Introduction

Predation: $(+,\ -)$

The Predator-Prey Equations

Competition: $(-,\ -)$

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End of Section

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$\rightsquigarrow$ We will therefore only discuss predation.

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- 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)*.

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

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- We will begin by analysing the steady states of the system.

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- Thus at the two steady states the Jacobian matrix is

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

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$\hookrightarrow$ A few observations based on this model:

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- The nullclines are the horizontal line $y = a/b$ and the vertical line $x = c/d$.

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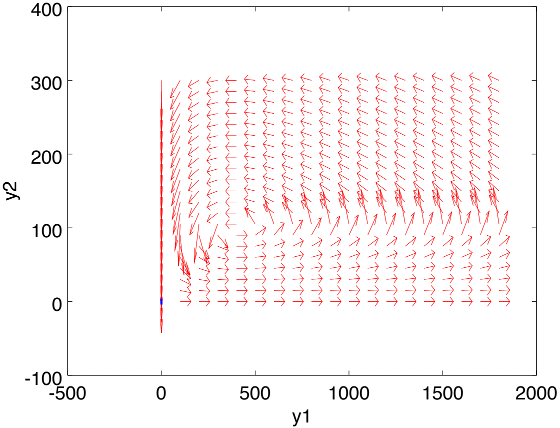
- The nullclines are the horizontal line $y = a/b$ and the vertical line $x = c/d$.
- We now have almost enough information to sketch a phase plane plot.

  We could, for example, now just evaluate and plot the vector $\left(\dfrac{dx}{dt}, \dfrac{dy}{dt}\right)$ at four points in the four regions of the first quadrant delineated by the nullclines.

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



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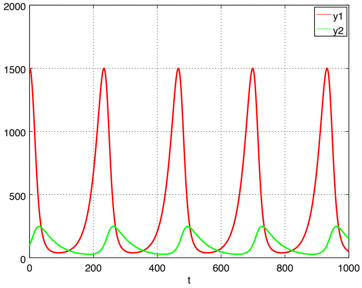
- We will solve this using a fourth order Runge-Kutta method. Note the cyclical time plots and the clear identification of the non-zero steady state, $\left(\boldsymbol{\frac{c}{d}}, \boldsymbol{\frac{a}{b}}\right) \mathbf{= (400, 100)}$, as a **centre** in the phase plane plot.



$\hookrightarrow$ 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.

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$\succ$ This technique of elminating 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.

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5. See if any further simplifications are possible. For example, redefining common ratios as new parameters.

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- Obviously this simplified, dimensionless system is easier to analyse than the original **Predator-Prey** equations.

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

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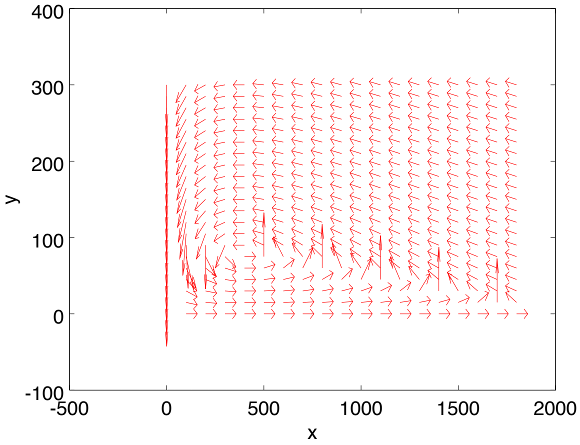
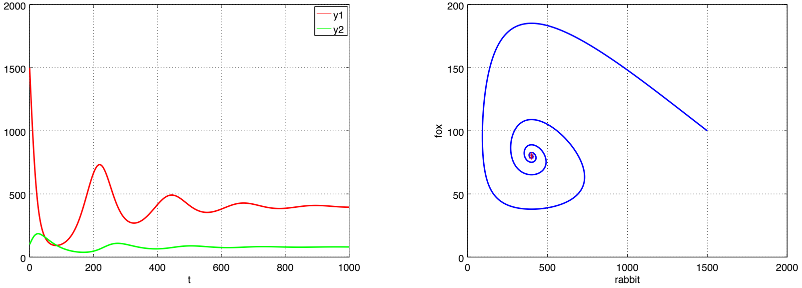
↪ Here is a direction field plot for the case $a = 0.05$, $b = \dfrac{a}{100} = 0.0005$, $c = 0.02$, $d = \dfrac{c}{400} = 0.00005$, and $K = 2000$ with non-zero steady state $(400, 80)$, suggesting it might an asymptotically stable spiral point *(although an argument could also be made for it being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





$\hookrightarrow$ 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.

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- If, on the other hand, as in the example phase plane plots a few slides back, we have $\boldsymbol{ac < 4d^2K^2 - 4cd}$ so that the discriminant is negative, then the steady state is an asymptotically stable spiral.

