

Introduction

Predation: $(+, -)$

Competition: $(-, -)$

Introduction

Predation: $(+, -)$

The Predator-Prey Equations

Competition: $(-, -)$

- ↪ We now turn our attention to biological systems modelled by systems of differential equations. In particular, we look at the *population dynamics* (recalling from **Lecture 3** that this term encompasses a wide range of phenomena) of *interacting species*.
- ↪ I really want to emphasise, however, that at this stage you have the tools from **Lecture 4** to deal with anything (biological or otherwise) modelled by a system of ODEs. It's important that you realise this.
- ↪ We will classify interaction between two species according to how each of the species benefits in relation to the other (+ versus -):
 1. **Predation or Parasitism** : (+, -)
 2. **Competition**: (-, -)
 3. **Mutualism**: (+, +)
- ▶ In this lecture, we will focus on the first two categories.
- ▶ Since some models we consider will be of two species, it is important to note that unless modelling a closed system with two species, a two-species model will typically not fully reflect the complex relationships between multiple species in nature. However it is an important first step to understanding these.

End of Section

Predation: (+, -)

- ↪ First note that *parasitism* and *predation* are essentially equivalent, but the presence of an annual cycle for most host-parasite relationships caused by what are typically discrete, non-overlapping generations, means that *parasitism* is typically modelled by systems of difference equations (discrete).
- In contrast, predator-prey relationships do not have that discrete structure and thus *predation* is typically modelled by systems of ODEs (continuous).
- ↪ We will therefore only discuss predation.

The Predator-Prey/Lotka-Volterra Equations

- We begin with the classic example, the **Lotka-Volterra** or **Predator-Prey** system of 2 equations.
- ▶ Background: Records of Lynx (predator) and Hare (prey) populations kept since the 1840s by the Hudson Bay Company in Canada have shown regular cyclical rises and falls in the population of the species. More recently, in the 1920's Vito Volterra, a mathematician specialising in differential and integral equations, developed the mathematical model for this behaviour in response to a question by his future son-in-law (a marine biologist) about similar cyclical behaviour he had observed in predator and prey fish species populations in the Mediterranean. At about the same time, independently, Alfred Lotka developed the same equations.
 - ▶ The Predator-Prey equations are more focussed on describing the qualitative behaviour of predator versus prey population dynamics than on providing specific predictions of populations (*there are refinements of this model which better serve that latter purpose*).

- Based on observing the behaviour of predator-prey population trends, here are the assumptions that went into that classical model:
- ▶ The prey species grows in an unlimited way at a rate proportional to the current population **if there are no predators**.
 - ▶ The predator species dies out at a rate proportional to its current population **if there are no prey**.
 - ▶ The number of encounters between the predator and prey is proportional to the product of their populations.
 - ▶ An encounter between a predator and a prey typically benefits the growth of the predator population and inhibits the growth of the prey population.
- Using these assumptions, let $x(t)$ be the prey population and $y(t)$ be the predator population. The equations are:

$$\begin{aligned}\frac{dx}{dt} &= ax - bxy \\ \frac{dy}{dt} &= -cy + dxy\end{aligned}$$

where a , b , c , d are positive constants.

$$\begin{array}{lcl} \text{REMINDER:} & \frac{dx}{dt} & = ax - bxy \\ & \frac{dy}{dt} & = -cy + dxy \end{array}$$

- ↪ This is a *nonlinear, autonomous* system of ODEs.
- ↪ a is the **net growth rate** of the prey population, so that in the absence of prey we just get the **Malthusian equation** for the prey. Similarly, c is the **net death/mortality rate** of the predator, and not surprisingly in the absence of prey the predator dies out.
- ▶ The form of the encounter rate comes from the **law of mass action**, which in its original chemical context says that:
 The rate of molecular collisions/reaction of two chemical species in a dilute gas or solution is proportional to the product of their two concentrations.
- ▶ In its original chemical context, the **law of mass action** is used to model the changing concentrations of chemical substances in biological systems in the field of biochemical kinetics, of which Michaelis-Menten kinetics (and the associated system of ODEs) is a famous example. This key biochemical law is however also used in other contexts such as disease modelling and population interactions to derive models of these phenomena, although in these other cases it is often only an approximation of what really happens.
- ↪ We will begin by analysing the steady states of the system.

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| REMINDER: | $\frac{dx}{dt}$ | = | $ax - bxy$ |
| | $\frac{dy}{dt}$ | = | $-cy + dxy$ |

→ It is relatively easy to determine that the two steady states for the Lotka-Volterra system of equations are:

$$\vec{ss1} = (0, 0) \quad \text{and} \quad \vec{ss2} = \left(\frac{c}{d}, \frac{a}{b} \right).$$

- ▶ The Jacobian matrix (also called the *community matrix*, in the context of ecology) of the right hand side vector function for the ODE system is $J(x, y) = \begin{pmatrix} a - by & -bx \\ dy & dx - c \end{pmatrix}$
- ▶ Thus at the two steady states the Jacobian matrix is

$$J(0, 0) = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix} \quad \text{and} \quad J\left(\frac{c}{d}, \frac{a}{b}\right) = \begin{pmatrix} 0 & -\frac{bc}{d} \\ \frac{da}{b} & 0 \end{pmatrix}$$

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| REMINDER: $J(0, 0) = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix}$ and $J\left(\frac{c}{d}, \frac{a}{b}\right) = \begin{pmatrix} 0 & -\frac{bc}{d} \\ \frac{da}{b} & 0 \end{pmatrix}$ |
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→ It is clear that for diagonal matrix $J(0, 0)$ the eigenvalues are $\lambda_1 = a > 0$, $\lambda_2 = -c < 0$ so that $(0, 0)$ is an (unstable) **saddle point** of the system.

