

# MSc Computational Methods in Ecology and Evolution

## Maths for Biology

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## Solvable ODEs in 1 and 2 dimensions

### Question 1 Analytical solution to logistic ODE

The following 1<sup>st</sup> order differential equation for population growth with a limited carrying capacity was studied in the lectures:

$$\frac{dx}{dt} = \nu x \left(1 - \frac{x}{K}\right),$$

where  $x(t)$  is the population size at time  $t$ ,  $\nu$  is the growth rate and  $K$ , is the carrying capacity.

- a) Use the transformation  $\tau = \nu t$  and  $z = x/K$  to simplify the ODE to

$$\frac{dz}{d\tau} = z(1 - z)$$

This process is called non-dimensionalisation and is the ODE expressed in natural dimensionless or scaled population size  $z$  and dimensionless time  $\tau$ . Why is this useful?

- b) Using separation of variables and then partial fractions find a closed-form analytical solution  $z(\tau)$  given the initial condition  $z(0) = z_0$ .
- c) Express the result in terms of the actual population size and time,  $x(t)$ : check the expression has the correct limit as  $t \rightarrow 0$ .
- d) What happens if the initial condition is  $x_0 = 0$ , or  $x_0 = K$ ? Comment on this result in relation to the fixed points of the system.
- e) Show from the analytical expression for  $x(t)$  that its limit as  $t \rightarrow \infty$  is  $x(t \rightarrow \infty) = K$ .
- f) In which limit (for what range of times and which initial conditions) does the expression  $x(t)$  become approximately exponential? What is this approximate expression?
- g) Use the full expression for population growth to show that the time  $t^*$  at which the population reaches  $\frac{K}{2}$ , in terms of  $\nu, x_0$  &  $K$  is

$$t^* = \frac{1}{\nu} \ln \left( \frac{K - x_0}{x_0} \right)$$

Comment on result for  $x_0 > K/2$ .

(Hint: It might be less messy to first consider  $z(\tau = \nu t^*) = 1/2$ , and then substitute values for  $z_0$ )

Answer:

a) LHS :  $\frac{du}{dt} = \frac{dz}{dt} \frac{du}{dz} = v \frac{du}{dz} = v \frac{d(vKz)}{dz} = vK \frac{dz}{dz}$

RHS :  $vK(1-z)$

$$\Rightarrow vK \frac{dz}{dz} = vK z(1-z) \quad \Rightarrow \frac{dz}{dz} = z(1-z)$$

b)  $\int_0^{\tau} dz' = \int_{z_0}^z \frac{dz'}{z'(1-z')}$

$$\tau = \int_{z_0}^z \frac{dz'}{z'(1-z')}$$

- re-express RHS using partial fractions:

$$\frac{A}{z} + \frac{B}{1-z} = \frac{A(1-z) + Bz}{z(1-z)} \quad \Rightarrow \text{Need } A + (B-A)z = 1$$

$$\Rightarrow A=1 \quad B=1$$

$$\Rightarrow \tau = \int_{z_0}^z dz' \left( \frac{1}{z'} + \frac{1}{1-z'} \right)$$

$$= \left[ \ln(z') \right]_{z_0}^z - \left[ \ln(1-z') \right]_{z_0}^z$$

$$= \ln\left(\frac{z}{z_0}\right) - \ln\left(\frac{1-z}{1-z_0}\right)$$

$$\tau = \ln\left(\frac{z(1-z_0)}{z_0(1-z)}\right)$$

$$\Rightarrow z_0(1-z)e^{\tau} = z(1-z_0)$$

$$\Rightarrow e^{\tau} = \frac{z(1-z_0)}{z_0(1-z)}$$

$$\Rightarrow z_0e^{\tau} = z[(1-z_0) + z_0e^{\tau}]$$

$$\Rightarrow Z(\tau) = \frac{z_0e^{\tau}}{1-z_0 + z_0e^{\tau}}$$

$$c) \quad z = x/K \quad ; \quad z_0 = x_0/K \quad ; \quad z = vt$$

$$\Rightarrow \frac{n}{K} = \frac{\left(\frac{n_0}{K}\right)e^{vt}}{\left(1 - \frac{n_0}{K}\right) + \frac{x_0}{K}e^{vt}}$$

$$= \frac{n_0 e^{vt}}{K - n_0 + x_0 e^{vt}}$$

$$\Rightarrow n(t) = \frac{x_0 K e^{vt}}{K - n_0 + x_0 e^{vt}}$$

$$\text{Check, } n(0) = \frac{n_0 K}{K - n_0 + x_0} = n_0 //$$

$$d) \quad n_0 = 0 : \quad n(t) = \frac{0}{K} = 0 \quad \forall t.$$

$$K : \quad n(t) = \frac{K^2 e^{vt}}{K - K + K e^{vt}} = K //$$

- As the initial condition is equal to the fixed points, we should find exactly this, that the solution is unchanged over time.

$$e) \quad n(t \rightarrow \infty) \approx \frac{n_0 K e^{vt}}{n_0 e^{vt}} = K$$

$$f) \quad \text{if } n_0 e^{vt} \ll K - n_0 \text{ then } n(t) \approx \frac{n_0 K}{K - n_0} e^{vt}$$

- However, this can only be satisfied  $n_0 \ll K/2$ : this can be seen easily

if we re-arrange the above by setting  $t=0$  &  $x_0 = K/2$

in the above expression,  $x_0 \ll K - x_0$

$$\frac{K}{2} \ll K/2 \quad \text{which is a contradiction}$$

$$g) \quad n(t) = \frac{x_0 K e^{rt}}{K - x_0 + x_0 e^{rt}} = \frac{K}{2}$$

$$z(t) = \frac{z_0 e^{rt}}{1 - z_0 + z_0 e^{rt}} = \frac{1}{2}$$

$$\Rightarrow z_0 e^{rt} = \frac{1}{2}(1 - z_0 + z_0 e^{rt})$$

$$z_0(1 - \frac{1}{2})e^{rt} = \frac{1}{2}(1 - z_0)$$

$$\frac{z_0}{2} e^{rt} = \frac{1}{2}(1 - z_0)$$

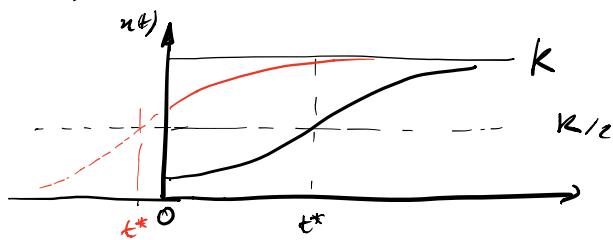
$$\Rightarrow t^* = \frac{1}{r} \ln\left(\frac{1 - z_0}{z_0}\right)$$