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- 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

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- 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

$\boxed{\text{End of Section}}$

Competition: $(-, -)$

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$\hookrightarrow$ 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 $-\dfrac{U_i}{K_i}$ 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.

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- 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

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  1. We will non-dimensionalise U_1 to get u, U_2 to get v, and t to get τ.
  2. Let $\boldsymbol{U_1(t) = a_1 u, \quad U_2(t) = a_2 v, \quad \text{and} \quad t = a_3 \tau}$, where a_1, a_2, and a_3 are the three undetermined coefficients to be found.
  3. $$\frac{dU_1}{dt} = \frac{dU_1}{du}\left(\frac{du}{d\tau}\frac{d\tau}{dt}\right) = \left(\frac{a_1}{a_3}\right)\frac{du}{d\tau} = r_1 a_1 u \left(1 - \frac{a_1 u + \alpha a_2 v}{K_1}\right) \quad \Rightarrow$$

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

Similarly,

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

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

Nondimensionalisation of the Competition Equations

↪ EXAMPLE 3 Nondimensionalise the equations

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

- 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 $\boldsymbol{U_1(t) = a_1 u}$, $\boldsymbol{U_2(t) = a_2 v}$, **and** $\boldsymbol{t = a_3 \tau}$, where a_1, a_2, and a_3 are the three undetermined coefficients to be found.
  3. $$\frac{dU_1}{dt} = \frac{dU_1}{du}\left(\frac{du}{d\tau}\frac{d\tau}{dt}\right) = \left(\frac{a_1}{a_3}\right)\frac{du}{d\tau} = r_1 a_1 u\left(1 - \frac{a_1 u + \alpha a_2 v}{K_1}\right) \quad \Rightarrow$$

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

     Similarly,

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

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

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

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

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

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

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$a_3 = \dfrac{1}{r_1}$ $(\Rightarrow \tau = r_1 t)$ then to get $\dfrac{a_1}{K_1} = 1$, *let* $a_1 = K_1$ $(\Rightarrow u = \dfrac{U_1}{K_1})$. The equations then become $\dfrac{du}{d\tau} = u\left(1 - u - \dfrac{\alpha a_2}{K_1} v\right)$, $\dfrac{dv}{d\tau} = \dfrac{r_2}{r_1} v \left(1 - \dfrac{a_2 v}{K_2} - \dfrac{\beta K_1}{K_2} u\right)$

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

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

$a_2 =$

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

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

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

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

$a_3 = \dfrac{1}{r_1}$ $(\Rightarrow \tau = r_1 t)$ then to get $\dfrac{a_1}{K_1} = 1$, *let* $a_1 = K_1$ $(\Rightarrow u = \dfrac{U_1}{K_1})$. The equations then become $\dfrac{du}{d\tau} = u\left(1 - u - \dfrac{\alpha a_2}{K_1} v\right)$, $\dfrac{dv}{d\tau} = \dfrac{r_2}{r_1} v\left(1 - \dfrac{a_2 v}{K_2} - \dfrac{\beta K_1}{K_2} u\right)$

from which it is clear to see that a good choice for a_2 is $a_2 = K_2$ $(\Rightarrow v = \dfrac{U_2}{K_2})$; so the equations become

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

5. The ratios seen in the above equations suggest the definition of variables $\boldsymbol{a = \dfrac{\alpha K_2}{K_1},\ b = \dfrac{\beta K_1}{K_2},\ c = \dfrac{r_2}{r_1}}$.

REMINDER: $\dfrac{du}{d\tau} = u\left(1 - u - \dfrac{\alpha K_2}{K_1} v\right), \quad \dfrac{dv}{d\tau} = \dfrac{r_2}{r_1} v\left(1 - v - \dfrac{\beta K_1}{K_2} u\right)$, with $u = \dfrac{U_1}{K_1},\ v = \dfrac{U_2}{K_2},\ \tau = \dfrac{t}{r_1}$ then we define $a = \dfrac{\alpha K_2}{K_1},\ b = \dfrac{\beta K_1}{K_2},\ c = \dfrac{r_2}{r_1}$

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

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

$\hookrightarrow$ So the dimensionless equation only has THREE parameters, a, b, and c as compared to the original equations which had SIX.

REMINDER: $\dfrac{du}{d\tau} = u\left(1 - u - \dfrac{\alpha K_2}{K_1} v\right), \quad \dfrac{dv}{d\tau} = \dfrac{r_2}{r_1} v\left(1 - v - \dfrac{\beta K_1}{K_2} u\right)$, with
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$$(0,0), \quad (0,1), \quad (1,0), \quad \textit{and} \quad \left(\frac{1-a}{1-ab}, \ \frac{1-b}{1-ab}\right).$$

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⇝ 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.