→ Meanwhile, the eigenvalues for $J\left(\frac{c}{d}, \frac{a}{b}\right)$ are obtained by solving $\lambda^2 + \frac{bacd}{bd} = 0 \Rightarrow \lambda_{1,2} = \pm \sqrt{ac} i$.

So at this stage we cannot be sure what type of steady state is at $\left(\frac{c}{d}, \frac{a}{b}\right)$. It might be a centre as suggested by the eigenvalues, but because this is a nonlinear system of ODEs it may also be a spiral point (asymptotically stable or unstable).

- We will later see by analytically solving the system of ODEs and by looking at direction fields and numerical solutions that there is in fact a (stable) **centre** at $\left(\frac{c}{d}, \frac{a}{b}\right)$.

$$\text{REMINDER: } J(0, 0) = \begin{pmatrix} a & 0 \\ 0 & -c \end{pmatrix} \Rightarrow \lambda_{1,2} = a, -c \text{ and } J\left(\frac{c}{d}, \frac{a}{b}\right) = \begin{pmatrix} 0 & -\frac{bc}{d} \\ \frac{da}{b} & 0 \end{pmatrix} \Rightarrow \lambda_{1,2} = \pm \sqrt{ac} i$$

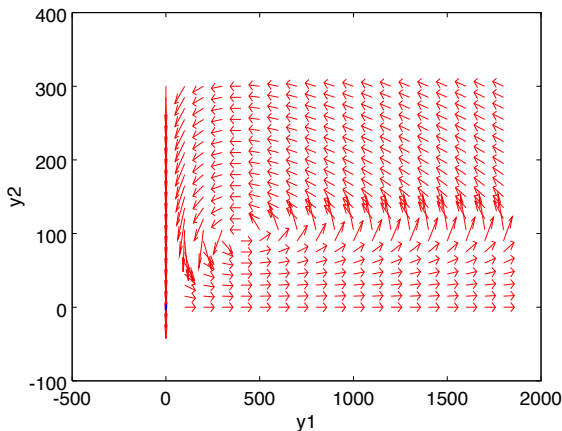
→ A few observations based on this model:

- ▶ Counterintuitively, the non-zero steady state of the prey, $\frac{c}{d}$, depends on the parameters associated with the predator, and is independent of the prey's own growth or mortality rate.
- ▶ Similarly, the non-zero steady state of the predator, $\frac{a}{b}$, depends on the parameters associated with the prey, and is independent of the predator's own growth or mortality rate.
- ▶ The nullclines are the horizontal line $y = a/b$ and the vertical line $x = c/d$.
- ▶ We now have almost enough information to sketch a phase plane plot.

We could, for example, now just evaluate and plot the vector

$\left(\frac{dx}{dt}, \frac{dy}{dt}\right)$ at four points in the four regions of the first quadrant delineated by the nullclines.

↪ Instead here is a direction field plot for the case $a = 0.05$, $b = \frac{a}{100} = 0.0005$, $c = 0.02$, and $d = \frac{c}{400} = 0.00005$, with non-zero steady state $(400, 100)$, suggesting that it is a centre.

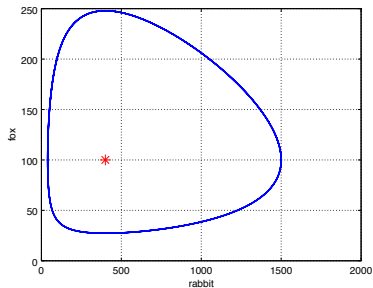
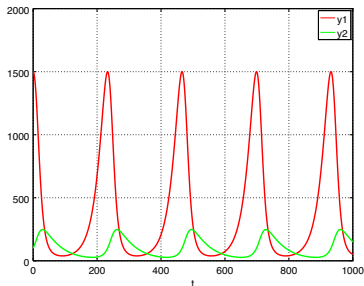


→ **EXAMPLE 1** We look at the solution to a predator prey problem in which the predators are foxes and the prey are rabbits. The following parameters will be used:

$$a = 0.05, \quad b = \frac{a}{100} = 0.0005, \quad c = 0.02, \quad \text{and} \quad d = \frac{c}{400} = 0.00005.$$

$$t \in [0, 1000], \quad x(0) = 1500, \quad y(0) = 100.$$

- ▶ We will solve this using a fourth order Runge-Kutta method. Note the cyclical time plots and the clear identification of the non-zero steady state, $\left(\frac{c}{d}, \frac{a}{b}\right) = (400, 100)$, as a **centre** in the phase plane plot.



→ Solution of a fox rabbit predator prey problem, with 100 foxes and 1500 rabbits at the start. Note the cyclical nature of the time plots and the confirmation in the phase plane plot that the non-zero steady state is a centre. That steady state, 400 rabbits and 100 foxes, is indicated by a red star, *, on the phase plane plot.