$$z_0 = \frac{n_0}{K}$$

$$\Rightarrow t^* = \frac{1}{r} \ln\left(\frac{1 - \frac{n_0}{K}}{\frac{n_0}{K}}\right)$$

$$= \frac{1}{r} \ln\left(\frac{K - n_0}{n_0}\right)$$

- if  $n_0 > \frac{K}{2}$  then  $K - n_0 < n_0$  & then  $t^*$  is negative, which indicates that the solution does not make sense physically/biologically, but nonetheless it is simply the result that to reach  $x_{\frac{K}{2}}$  you need to go backward in time.



**Question 2** Mutation-selection balance in deterministic population genetics

An ODE that describes both selection on a mutant allele and mutation between mutant and wild type alleles is

$$\frac{dx}{dt} = sx(1-x) + \mu(1-2x)$$

Where  $x(t)$  is the frequency of the mutant allele that has selective advantage  $s$  and  $\mu$  the mutation rate.

- a) The first term on the RHS represents selection; give an intuitive explanation for why this has the form  $x(1-x)$  (Hint: refer to the logistic equation)
- b) Explain the form for the 2<sup>nd</sup> term on the RHS, which represents mutation, in terms of the flux of mutations from wild type to mutant + flux of mutants from mutant to wild type.
- c) This ODE can't be solved analytically in this form, but we can study its fixed points. i) is  $x = 0$  a fixed point? Why not? ii) Set the LHS to zero and show the fixed points  $x^*$  are given by

$$x^* = \frac{(s - 2\mu)^2 \pm \sqrt{(s - 2\mu)^2 + 4\mu s}}{2s}$$

iii) argue that the negative sign solution is unphysical.

- d) Rearrange this solution in the following form

$$x^* = \frac{\left(1 - \frac{2\mu}{s}\right) + \sqrt{1 + \frac{4\mu^2}{s^2}}}{2}$$

- e) As this solution is only a function of  $\frac{\mu}{s}$  we can plot  $x^*$  vs  $\frac{\mu}{s}$ . Do this plot for  $0 \leq \frac{\mu}{s} \leq 10$ . What do you notice – explain your result in terms of the balance between mutation and selection.
- f) In the case that the mutant is deleterious ( $s = -s_d; s_d > 0$ ), i) why would we **not** expect the mutant to be removed? We would expect  $x \ll 1$ , and ii) show that the approximate form for the above ODE is

$$\frac{dx}{dt} = -s_d x(1-x) + \mu(1-2x) \approx -(s_d + 2\mu)x + \mu.$$

iii) What is the fixed point solution  $x^*$  for this ODE?

- g) Using the integrating factor method, show the solution to this equation, with initial condition  $x(0) = 0$ , is

$$x(t) = \frac{\mu}{s_d + 2\mu} \left(1 - e^{-(s_d + 2\mu)t}\right)$$

- h) Evaluate the limits of this solution for i)  $t \rightarrow 0$  & ii)  $t \rightarrow \infty$ . Check your answer to ii) agrees with f)ii). Your answer to i) indicates that the initial increase in frequency is independent of selection – why is this so?
- i) Typically, in evolution  $\mu \ll s_d$ . Show that the simplified solution is

$$x(t) = \frac{\mu}{s_d} (1 - e^{-s_d t})$$

and that the fixed point is  $x^* \approx \mu/s_d$ .

a) Here as we are dealing with frequencies which have a maximum value of  $x=1$  & the growth of the mutant depends on displacing the WT which have freq  $1-x$  the "effective" growth rate of an allele is  $s(1-x)$  which gives a logistic ODE  $\frac{dx}{dt} = s x(1-x)$  with carrying capacity  $K=1$ .

b)  $\mu$  is the mutation rate from WT  $\rightarrow$  mutant & mutant  $\rightarrow$  WT.

$\Rightarrow$  flux of mutations that give WT  $\rightarrow$  mutant

$$= (\text{freq WT}) \times \mu = (1-x)\mu \quad \textcircled{1}$$

$\times$  flux of mutations that give mutant  $\rightarrow$  WT

$$= (\text{freq mutant}) \times \mu = x\mu \quad \textcircled{2}$$

$\Rightarrow$  Mechanism ① increases freq of mutant  
 " " ② reduces " of mutant.

$$\begin{aligned} \Rightarrow \text{Net flux} &= \textcircled{1} - \textcircled{2} = \mu(1-x) - \mu x \\ &= \mu(1-2x) \end{aligned}$$

c)

$$\frac{dn}{dt} = sn(1-n) + \mu(1-2n).$$

i) subat  $n=0 \Rightarrow \frac{dn}{dt} = \mu \neq 0$

$\rightarrow$  this cannot be a fixed point since numbers are always converging WT  $\rightarrow$  mutant.

ii) Fixed points:  $\Rightarrow sn - sn^2 + \mu - 2\mu n = 0$ .

$$-sn^2 + (s-2\mu)n + \mu = 0.$$

$$\Rightarrow sn^2 - (s-2\mu)n - \mu = 0.$$

$$\Rightarrow n^* = \frac{(s-2\mu) \pm \sqrt{(s-2\mu)^2 + 4\mu s}}{2s} = 0.$$

(By quadratic formula)

iii) since the term under the must be greater than  $s-2\mu$   
 i.e.  $\sqrt{(s-2\mu)^2 + 4\mu s} > s-2\mu$ , this would give  $n^* < 0$ , which  
 is not possible.

d)  $n^* = \frac{(-2\mu) + (s-2\mu)\sqrt{1 + \frac{4\mu s}{(s-2\mu)^2}}}{2s}$

$$= \frac{(s-2\mu)}{2s} \left( 1 + \sqrt{1 + \frac{4\mu s}{(s-2\mu)^2}} \right)$$

