b}{a}$

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

S.O.V.

$$\ln n - \ln\left(1 - \frac{n}{K}\right) = rt + c$$

solve for n

$$\ln \frac{1 - \frac{n}{K}\,(K)}{n\,(K)} = -rt - c$$

$$\ln \frac{\frac{1}{n}(K-n)}{\frac{1}{n}(Kn)} = -rt - c$$

$$e^{\ln \frac{\frac{K}{n} - 1}{K}} = e^{-rt-c}$$

$$\frac{\frac{K}{n} - 1}{K} = e^{-rt} e^{-c}$$

$$1 + \frac{K}{n} - 1 = Ke^{-c}e^{-rt} + 1$$

$$\frac{K}{n} = 1 + Ke^{-c}e^{-rt}$$

$$\frac{K}{1 + K\underbrace{e^{-c}}_{C = e^{-c}}e^{-rt}} = n$$

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

integration

Revisiting Logistic Growth

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

ODE

leads to a solution

K carrying capacity

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

solution

constant

intrinsic growth rate

① $t = 0$? initial value?

② $t \to \infty$?

long-time limit as the system evolves

(hint: vector fields.)

ended up at K.

Revisiting Logistic Growth

family of solutions

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) \quad \rightarrow \quad n(t) = \frac{K}{1 + CKe^{-rt}}$$

$\longrightarrow n(t) = \dfrac{K}{1 + \frac{1}{K}\left(\frac{K}{n_0} - 1\right)Ke^{-rt}}$

What happens when $t = 0$?

$t=0 \quad n(0) = n_0$ placeholder

$n(0) = \dfrac{K}{1 + CK\cancel{e^0}_1} = n_0$

$\dfrac{K}{n_0} = 1 + CK$

$\dfrac{K}{n_0} - 1 = CK$

$\dfrac{1}{K}\left(\dfrac{K}{n_0} - 1\right) = C$

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

particular solution

What happens when $t \rightarrow \infty$?

$\lim_{t \to \infty} n(t) = \lim_{t \to \infty} \dfrac{K}{1 + CKe^{-rt}}$

$\boxed{e^{-rt} \longrightarrow e^{-huge} = 0}$

$= \dfrac{K}{1 + CK \cdot 0} = \boxed{K}$

as time gets really large, n approaches the carrying capacity!

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.

$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) \qquad n(t) = \frac{K}{1 + CKe^{-rt}}$$