The Analytic Solution of the Predator-Prey System

→ We will use the Lotka-Volterra ODE system, $\frac{dx}{dt} = ax - bxy$, $\frac{dy}{dt} = -cy + dxy$, to show that it is sometimes possible to solve nonlinear systems; The trick is to convert it into a single differential equation in terms of $\frac{dy}{dx}$, and solve this equation in the phase space.

► As in **Lecture 4**, we use the chain rule to write

$$\frac{dy}{dx} = \frac{dy/dt}{dx/dt} = \frac{-cy + dxy}{ax - bxy} = \frac{y(dx - c)}{x(a - by)}.$$

This is a separable differential equation:

$$\frac{a - by}{y} dy = \frac{dx - c}{x} dx \Rightarrow \int \left(\frac{a}{y} - b \right) dy = \int \left(d - \frac{c}{x} \right) dx$$

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| REMINDER: $\int \left(\frac{a}{y} - b \right) dy = \int \left(d - \frac{c}{x} \right) dx$ |
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↪ So, where K is an arbitrary constant,

$$a \ln(y) - by = dx - c \ln(x) + K \Rightarrow a \ln(y) + c \ln(x) - by - dx = K.$$

- ▶ While this solution is not explicit, we could plot it for a given K (*i.e., initial condition*) by picking values of one variable and solving the resulting nonlinear equation (*using an algorithm like the Bisection method or Newton's method or Matlab's `fzero()`*) to find the corresponding value(s) of the other variable.
- This technique of eliminating the time variable and solving the equation as a single ODE in phase space is one possible way to find the solution of a nonlinear system of ODEs.

Nondimensionalisation of the Predator-Prey Equations

→ I will use the **Lotka-Volterra** equations to demonstrate a somewhat more systematic way (compared to how this was done in **Lecture 3**) to approach non-dimensionalisation of a set of equations.

→ This is a variation on the *Method of Undetermined Coefficients*:

1. First identify the variables (dependent, independent) you wish to non-dimensionalise and pick corresponding names for the non-dimensionalised form of those variables.
2. Set each of the variables to be non-dimensionalised equal to an *undetermined coefficient* multiplied by the non-dimensional name of that variable.
3. Rewrite the differential equation(s) in terms of these new dimensionless variables. **NOTE: often the chain rule is needed here.**
4. Select *appropriate* definitions for the *undetermined coefficients* from STEP 2 so that the equation(s) is (are) as simple as possible. **NOTE there are usually many possible ways of defining these undetermined coefficients which result in simplified dimensionless equation(s).**
5. See if any further simplifications are possible. For example, redefining common ratios as new parameters.

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| REMINDER: | $\frac{dx}{dt}$ | = | $ax - bxy$ |
| | $\frac{dy}{dt}$ | = | $-cy + dxy$ |

We will go through those five steps for the **Lotka-Volterra** equations:

1. We will non-dimensionalise $x(t)$ and $y(t)$ - the prey and predator (respectively) populations at time t , as well as the independent variable t . The new variables will be called u , v and τ respectively.
2. Let $\mathbf{x}(\mathbf{t}) = \mathbf{e}_1 \mathbf{u}$, $\mathbf{y}(\mathbf{t}) = \mathbf{e}_2 \mathbf{v}$, and $\mathbf{t} = \mathbf{e}_3 \tau$, where e_1 , e_2 , and e_3 are the three undetermined coefficients to be found.

NOTE: if we take the dimension of population measure to be P , then $[e_1] = [e_2] = P$ and $[e_3] = T$.

3. Using the chain rule twice,

$$\frac{dx}{dt} = \frac{dx}{du} \left(\frac{du}{d\tau} \right) = \frac{dx}{du} \left(\frac{du}{d\tau} \frac{d\tau}{dt} \right) = e_1 \frac{du}{d\tau} \frac{1}{e_3} = \left(\frac{e_1}{e_3} \right) \frac{du}{d\tau}.$$

$$\text{So } \left(\frac{e_1}{e_3} \right) \frac{du}{d\tau} = a(e_1 u) - b(e_1 u)(e_2 v) \Rightarrow \frac{du}{d\tau} = ae_3 u - be_2 e_3 uv$$

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| REMINDER: $\frac{dx}{dt} = ax - bxy$ $\frac{dy}{dt} = -cy + dxy$, $x(t) = e_1 u$, $y(t) = e_2 v$, and $t = e_3 \tau \Rightarrow \frac{du}{d\tau} = ae_3 u - be_2 e_3 uv$ |
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3. (continued) Similarly,

$$\frac{dy}{dt} = \frac{dy}{dv} \left(\frac{dv}{dt} \right) = \frac{dy}{dv} \left(\frac{dv}{d\tau} \frac{d\tau}{dt} \right) = e_2 \frac{dv}{d\tau} \frac{1}{e_3} = \left(\frac{e_2}{e_3} \right) \frac{dv}{d\tau}.$$

$$\text{So } \left(\frac{e_2}{e_3} \right) \frac{dv}{d\tau} = -c(e_2 v) + d(e_1 u)(e_2 v) \Rightarrow \frac{dv}{d\tau} = -ce_3 v + de_1 e_3 uv.$$

So the new system of ODEs is

$$\frac{du}{d\tau} = ae_3 u - be_2 e_3 uv, \quad \frac{dv}{d\tau} = -ce_3 v + de_1 e_3 uv.$$