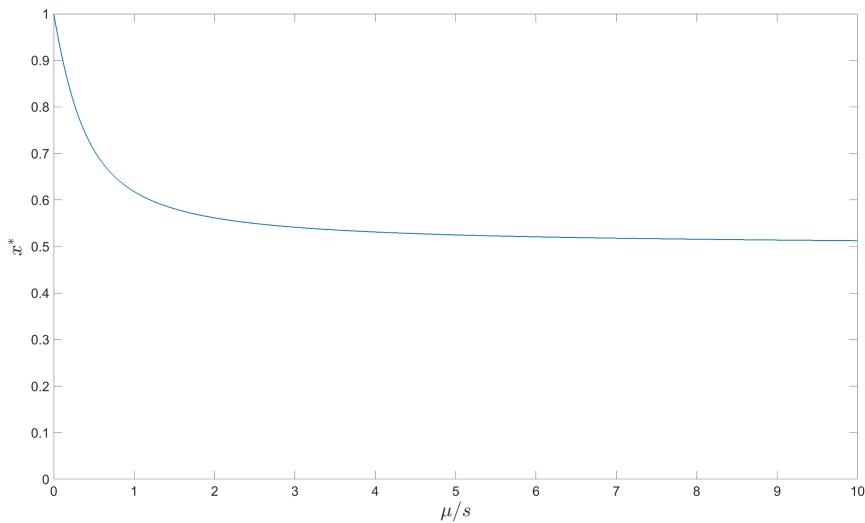
$$= \frac{1}{2} \left( 1 - \frac{2\mu}{S} \right) \left( 1 + \sqrt{1 + \frac{4\mu/s}{\left( 1 - \frac{2\mu}{S} \right)^2}} \right)$$

$$\chi^2 = \frac{(S-2\mu) \pm \sqrt{(S-2\mu)^2 + 4\mu s}}{2s} = 0.$$

$$= \frac{1}{2} \left( 1 - \frac{2\mu}{S} \right) \pm \sqrt{\left( 1 - \frac{2\mu}{S} \right)^2 + \frac{4\mu s}{S}}$$

$$\sqrt{1 - 4\mu/s + \frac{4\mu^2}{S^2} + \frac{4\mu s}{S}}$$

$$= \frac{1}{2} \left[ \left( 1 - \frac{2\mu}{S} \right) + \sqrt{1 + \frac{4\mu^2}{S^2}} \right]$$



As  $\mu/s$  increases, mutation becomes more & more important compared to selection, and this reduces the frequency of the mutant. When  $\mu/s \gg 1$  mutation completely dominates selection; the steady-state then arises when the number (or flux) of mutations  $\rightarrow$  mutant exactly balances mutant  $\rightarrow$  wild-type.

This happens when  $\mu x^* = \mu(1-x^*) \Rightarrow 2x^* = 1 \Rightarrow x^* = \frac{1}{2}$  & hence the asymptote seen in the graph.

f) i) as for the case in c) even though the mutant is deleterious there are mutations from WT  $\rightarrow$  mutant which prevent the mutant from being removed. For this reason, the mutant is maintained at small frequencies  $n \ll 1$ .

$$\begin{aligned} \text{i)} \quad \frac{dn}{dt} &= -S_d n(1-n) + \mu(1-2n) \\ &= -S_d(n - n^2) + \mu(1 - 2n) \\ &\approx -S_d n - 2\mu n + \mu \quad \text{as } n \ll 1 \Rightarrow n^2 \ll n \\ &= -(S_d + 2\mu)n + \mu \end{aligned}$$

$$\begin{aligned} \text{ii)} \quad \frac{dn}{dt} &= 0 \quad \Rightarrow \mu = (S_d + 2\mu)x^* \\ &\Rightarrow x^* = \mu / (S_d + 2\mu) \end{aligned}$$

j) Let  $\alpha = S_d + 2\mu$

$$\Rightarrow \frac{dy}{dt} + \alpha y = \mu$$

$$\frac{d}{dt}(e^{\alpha t} u) = \mu e^{\alpha t}$$

$$ne^{\alpha t} = \mu \int e^{\alpha t} dt + C$$

$$\Rightarrow n = \frac{\mu}{\alpha} + C e^{-\alpha t}$$

$$\begin{aligned} \frac{d}{dt}(e^{\alpha t} u) &= u \frac{d}{dt} e^{\alpha t} + e^{\alpha t} \frac{du}{dt} \\ &= \alpha x e^{\alpha t} + e^{\alpha t} \frac{du}{dt} \\ &= e^{\alpha t} (\alpha x + \frac{du}{dt}) \end{aligned}$$

\* Use initial condition to find const C

$$n(0) = \frac{M}{\alpha} + C = 0 \quad \Rightarrow C = -\frac{M}{\alpha}.$$

$$\begin{aligned} \Rightarrow n(t) &= \frac{M}{\alpha} (1 - e^{-\alpha t}) \\ &= \frac{M}{Sd+2\mu} \left( 1 - e^{-(Sd+2\mu)t} \right) \end{aligned}$$

ii) i)  $t \rightarrow 0$  : Taylor expansion of  $e^{-x} = 1 - x + O(x^2)$   
 $\Rightarrow e^{-(Sd+2\mu)t} \approx 1 - (Sd+2\mu)t \text{ as } t \rightarrow 0.$

$$\begin{aligned} n(t) &\approx \frac{M}{Sd+2\mu} \left( 1 - (1 - (Sd+2\mu)t) \right) \\ &= \frac{M}{Sd+2\mu} (Sd+2\mu)t \\ &= \mu t \end{aligned}$$

$\Rightarrow$  initial increase is independent of selection as  $x > 0 \Rightarrow \frac{dx}{dt} = -\alpha x + \mu$   
 $\Rightarrow \frac{dx}{dt} = \mu$   
 $\Rightarrow \int dx = \mu \int dt$   
 $\Rightarrow x = \mu t.$

$$\text{ii)} \quad t \rightarrow \infty \quad e^{-x} \rightarrow 0 \quad \Rightarrow e^{-(Sd+2\mu)t} \rightarrow 0$$

$$\Rightarrow n(t) \rightarrow \frac{M}{Sd+2\mu} = x^*$$

i) if  $\mu \ll \delta_d$ .  $\Rightarrow \alpha = \delta_d + 2\mu \approx \delta_d$ .

$$\Rightarrow n(t) = \frac{\mu}{\delta_d} (1 - e^{-\delta_d t})$$

$$n(t \rightarrow \infty) = \frac{\mu}{\delta_d} = n^*$$

**Question 3.**

The following system of linear 2D system of ODEs is given by

$$\begin{aligned}\dot{x} &= y \\ \dot{y} &= x\end{aligned}$$

Here, we will find the eigenvalues and eigenvectors of its corresponding 2x2 matrix

$$\mathbf{A} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$$

- a) Find the eigenvalues and eigenvectors of this matrix.
- b) Use these to sketch the phase-portrait for this system, indicating the fixed point and its stability.
- c) Find the solution for  $x(t)$  and  $y(t)$  for the initial condition  $x(0) = x_0 = -2$  and  $y(0) = y_0 = 1$ . Sketch this solution on the same phase-plane as  $t$  progresses from  $t = 0$  to  $t \rightarrow \infty$ .
- d) Repeat a) to c) for the linear system

$$\begin{aligned}\dot{x} &= -3x + 2y \\ \dot{y} &= -2y + x\end{aligned}$$

and indicate which are the “fast” and “slow” eigendirections on the phase plot.

$$\begin{array}{l} \dot{x} = y \\ \dot{y} = u \end{array} \Rightarrow A = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix} \quad \text{Tr } A = 0 \quad \det A = -1$$

$$\lambda = \frac{\pm\sqrt{9}}{2} = \pm 1$$

$$\lambda_1 = 1$$

$$v_1 : \begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix} \begin{pmatrix} v_{11} \\ v_{12} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$$\Rightarrow -v_{11} + v_{21} = 0 \Rightarrow v_{11} = v_{21} \Rightarrow v_1 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

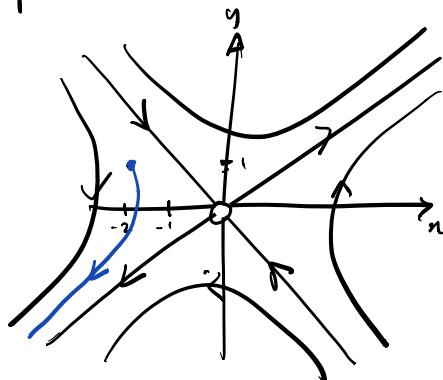
$$\lambda_2 = -1$$

$$v_2 : \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} v_{21} \\ v_{22} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$$\Rightarrow v_{12} + v_{22} = 0 \Rightarrow v_2 = \begin{pmatrix} 1 \\ -1 \end{pmatrix}$$

$$\Rightarrow \frac{d \underline{u}}{dt} = \underline{A} \underline{u}$$

$\Rightarrow$  sketch phase-portrait.



$\Rightarrow$  Find solution for  $x_0 = -2$ ;  $y_0 = 1$  & indicate approximately this solution as  $t$  progresses from  $0 \rightarrow \infty$

$$\underline{x}(t) = c_1 \underline{v}_1 e^{\lambda_1 t} + c_2 \underline{v}_2 e^{\lambda_2 t}$$

$$\Rightarrow \begin{pmatrix} x \\ y \end{pmatrix} = c_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} e^t + c_2 \begin{pmatrix} 1 \\ -1 \end{pmatrix} e^{-t}$$

$$\begin{pmatrix} x(0) \\ y(0) \end{pmatrix} = c_1 \begin{pmatrix} 1 \\ 1 \end{pmatrix} + c_2 \begin{pmatrix} 1 \\ -1 \end{pmatrix} = \begin{pmatrix} -2 \\ 1 \end{pmatrix}$$

$$\Rightarrow c_1 + c_2 = -2$$

$$c_1 - c_2 = 1 \quad \Rightarrow c_1 = 1 + c_2$$

$$\Rightarrow 1 + 2c_2 = -2 \Rightarrow c_2 = \frac{1}{2}(-3) = -\frac{3}{2}$$

$$\Rightarrow c_1 = -\frac{1}{2}$$

$$\Rightarrow \begin{pmatrix} x \\ y \end{pmatrix} = -\frac{1}{2} \begin{pmatrix} 1 \\ 1 \end{pmatrix} e^t + -\frac{3}{2} \begin{pmatrix} 1 \\ -1 \end{pmatrix} e^{-t}$$

$$\begin{pmatrix} x(0) \\ y(0) \end{pmatrix} = -\frac{1}{2} \begin{pmatrix} 1 \\ 1 \end{pmatrix} - \frac{3}{2} \begin{pmatrix} 1 \\ -1 \end{pmatrix} = \begin{pmatrix} -2 \\ 1 \end{pmatrix} //$$

Repeat for  $\dot{x} = -3x + 2y$   
 $\dot{y} = -2y + x$

$$\Gamma \quad A = \begin{pmatrix} 3 & 2 \\ 1 & -2 \end{pmatrix} \quad \text{Tr}A = -5 \quad \det A = 6 - 2 = 4$$

$$\lambda = \frac{-5 \pm \sqrt{25-16}}{2} = \frac{-5 \pm 3}{2}$$

$$= -4, -1$$

$$\underline{v}_1 = \begin{pmatrix} -3+9 & 2 \\ 1 & -2+4 \end{pmatrix} \begin{pmatrix} v_{11} \\ v_{21} \end{pmatrix} = \begin{pmatrix} 0 \\ 2 \end{pmatrix}$$

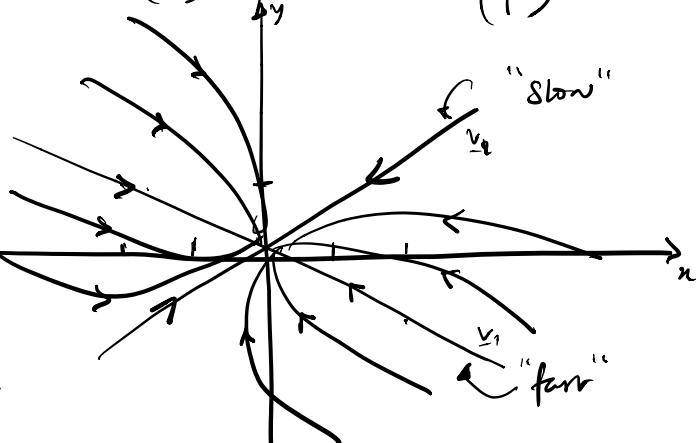
$$\Rightarrow \begin{pmatrix} 1 & 2 \\ 1 & 2 \end{pmatrix} \begin{pmatrix} v_{11} \\ v_{21} \end{pmatrix} = \begin{pmatrix} 0 \\ 2 \end{pmatrix}$$

$$\Rightarrow v_{11} + 2v_{21} = 0 \Rightarrow \frac{v_{11}}{v_{21}} = -2 \Rightarrow \underline{v}_1 = \begin{pmatrix} -2 \\ 1 \end{pmatrix}$$

$$\underline{v}_2 = \begin{pmatrix} -2 & 2 \\ 1 & -1 \end{pmatrix} \begin{pmatrix} v_{12} \\ v_{22} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \cancel{\text{X}}$$

$$\Rightarrow 2v_{12} - 2v_{22} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} = \underline{v}_2 = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

\* Both eigenvalues are  
 -ve  $\Rightarrow$  stable  
 curves decay to  
 origin &  
 arrows are inwards.