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| REMINDER: $\frac{du}{d\tau} = ae_3u - be_2e_3uv,$ $\frac{dv}{d\tau} = -ce_3v + de_1e_3uv$ |
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4. Focussing on simplifying the first equation, one possibility is to let

$$e_3 = \frac{1}{a} \quad (\Rightarrow \tau = at) \quad \text{then to get } be_2e_3 = 1, \quad \text{let } e_2 = \frac{a}{b} \quad (\Rightarrow v = \frac{b}{a}y).$$

The equations then become $\frac{du}{d\tau} = u - uv,$ $\frac{dv}{d\tau} = -\frac{c}{a}v + \frac{d}{a}e_1uv.$

The “logical” choice then is to let $e_1 = \frac{a}{d} \quad (\Rightarrow u = \frac{d}{a}x)$ so that

$$\frac{du}{d\tau} = u - uv, \quad \frac{dv}{d\tau} = -\frac{c}{a}v + uv,$$

and $\alpha = \frac{c}{a}$ (\rightsquigarrow this is [step 5](#)) is now the ONLY parameter (compared to 4 originally) in the system of ODEs.

→ The system of equations is now

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| $\frac{du}{d\tau} = u - uv,$ | $\frac{dv}{d\tau} = -\alpha v + uv$ |
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► Obviously this simplified, dimensionless system is easier to analyse than the original **Predator-Prey** equations.

A Slight Modification to the Predator-Prey Equations

→ **EXAMPLE 2**: We will make the assumption that the prey population now follows the more realistic **Logistic ODE** in the absence of the predator. Thus, where K is the prey carrying capacity in the absence of a predator, the equations become

$$\begin{aligned}\frac{dx}{dt} &= ax \left(1 - \frac{x}{K}\right) - bxy \\ \frac{dy}{dt} &= -cy + dxy\end{aligned}.$$

- The steady states are now the solutions to

$$ax \left(1 - \frac{x}{K}\right) - bxy = 0 \Rightarrow ax \left(1 - \frac{x}{K}\right) = bxy \quad \text{and} \quad -cy + dxy = 0 \Rightarrow y(dx - c) = 0.$$

The last equation gives $y = 0$ or $x = c/d$. First, if $y = 0$ then plugging this into the dx/dt equation we $x = 0$ or $x = K$. Thus

$(0, 0)$ and $(K, 0)$ are two steady states, but we ignore them since they are not *really biologically relevant*.

↪ The only *biologically relevant* steady state is when $x = c/d$. We plug this into the first (dx/dt) equation to get

$$\frac{ac}{d} \left(1 - \frac{c}{dK}\right) = b \frac{c}{d} y \quad \Rightarrow \quad ac \left(1 - \frac{c}{dK}\right) = bcy \quad \Rightarrow$$

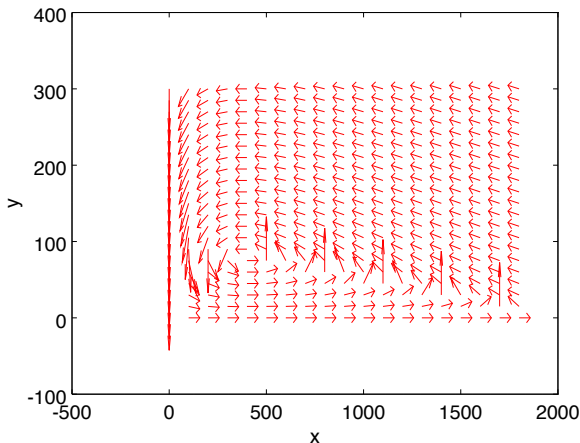
$$y = \frac{a}{b} \left(1 - \frac{c}{dK}\right) = \frac{a}{b} - \frac{ac}{bdK}.$$

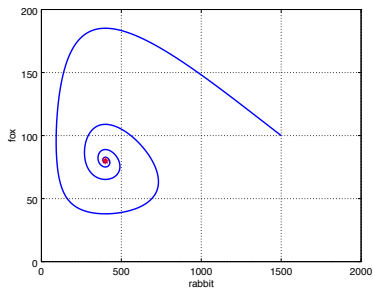
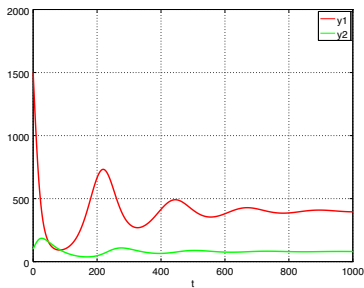
Thus the only biologically relevant steady state is

$$\left(\frac{c}{d}, \quad \frac{a}{b} - \frac{ac}{bdK} \right).$$

- ★ NOTE how this is like the *biologically relevant* steady state for the original **Lotka-Volterra** equations, $\left(\frac{c}{d}, \frac{a}{b}\right)$, but with a decrease in the predator population by $\frac{ac}{bdK}$.

→ Here is a direction field plot for the case $a = 0.05$, $b = \frac{a}{100} = 0.0005$, $c = 0.02$, $d = \frac{c}{400} = 0.00005$, and $K = 2000$ with non-zero steady state $(400, 80)$, suggesting it might an asymptotically stable spiral point (although an argument could also be made for it being a “centre”).