**Question 4.**

Consider the following linear 2D system of ODEs:

$$\begin{aligned}\dot{x} &= -y \\ \dot{y} &= x\end{aligned}$$

The matrix representation gives rise to the following 2x2 matrix:

$$\mathbf{A} = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$$

- a) Show that the eigenvalues of  $\mathbf{A}$  are given by  $\lambda = \pm i$ .
- b) Sketch the phase-portrait.
- c) The imaginary eigenvalues indicate the nature of  $\mathbf{A}$  is to rotate vectors and so we cannot define eigenvectors in the conventional sense – we can have complex eigenvectors, but we cannot associate it with a fixed direction on a 2D plane. However, this rotational nature suggests the solution:

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

where you should recognise the familiar rotation matrix. Verify that this indeed is the solution for the initial condition  $x(0) = x_0$  and  $y(0) = y_0$ , by separately calculating  $\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix}$  and  $\mathbf{A}\underline{x}$  and showing them to be equal.

- d) Without calculation what would the dynamics for the following matrix look like

$$\mathbf{B} = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}$$

Give your reasoning. (Hint: this matrix is effectively like swapping the  $x$  and  $y$ -axis and then relabelling them, so in which case what would happen to an anti-clockwise rotation, which occurs with  $\mathbf{A}$ ).

$$\begin{matrix} \dot{x} = -y \\ \dot{y} = x \end{matrix} \Rightarrow A = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$$

a)  $\Rightarrow \text{Tr } A = 0 ; \det A = 0 - - 1 = 1$

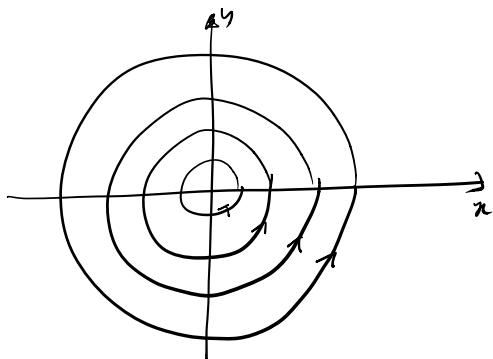
$$\Rightarrow \lambda = \frac{\text{Tr } A \pm \sqrt{\text{Tr } A - 4 \det A}}{2}$$

$$= \frac{0 \pm \sqrt{-4}}{2}$$

$$= \pm \frac{\sqrt{4}}{2} i$$

$$= \pm i$$

- b) The pure imaginary eigenvalues indicate rotation  
 $\Rightarrow$  the type of phase portrait is a neutral centre with  
 a rotation anti-clockwise.



$\rightarrow$  how do we know it is anti-clockwise?

$\rightarrow$  Examine the action of the matrix  $A = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$  if rotates vectors anti-clockwise.

$$c) \quad \begin{aligned} \dot{x} &= -y \\ \dot{y} &= x \end{aligned} \Rightarrow \begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

$\rightarrow$  Want to show the solution given in the question on LHS equals RHS.

$$\text{LHS: } \begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} = \begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \frac{d}{dt} \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$\rightarrow$  We could multiply components out, but there is no need, as the matrix  $A$  is the only part that has a time-dependence, as so we can differentiate each element.

$$\Rightarrow \frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \frac{1}{t} \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$= \begin{pmatrix} -\sin t & -\cos t \\ \cos t & -\sin t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

RHS

$$\begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$= \begin{pmatrix} -\sin t & -\cos t \\ \cos t & -\sin t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

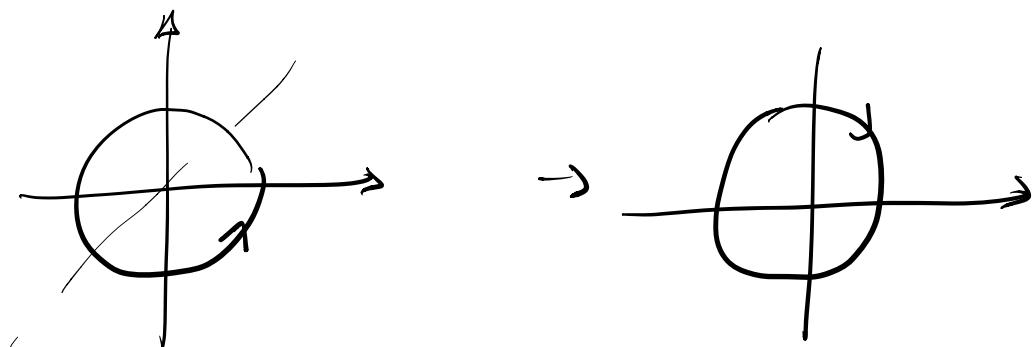
$$\Rightarrow \text{LHS} = \text{RHS} //$$

d) The matrix  $\underline{\underline{B}} = \begin{pmatrix} 0 & 1 \\ -1 & 0 \end{pmatrix}$  corresponds to the pair of ODEs.

$$\frac{du}{dt} = g$$

$$\frac{dy}{dt} = -u$$

→ This is essentially the same eqs as for  $\underline{\underline{A}}$  but  $x \rightarrow y$  &  $y \rightarrow x$   
 → the phase-portrait for  $\underline{\underline{B}}$  can be obtained by reflecting the phase-portrait  
 for  $\underline{\underline{A}}$  about the main diagonal.



\* Alternatively by examining the action of  $\underline{\underline{B}}$  on vectors we can see it rotates them clockwise.

### Question 5.

Consider the following linear 2D system of ODEs:

$$\begin{aligned}\dot{x} &= -x - y \\ \dot{y} &= x - y\end{aligned}$$

Which we studied in the lectures. The matrix representation gives rise to the following 2x2 matrix:

$$\mathbf{A} = \begin{pmatrix} -1 & -1 \\ 1 & -1 \end{pmatrix}$$

- a)** Show that the eigenvalues of  $\mathbf{A}$  are given by  $\lambda = -1 \pm i$ .
- b)** What is the real part of the eigenvalue and what does it indicate about the dynamics?
- c)** What does the presence of an imaginary part indicate?
- d)** Sketch the phase portrait.
- e)** The solution to this as shown in the lectures is

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = e^{-t} \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

where you should recognise the familiar rotation matrix. Verify that this indeed is the solution for the initial condition  $x(0) = x_0$  and  $y(0) = y_0$ , by separately calculating  $\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix}$  and  $\mathbf{A}\underline{x}$  and showing them to be equal.

- f)** If the matrix is now

$$\mathbf{B} = \begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix}$$

Without calculation can you predict what the dynamics of this matrix look like? Give your reasoning and sketch the phase portrait. Confirm that the real part of the eigenvalues of this matrix are positive ( $\text{Re}(\lambda) > 0$ ).

$$a) \quad \underline{\underline{A}} = \begin{pmatrix} -1 & -1 \\ 1 & -1 \end{pmatrix} \quad \text{Tr}(\underline{\underline{A}}) = -2$$

$$|\underline{\underline{A}}| = 1 - -1 = 2$$

$$\Rightarrow \lambda = \frac{-2 \pm \sqrt{4 - 4 \times 2}}{2} = -1 \pm \frac{\sqrt{-4}}{2}$$

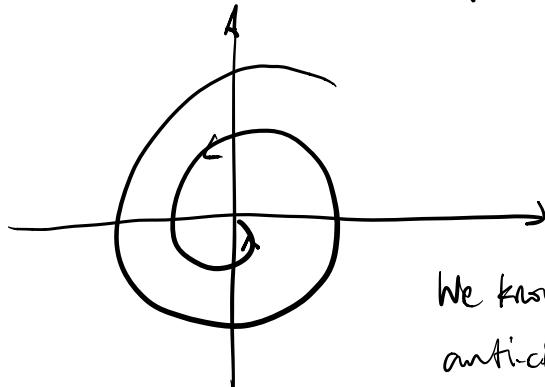
$$= -1 \pm \frac{2i}{2} \quad i = \sqrt{-1}$$

$$= -1 \pm i$$

- b) The Real part of the eigenvalue  $\text{Re}(\lambda)$  indicates whether trajectories are stable or not  
 $\Rightarrow$  Here  $\text{Re}(\lambda) < 0 \Rightarrow$  trajectories are stable & solutions tend to  $x=0, y=0$  for  $t \rightarrow \infty$

c) The presence of an imaginary part to the eigenvalues induces rotational/oscillatory motion.

d) We have a stable spiral, which is rotatory anti-clockwise.



Why anti-clockwise?

$$\underline{\underline{A}} = \begin{pmatrix} -1 & 0 \\ 0 & -1 \end{pmatrix} + \begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$$

We know matrix  $\begin{pmatrix} 0 & -1 \\ 1 & 0 \end{pmatrix}$  represents rotation anti-clockwise so we expect the spirals will be anti-clockwise also.

$$e) \begin{pmatrix} n(t) \\ y(t) \end{pmatrix} = e^{-t} \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$= \begin{pmatrix} e^{-t} \cos t & -e^{-t} \sin t \\ e^{-t} \sin t & e^{-t} \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$\Rightarrow \frac{d}{dt} \begin{pmatrix} n(t) \\ y(t) \end{pmatrix} = \begin{pmatrix} \frac{d}{dt}(e^{-t} \cos t) & -\frac{d}{dt}(e^{-t} \sin t) \\ \frac{d}{dt}(e^{-t} \sin t) & \frac{d}{dt}(e^{-t} \cos t) \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$\begin{aligned} \frac{d}{dt}(e^{-t} \cos t) &= \cos t (-e^{-t}) + e^{-t} (-\sin t) \\ &= -e^{-t} (\sin t + \cos t) \end{aligned}$$

$$\begin{aligned} \frac{d}{dt}(e^{-t} \sin t) &= \sin t (-e^{-t}) + e^{-t} \cos t \\ &= e^{-t} (\cos t - \sin t) \end{aligned}$$

$$\Rightarrow \frac{d}{dt} \begin{pmatrix} n \\ y \end{pmatrix} = \begin{pmatrix} -e^{-t}(\sin t + \cos t) & -e^{-t}(\cos t - \sin t) \\ e^{-t}(\cos t - \sin t) & -e^{-t}(\sin t + \cos t) \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$= -e^{-t} \begin{pmatrix} \sin t + \cos t & \cos t - \sin t \\ \sin t - \cos t & \sin t + \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$\underline{A} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} -1 & -1 \\ 1 & -1 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

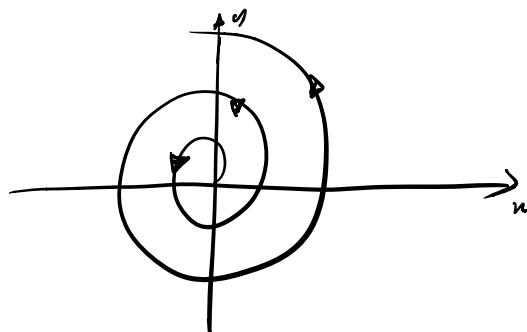
$$= e^{-t} \begin{pmatrix} -1 & -1 \\ 1 & -1 \end{pmatrix} \begin{pmatrix} \cos t & -\sin t \\ \sin t & \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$= e^{-t} \begin{pmatrix} -\cos t - \sin t & \sin t - \cos t \\ \cos t - \sin t & -\sin t - \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix}$$

$$= -e^{-t} \begin{pmatrix} \sin t + \cos t & \cos t - \sin t \\ \sin t - \cos t & \sin t + \cos t \end{pmatrix} \begin{pmatrix} x_0 \\ y_0 \end{pmatrix} //$$

f)  $\underline{B} = \begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix}$  compared to  $\underline{A} = \begin{pmatrix} -1 & -1 \\ 1 & -1 \end{pmatrix}$