→ Solution of a fox-rabbit modified predator prey problem (with **Logistic** prey equation when $y = 0$, and with $K = 2000$), with 100 foxes and 1500 rabbits at the start. Note the diminishing oscillatory nature of both time plots and the confirmation in the phase plane plot that the non-zero steady state is an asymptotically stable spiral. That steady state, 400 rabbits and 80 foxes, is indicated by a red star, *, on the phase plane plot. Compare to the earlier graphs in EXAMPLE 1 in which the unmodified **Predator-Prey** equations were solved instead.

→ More formally, the Jacobian for the modified **Predator-Prey** equations, $\frac{dx}{dt} = ax \left(1 - \frac{x}{K}\right) - bxy$, $\frac{dy}{dt} = -cy + dxy$, is

$$J(x, y) = \begin{pmatrix} a - \frac{2ax}{K} - by & -bx \\ \frac{dy}{dx} & dx - c \end{pmatrix}$$

► So

$$J\left(\frac{c}{d}, \frac{a}{b} - \frac{ac}{bdK}\right) = \begin{pmatrix} a - \frac{2ac}{dK} - a + \frac{ac}{dK} & -\frac{bc}{d} \\ \frac{da}{b} - \frac{ac}{bK} & c - c \end{pmatrix} = \begin{pmatrix} -\frac{ac}{dK} & -\frac{bc}{d} \\ \frac{daK - ac}{bK} & 0 \end{pmatrix}.$$

► The eigenvalues are the solutions λ to

$$-\lambda \left(-\frac{ac}{dK} - \lambda\right) + \frac{cadK - ac^2}{dK} = 0 \Rightarrow \lambda^2 + \frac{ac}{dK}\lambda + \frac{cadK - ac^2}{dK} = 0.$$

$$\Rightarrow dK\lambda^2 + ac\lambda + (acdK - ac^2) = 0 \Rightarrow \lambda = \frac{-ac \pm \sqrt{a^2c^2 - 4acd^2K^2 + 4ac^2dK}}{2dK}$$

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| REMINDER: Eigenvalues $\lambda = \frac{-ac \pm \sqrt{a^2c^2 - 4acd^2K^2 + 4ac^2dK}}{2dK}$ |
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→ The discriminant can be simplified to

$$ac(ac - 4d^2K^2 + 4cdK) = ac(ac + 4Kd[c - dK]).$$

- First note for the dy/dt steady state, $\frac{a}{b} - \frac{ac}{bdK} = \frac{a}{b} - \frac{a}{b}\left(\frac{c}{dK}\right)$, to be positive (and hence biologically relevant), we require that $1 > \frac{c}{dK} \Rightarrow dK > c \Rightarrow \mathbf{0} > \mathbf{c} - \mathbf{dK}$. Thus if the dy/dt steady state, $\frac{a}{b} - \frac{ac}{bdK}$, is a positive number, the discriminant is always $< a^2c^2$ hence each eigenvalue would be negative and the steady state would be an **asymptotically stable node**.
- If, on the other hand, as in the example phase plane plots a few slides back, we have $\mathbf{ac} < \mathbf{4d^2K^2} - \mathbf{4cd}$ so that the discriminant is negative, then the steady state is an **asymptotically stable spiral**.

- Thus we see that a minor change in the **Predator-Prey** equations results in a very dramatic change in the behaviour of the solutions. More generally, in the modified equation depending on the choice of parameters the steady state could be an asymptotically stable node or an asymptotically stable spiral point.
- ▶ The stable centre steady state for the **Lotka-Volterra** equations is therefore not *structurally stable* in that a tiny perturbation of the equation results in a qualitatively different solution behaviour. This is one criticism that has been levelled at the **Lotka-Volterra** equations and means they must be used with great care if one wishes to get accurate predictions of predator-prey behaviour.
 - ▶ Thus there are many variations of the **Lotka-Volterra** equations which are geared towards producing more realistic models.
 - ▶ Nevertheless, the **Lotka-Volterra** equations are a major contributor to the growth of mathematical ecology and serve the purpose of giving good qualitative information about simplified predator-prey interactions which can then be further refined.

Other Variations on/Alternatives to the Predator-Prey Equations

→ There are many possible variations of the Predator-Prey equations in which more realistic assumptions are made (for example, removing the assumption that a , b , c , and d are constants. There are also alternative predator-prey models.

There are many sources for reading more on these, for example:

- ▶ S.A. Levin, editor. *Frontiers in Mathematical Biology*, volume 100 of *Lect. Notes in Biomathematics*. Springer-Verlag, Berlin-Heidelberg-New York, 1994.
- ▶ R.M. Nisbet and W.S.C. Gurney. *Modelling Fluctuating Populations*. The Blackburn Press, New Jersey, 2004.
- ▶ The **Arditi-Ginzburg equations** - an alternative to the **Lotka-Volterra** predator-prey model. For an introduction see

https://en.wikipedia.org/wiki/Arditi-Ginzburg_equations

End of Section

Competition: (-, -)

- *The principle of competitive exclusion* or *Gause's law (of competitive exclusion)* - named after Russian biologist Georgy Gause - says essentially that if two (non-predator-prey) species live in the same area and share the same basic requirements¹, then they will compete for resources, habitat, territory, etc., and this competition will lead to the extinction of one of the species. This is a phenomenon that has often been observed in nature.
- However, what is very notable about *Gause's law* is that it is sometimes not true. Thus when we encounter a scenario in which two competitors *DO* coexist, *Gause's law* prompts us to examine the situation more closely in order to determine the reasons for this coexistence.