1. The diagonal elements are now positive instead of negative which suggests growth instead of decay
2. The off-diagonal elements are still  $(1, -1)$ , which is related to rotation  
→ expect an unstable (spiral) spiral



$$\underline{\underline{B}} = \begin{pmatrix} 1 & -1 \\ 1 & 1 \end{pmatrix} \quad \text{Tr}(\underline{\underline{B}}) = 2 \quad |\underline{\underline{B}}| = 2 \quad \Rightarrow \lambda = \frac{\text{Tr}(\underline{\underline{B}}) \pm \sqrt{\text{Tr}(\underline{\underline{B}})^2 - 4|\underline{\underline{B}}|}}{2}$$

$$= \frac{2 \pm \sqrt{4-8}}{2}$$

$$= 1 \pm i$$

$\Rightarrow \text{Re}(\lambda) > 0$  and the spiral is unstable. //

## Integration Practice

Integrate the following by finding the appropriate substitution

a)  $\int 2x\sqrt{x^2 + 1} dx$ ; b)  $\int 3x^2\sqrt{x^3 + 1} dx$ ; c)  $\int ax^{\alpha-1}(bx^\alpha + c)^\beta dx$ ; d)  $\int x \cos(x^2 + 3) dx$

e)  $\int_0^\infty xe^{-x^2} dx$ ; f)  $\int_0^\infty x^2 e^{-x^3} dx$ ; g)  $\int \frac{x+2}{x^2+4x} dx$ ; h)  $\int_0^{\pi/2} \frac{\cos x}{1+\sin^2 x} dx$  (Hint:  $\frac{d \tan^{-1}(x)}{dx} = \frac{1}{1+x^2}$ )

What is the general rule that allows integration by substitution to work? Why can't we integrate  $\int 2x^2\sqrt{x^2 + 1} dx$  this way?

Integrate by parts the following integral

i)  $\int xe^{-x} dx$ ; j)  $\int x \ln x dx$ ; k)  $\int \ln x dx$  (Hint:  $\ln x = 1 \times \ln x$ ); l)  $\int \cos^2 x dx$ ; m)  $\int e^{-x} \cos x dx$

Integrate the following using partial fractions

n)  $\int \frac{dx}{x(1-x)}$ ; o)  $\int \frac{dx}{x(1-x)(x+1)}$ ; p)  $\int \frac{xdx}{(x+1)^2}$

$$\begin{aligned} a) \int 2x\sqrt{x^2+1} dx ; u &= x^2+1 \quad du = 2x dx \quad | \quad b) \int 3x^2\sqrt{x^3+1} dx ; u &= x^3+1 \Rightarrow du = 3x^2 dx \\ &\Rightarrow = \int \sqrt{u} du = \frac{2}{3}u^{3/2} + C &= \int \sqrt{u} du = \frac{2}{3}u^{3/2} + C \\ &= \frac{2}{3}(x^2+1)^{3/2} + C &= \frac{2}{3}(x^3+1)^{3/2} + C \end{aligned}$$

$$c) \int a x^{\alpha-1} (bx^\alpha + c)^\beta dx ; u = bx^\alpha + c$$

$$du = \alpha b x^{\alpha-1} dx$$

$$= \frac{a}{\alpha b} \int u^\beta du = \frac{a}{\alpha b} \frac{1}{\beta+1} u^{\beta+1} = \frac{a}{\alpha b(\beta+1)} (bx^\alpha + c)^{\beta+1}$$

$$d) \int x \cos(x^2+3) dx ; u = x^2+3 \Rightarrow du = 2x dx$$

$$= \frac{1}{2} \int \cos u du = \frac{1}{2} \sin u + C$$

$$= \frac{1}{2} \sin(x^2+3)$$

$$e) \int_0^{\infty} x e^{-x^2} dx ; u = x^2 \quad du = 2x$$

$$\begin{aligned} &= \frac{1}{2} \int_0^{\infty} e^{-u} du = -\frac{1}{2} [e^{-u}]_0^{\infty} \\ &= -\frac{1}{2} [e^{-\infty} - 1] \\ &= 1/2 \end{aligned}$$

$$f) \int_0^{\infty} x^2 e^{-x^3} dx ; u = x^3 \quad du = 3x^2 dx$$

$$= \frac{1}{3} \int_0^{\infty} e^{-u} du = \frac{1}{3}$$

$$g) \int \frac{x+2}{x^2+4x} dx ; u = x^2+4x ; du = (2x+4)dx = 2(x+2)dx$$

$$\begin{aligned} &= \frac{1}{2} \int \frac{du}{u} = \frac{1}{2} \ln|u| + C \\ &= \frac{1}{2} \ln|x^2+4x| + C \end{aligned}$$

$$h) \int_0^{\pi/2} \frac{\cos u}{1+\sin^2 u} du ; u = \sin x ; du = \cos x dx$$

\* Also need to change limits due to substitution

$$\rightarrow \text{Upper limit } u_+ = \sin x_+ = \sin(\pi/2) = 1.$$

$$\text{Lower limit } u_- = \sin x_- = \sin(0) = 0.$$

$$\Rightarrow \int_0^{\pi/2} \frac{\cos u du}{1+\sin^2 u} = \int_0^1 \frac{du}{1+u^2}$$

$$\star \text{ Now from Q6 b) we know } \frac{d \tan^{-1} u}{du} = \frac{1}{1+u^2} \Rightarrow \int \frac{du}{1+u^2} = \tan^{-1} u + C$$

$$\begin{aligned} \Rightarrow \int_0^{\pi/2} \frac{\cos u \, du}{1 + \sin^2 u} &= \int_0^1 \frac{du}{1 + u^2} = [\tan^{-1} u]_0^1 \\ &= \tan^{-1}(1) - \tan^{-1}(0) \\ &= \pi/4 \end{aligned}$$

\* The general rule is that if the integral is of the form

$$I = \int f'(u) g(f(u)) \, du$$

then choose substitution  $u = f(x)$ , where  $du = f'(x)dx$

$$\Rightarrow I = \int g(u) \, du$$

\* By parts:

$$\begin{aligned} i) \quad \int u e^{-x} \, du ; \text{ choose } u = u \times \frac{du}{du} = e^{-x} \\ \Rightarrow \frac{du}{du} = 1 \times v = -e^{-x} \end{aligned}$$

$$\begin{aligned} \Rightarrow \int u e^{-x} \, du &= uv - \int (v \frac{du}{du}) \, du \\ &= -ue^{-x} - \int (-e^{-x} \times 1) \, du \\ &= -ue^{-x} - e^{-x} \\ &= -e^{-x}(1+u) + C \end{aligned}$$

j)  $\int x \ln x dx$ ; Don't know what integral of  $\ln x$  is (yet!).