¹Technically, we require that two species share the same *ecological niche*, meaning they interact identically with the same other species, require the same nutrients, live in the same habitats, . . . *i.e.* are largely identical in their core survival requirements

- In a basic model for competition between two species, we assume that each species grows according to the **Logistic ODE** if the other species is not present. So if $U_i(t)$ is the population of species i ($i = 1, 2$) at time t , then with *intrinsic growth rates* r_i and carrying capacities K_i ($i = 1, 2$), the equations so far are:

$$\frac{dU_1}{dt} = r_1 U_1 \left(1 - \frac{U_1}{K_1} \right) \quad \text{and} \quad \frac{dU_2}{dt} = r_2 U_2 \left(1 - \frac{U_2}{K_2} \right).$$

- However, when the two species *are* present and competing for resources etc., the presence of each species will have a negative impact on the growth rate of the other. If we think of the term $-\frac{U_i}{K_i}$ in each equation as the limiting effect on growth caused by competition within species i , then a sensible first assumption is that the effect of competition between the two species follows the same pattern.

→ Thus we add a term $-\frac{\alpha U_2}{K_1}$ to the second term in the product in the first equation, and similarly $-\frac{\beta U_1}{K_2}$ in the second equation. The new equations are

$$\frac{dU_1}{dt} = r_1 U_1 \left(1 - \frac{U_1 + \alpha U_2}{K_1} \right) \quad \text{and} \quad \frac{dU_2}{dt} = r_2 U_2 \left(1 - \frac{U_2 + \beta U_1}{K_2} \right).$$

- ▶ α and β can be thought of as (dimensionless - *do a dimensional analysis to see this*) coefficients which measure the relative competitiveness of the two species. For example, if the species are competing for a specific kind of food and each individual from species 1 eats four times as much of that food as each individual of species 2, then $\alpha = 4$ and $\beta = \frac{1}{4}$. In general, for two species in the same *ecological niche*, $\alpha\beta = 1$.
- ▶ We will *nondimensionalise* these equations to simplify them and reduce the number of parameters from 6 before doing any further analysis.

Nondimensionalisation of the Competition Equations

→ **EXAMPLE 3** Nondimensionalise the equations

$$\frac{dU_1}{dt} = r_1 U_1 \left(1 - \frac{U_1 + \alpha U_2}{K_1} \right) \quad \text{and} \quad \frac{dU_2}{dt} = r_2 U_2 \left(1 - \frac{U_2 + \beta U_1}{K_2} \right).$$

► **ANSWER** Using the five step procedure outlined earlier:

1. We will non-dimensionalise U_1 to get u , U_2 to get v , and t to get τ .
2. Let $U_1(t) = a_1 u$, $U_2(t) = a_2 v$, and $t = a_3 \tau$, where a_1 , a_2 , and a_3 are the three undetermined coefficients to be found.

$$3. \quad \frac{dU_1}{dt} = \frac{dU_1}{du} \left(\frac{du}{d\tau} \frac{d\tau}{dt} \right) = \left(\frac{a_1}{a_3} \right) \frac{du}{d\tau} = r_1 a_1 u \left(1 - \frac{a_1 u + \alpha a_2 v}{K_1} \right) \Rightarrow$$

$$\frac{du}{d\tau} = r_1 a_3 u \left(1 - \frac{a_1 u + \alpha a_2 v}{K_1} \right).$$

Similarly,

$$\frac{dU_2}{dt} = \frac{dU_2}{dv} \left(\frac{dv}{d\tau} \frac{d\tau}{dt} \right) = \left(\frac{a_2}{a_3} \right) \frac{dv}{d\tau} = r_2 a_2 v \left(1 - \frac{a_2 v + \beta a_1 u}{K_2} \right) \Rightarrow$$

$$\frac{dv}{d\tau} = r_2 a_3 v \left(1 - \frac{a_2 v + \beta a_1 u}{K_2} \right).$$

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| REMINDER: $\frac{du}{d\tau} = r_1 a_3 u \left(1 - \frac{a_1 u + \alpha a_2 v}{K_1}\right)$ and $\frac{dv}{d\tau} = r_2 a_3 v \left(1 - \frac{a_2 v + \beta a_1 u}{K_2}\right)$ |
|--|

4. Focussing on simplifying the first equation, one possibility is to let

$$a_3 = \frac{1}{r_1} \quad (\Rightarrow \tau = r_1 t) \quad \text{then to get } \frac{a_1}{K_1} = 1, \quad \text{let } a_1 = K_1 \quad (\Rightarrow u = \frac{U_1}{K_1}). \quad \text{The}$$

equations then become $\frac{du}{d\tau} = u \left(1 - u - \frac{\alpha a_2}{K_1} v\right), \quad \frac{dv}{d\tau} = \frac{r_2}{r_1} v \left(1 - \frac{a_2 v}{K_2} - \frac{\beta K_1}{K_2} u\right)$

from which it is clear to see that a good choice for a_2 is

$$a_2 = K_2 \quad (\Rightarrow v = \frac{U_2}{K_2}); \text{ so the equations become}$$

$$\frac{du}{d\tau} = u \left(1 - u - \frac{\alpha K_2}{K_1} v\right), \quad \frac{dv}{d\tau} = \frac{r_2}{r_1} v \left(1 - v - \frac{\beta K_1}{K_2} u\right)$$

5. The ratios seen in the above equations suggest the definition of

$$\text{variables } \mathbf{a} = \frac{\alpha K_2}{K_1}, \quad \mathbf{b} = \frac{\beta K_1}{K_2}, \quad \mathbf{c} = \frac{r_2}{r_1}.$$

REMINDER: $\frac{du}{d\tau} = u \left(1 - u - \frac{\alpha K_2}{K_1} v \right)$, $\frac{dv}{d\tau} = \frac{r_2}{r_1} v \left(1 - v - \frac{\beta K_1}{K_2} u \right)$, with

$$u = \frac{U_1}{K_1}, \quad v = \frac{U_2}{K_2}, \quad \tau = \frac{t}{r_1} \text{ then we define } a = \frac{\alpha K_2}{K_1}, \quad b = \frac{\beta K_1}{K_2}, \quad c = \frac{r_2}{r_1}$$

5. (continued) Thus the final form of the dimensionless competition equations is

$$\frac{du}{d\tau} = u(1 - u - av), \quad \frac{dv}{d\tau} = cv(1 - v - bu).$$

- ↪ So the dimensionless equation only has THREE parameters, a , b , and c as compared to the original equations which had SIX. Each dimensionless population is given as a proportion of the carrying capacity for that species (in the absence of the other species).

| |
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| REMINDER: $\frac{du}{d\tau} = u(1 - u - av), \quad \frac{dv}{d\tau} = cv(1 - v - bu)$ |
|---|

→ The steady states can be easily shown to be

$$(0, 0), \quad (0, 1), \quad (1, 0), \quad \text{and} \quad \left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab} \right).$$

↪ So all steady states except the last one reflect *Gause's law (of competitive exclusion)* in which one of the species dies out. Only the last steady state is one in which there is coexistence of the two species.

→ The Jacobian matrix is

$$J(u, v) = \begin{pmatrix} 1 - 2u - av & -ua \\ -bcv & c - 2cv - bcu \end{pmatrix}$$

- So $J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & c \end{pmatrix}$ and therefore the eigenvalues are 1 and c , both > 0 , meaning that the origin is an *unstable node*.

REMINDER: $\frac{du}{d\tau} = u(1 - u - av)$, $\frac{dv}{d\tau} = cv(1 - v - bu)$, steady states

$$(0, 0), (0, 1), (1, 0), \text{ and } \left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab} \right) \text{ with } J(u, v) = \begin{pmatrix} 1-2u-av & -ua \\ -bcv & c-2cv-bcu \end{pmatrix}$$

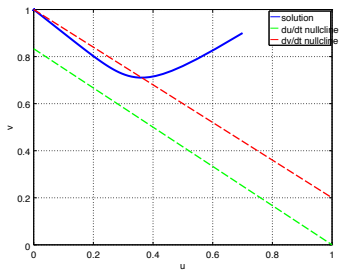
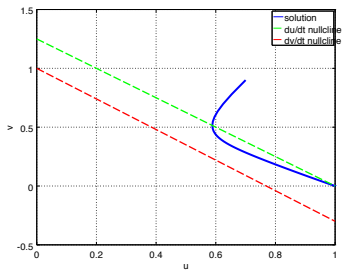
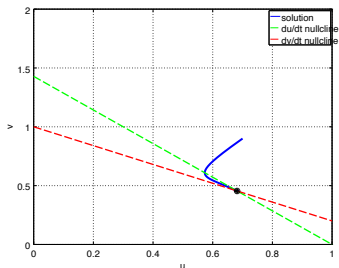
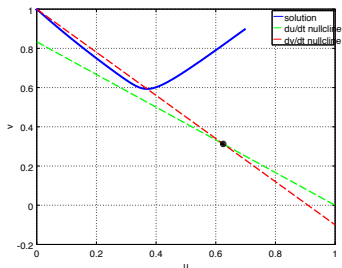
- $J(0, 1) = \begin{pmatrix} 1-a & 0 \\ -bc & -c \end{pmatrix}$ so the eigenvalues are $1-a$ and $-c$.
 So if $1-a < 0 \Rightarrow a > 1$ both eigenvalues are negative and $(0, 1)$ is an **asymptotically stable node**; meanwhile if $a < 1$ one eigenvalue is positive and the other is negative meaning that $(0, 1)$ is an **unstable saddle point**.
- $J(1, 0) = \begin{pmatrix} -1 & -a \\ 0 & c(1-b) \end{pmatrix}$ so the eigenvalues are -1 and $c(1-b)$.
 So if $1-b < 0 \Rightarrow b > 1$ both eigenvalues are negative and $(1, 0)$ is an **asymptotically stable node**; meanwhile if $b < 1$ one eigenvalue is positive and the other is negative meaning that $(1, 0)$ is an **unstable saddle point**.