$\Delta$  choose

$$u = \ln x \quad \frac{du}{dx} = x$$

$$\cancel{\frac{du}{dx}} = \frac{1}{x} \quad v = \frac{1}{2}x^2$$

$$\begin{aligned} \Rightarrow \int x \ln x dx &= \frac{1}{2}x^2 \ln x - \int \frac{1}{2}x^2 \times \frac{1}{x} dx \\ &= \frac{1}{2}x^2 \ln x - \frac{1}{2} \int x dx \\ &= \frac{1}{2}x^2 \ln x - \frac{1}{4}x^2 \\ &= \frac{1}{2}x^2(\ln x - 1/2) + C \end{aligned}$$

k)  $\int \ln x dx = \int 1 \times \ln(x) dx \Rightarrow u = \ln x \quad \frac{du}{dx} = 1$

$$\frac{du}{dx} = \frac{1}{x} \quad v = x$$

$$\begin{aligned} \Rightarrow \int \ln x dx &= x \ln x - \int 1 dx \\ &= x \ln x - x + C \end{aligned}$$

l)  $\int \cos^2(u) du$ ;  $u = \cos x \quad \frac{du}{dx} = \cos x.$

$$\frac{du}{dx} = -\sin x \quad v = \sin x.$$

$$\begin{aligned} \Rightarrow \int \cos^2 u du &= \sin u \cos x + \int \sin^2(u) du. \\ &= \sin u \cos x + \int (1 - \cos^2(u)) du. \\ &= \sin u \cos x + u - \int \cos^2(u) du. \end{aligned}$$

$$\Rightarrow 2 \int \cos^2(u) du = \sin u \cos x + u,$$

$$\Rightarrow \int \cos^2(u) du = \frac{1}{2}(\sin u \cos x + u) + C \quad (= \frac{x}{2} + \frac{1}{4}\sin(2x))$$

$$m) \int e^{-x} \cos x \, dx ; \quad u = e^{-x} \quad \frac{du}{dx} = -e^{-x} \\ \frac{du}{dx} = -e^{-x} \quad v = \sin x.$$

$$\Rightarrow \int e^{-x} \cos x \, dx = e^{-x} \sin x + \int e^{-x} \sin x \, dx \quad ①$$

\* Do another round & by parts:

$$\int e^{-x} \sin x \, dx ; \quad u = e^{-x} \quad \frac{du}{dx} = -e^{-x} \\ \frac{du}{dx} = -e^{-x} \quad v = -\cos x$$

$$\Rightarrow \int e^{-x} \sin x \, dx = -e^{-x} \cos x - \int e^{-x} \cos x \, dx \quad ②.$$

Plugging ② back into ①

$$\int e^{-x} \cos x \, dx = e^{-x} \sin x - e^{-x} \cos x - \int e^{-x} \cos x \, dx,$$

$$\Rightarrow 2 \int e^{-x} \cos x \, dx = e^{-x} (\sin x - \cos x)$$

$$\Rightarrow \int e^{-x} \cos x \, dx = \frac{1}{2} e^{-x} (\sin x - \cos x) + C$$

\* Partial fractions:

$$n) \int \frac{dx}{x(1-x)} ; \text{ We know we can arrange integrand as}$$

$$\frac{1}{x(1-x)} = \frac{A}{x} + \frac{B}{1-x}$$

$\rightarrow$  Need to find A & B to satisfy this:

$$\Rightarrow \frac{A}{n} + \frac{B}{1-n} = \frac{A(1-n) + Bn}{n(1-n)} = \frac{A + (B-A)n}{n(1-n)}$$

$$\Rightarrow A + (B-A)n = 1$$

$\Rightarrow$  there are no  $n$  terms on RHS  $\Rightarrow B-A=0$  or  $A=B$ .

& the constant term  $A=1$ .

$$\Rightarrow A=B=1$$

$$\Rightarrow \int \frac{du}{u(1-u)} = \int du \left( \frac{1}{u} + \frac{1}{1-u} \right)$$

$$= \ln|u| - \ln(1-u) + C$$

$$\textcircled{o}) \quad \int \frac{du}{u(1-u)(1+u)} \Rightarrow \frac{A}{u} + \frac{B}{1-u} + \frac{C}{1+u}$$

$$\Rightarrow A(1-u)(1+u) + B u(1+u) + C u(1-u) = 1$$

$$\Rightarrow A(1-u^2) + B(u+u^2) + C(u-u^2) = 1$$

$$\Rightarrow \underset{\textcircled{1}}{A} + \underset{\textcircled{2}}{(B+C)u} + \underset{\textcircled{3}}{(B-C-A)u^2} = 1$$

$$\textcircled{1} \quad A=1 \quad ; \quad \textcircled{2} \quad B+C=0 \quad \textcircled{3} \quad B-C-A=0$$

$$\Rightarrow B=-C \qquad \qquad \qquad 2B-1=0$$

$$\Rightarrow B=\frac{1}{2} \quad \Rightarrow C=-\frac{1}{2}$$

$$\Rightarrow \int \frac{dx}{n(1-x)(1+x)} = \int dx \left( \frac{1}{x} + \frac{1/2}{1-x} - \frac{1/2}{1+x} \right)$$

$$= \ln|x| - \frac{1}{2} \ln|1-x| - \frac{1}{2} \ln|1+x| + C$$

p)  $\int \frac{x}{(1+x)^2} dx$  : We have a repeated factor  $\Rightarrow$  the general form is now:

$$\frac{x}{(1+x)^2} = \frac{A}{1+x} + \frac{B}{(1+x)^2}$$

$$\Rightarrow \frac{A(1+x)^2 + B(1+x)}{(1+x)(1+x)^2} = \frac{A(1+x) + B}{(1+x)^2}$$

$$\Rightarrow A + B + Ax = x.$$

$$\Rightarrow A = 1 \quad \& \quad B = -A = -1$$

$$\Rightarrow \int \frac{x dx}{(1+x)^2} = \int dx \left( \frac{1}{1+x} - \frac{1}{(1+x)^2} \right)$$

$$= \ln|1+x| + \frac{1}{1+x} + C$$