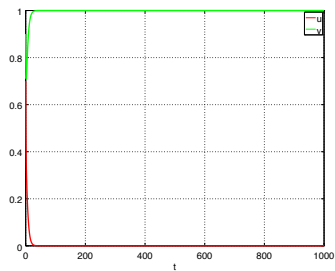
REMINDER: $\frac{du}{d\tau} = u(1 - u - av)$, $\frac{dv}{d\tau} = cv(1 - v - bu)$, steady states

$(0, 0)$, $(0, 1)$, $(1, 0)$, and $\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$ with $J(u, v) = \begin{pmatrix} 1 - 2u - av & -ua \\ -bcv & c - 2cv - bcu \end{pmatrix}$

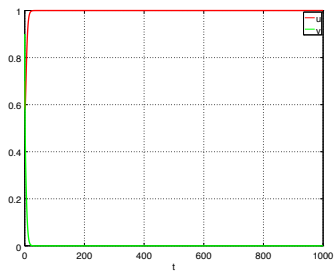
- ▶ $J\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$ is a quite complicated expression so we will not examine it in this general context.
- ▶ Instead, we note from what we have already seen that the values $a = 1$ and $b = 1$ appear to be critical threshold values, so we will look at four cases when considering the behaviour of solutions:
 1. $a > 1, b < 1$
 2. $a < 1, b > 1$
 3. $a < 1, b < 1$
 4. $a > 1, b > 1$.
- ▶ We will look at a representative sample of phase plane plots, solution versus time plots, and direction fields for all four cases. *(NOTE the solution versus time plots will be for dimensionless time, but I will still label the horizontal axis t instead of τ).*

- ▶ Note that the steady state associated with coexistence, $\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$, exists in the first quadrant (hence is biologically realistic) only in CASES 3 ($a < 1, b < 1$) and 4 ($a > 1, b > 1$).
- ▶ In the following plots, the following data was used:
In all four cases, $c = \frac{r_2}{r_1} = 1$, the initial data was $u = 0.7, v = 0.9$.
 - ▶ CASE 1 $a = 1.2, b = 0.8$
 - ▶ CASE 2 $a = 0.8, b = 1.3$
 - ▶ CASE 3 $a = 0.7, b = 0.8$
 - ▶ CASE 4 $a = 1.2, b = 1.1$
- ▶ In CASES 3 and 4, the steady state $\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$ is indicated by a large black dot.
- ▶ The du/dt and dv/dt nullclines are also plotted, and we can see that the four cases correspond to different relative configurations of the nullclines in the biologically realistic first quadrant.

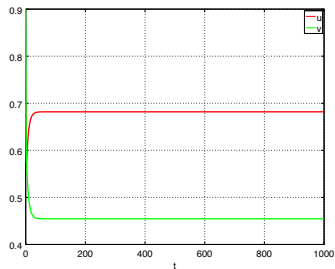
 $a > 1, b < 1$  $a < 1, b > 1$  $a < 1, b < 1$  $a > 1, b > 1$



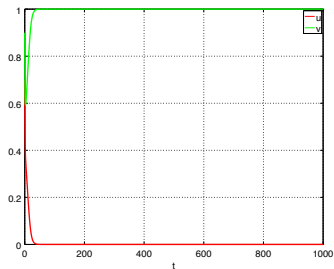
$$a > 1, b < 1$$



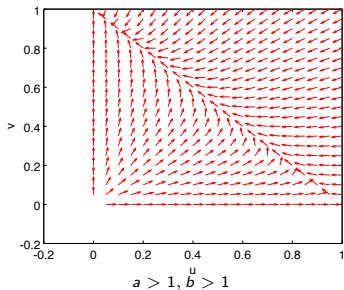
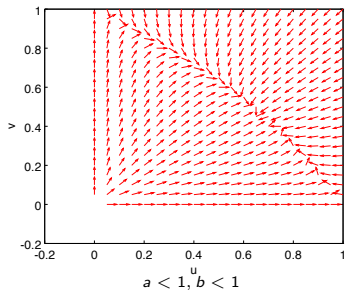
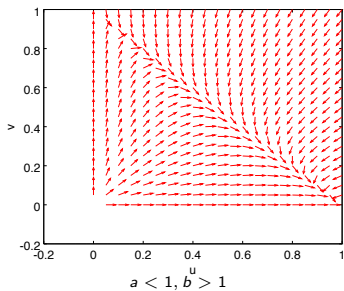
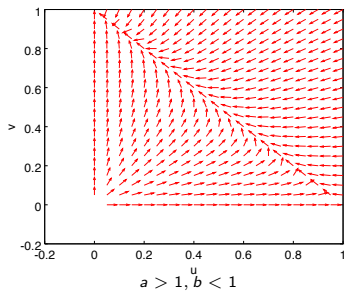
$$a < 1, b > 1$$



$$a < 1, b < 1$$



$$a > 1, b > 1$$



↪ Here are observations on stability based on the graphs and confirming the classification we did earlier for steady states:

1. $a > 1, b < 1$ Here, the second species always wins, thus steady state $(0, 1)$ is **asymptotically stable** and all other steady states are unstable.
2. $a < 1, b > 1$ Here, the first species always wins, thus steady state $(1, 0)$ is **asymptotically stable** and all other steady states are unstable.
3. $a < 1, b < 1$ Here, the two species coexist in the **asymptotically stable** steady state $\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$ and all other steady states are unstable.

However for competitive species occupying the same ecological niche, $ab = \alpha\beta$ must = 1, so a and b cannot both be less than 1. Hence this scenario is not possible.

4. $a > 1, b > 1$ Here, either species can win depending on the initial conditions. Notably, the coexistence steady state $\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$ is unstable in this case.
- So we have shown that in all cases, this model has a steady state in which one species wins and the other loses. Thus this model has been shown to exhibit *Gause's law (of competitive exclusion)*.

End of Section