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$$J(u,v) =$$

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

- 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: $\dfrac{du}{d\tau} = u\,(1 - u - av)\,, \quad \dfrac{dv}{d\tau} = cv\,(1 - v - bu)$, steady states $(0,0),\ (0,1),\ (1,0),\ \textit{and}\ \left(\dfrac{1-a}{1-ab},\ \dfrac{1-b}{1-ab}\right)$ with $J(u,v) =$

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- $J(0,1) = \begin{pmatrix} 1-a & 0 \\ -bc & -c \end{pmatrix}$ 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;

REMINDER: $\dfrac{du}{d\tau} = u\,(1 - u - av)\,, \quad \dfrac{dv}{d\tau} = cv\,(1 - v - bu)$, steady states
$(0,0),\ (0,1),\ (1,0),$ *and* $\left(\dfrac{1-a}{1-ab}, \dfrac{1-b}{1-ab}\right)$ with $J(u,v) = \begin{pmatrix} 1 - 2u - av & -ua \\ -bcv & c - 2cv - bcu \end{pmatrix}$

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  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.

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- $J(0,1) = \begin{pmatrix} 1-a & 0 \\ -bc & -c \end{pmatrix}$ 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;

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- $J(0,1) = \begin{pmatrix} 1-a & 0 \\ -bc & -c \end{pmatrix}$ 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.
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- $J\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$ is a quite complicated expression so we will not examine it in this general context.

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- $J\left(\frac{1-a}{1-ab}, \frac{1-b}{1-ab}\right)$ 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:

REMINDER: $\dfrac{du}{d\tau} = u\,(1 - u - av)\,, \quad \dfrac{dv}{d\tau} = cv\,(1 - v - bu)$, steady states $(0,0),\ (0,1),\ (1,0),\ \textit{and}\ \left(\dfrac{1-a}{1-ab}, \dfrac{1-b}{1-ab}\right)$ with $J(u,v) = \begin{pmatrix} 1 - 2u - av & -ua \\ -bcv & c - 2cv - bcu \end{pmatrix}$

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    1. $a > 1,\ b < 1$

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- 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. $a < 1,\ b > 1$

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- 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, $\left(\dfrac{1-a}{1-ab}, \dfrac{1-b}{1-ab}\right)$, exists in the first quadrant (hence is biologically realistic) only in CASES 3 ($a < 1$, $b < 1$) and 4 ($a > 1$, $b > 1$).
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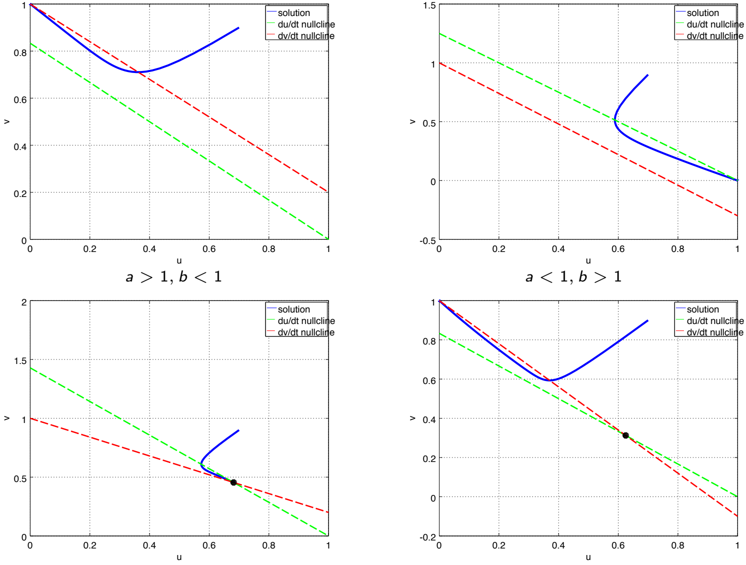
- In CASES 3 and 4, the steady state $\left(\dfrac{1-a}{1-ab}, \dfrac{1-b}{1-ab}\right)$ is indicated by a large black dot.
- The du/dt and dv/dt nullclines are also plotted, and we can see that the four cases correspond to different relative configurations of the nullclines in the biologically realistic first quadrant.



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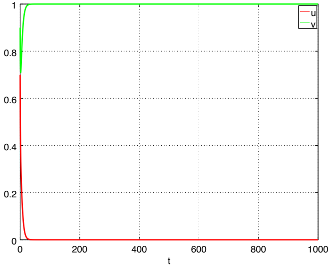

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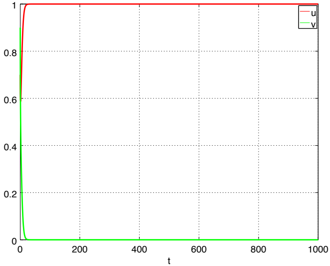

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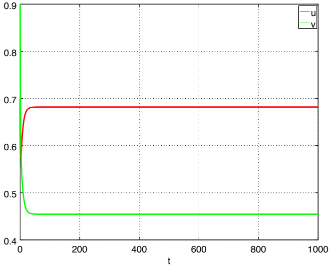

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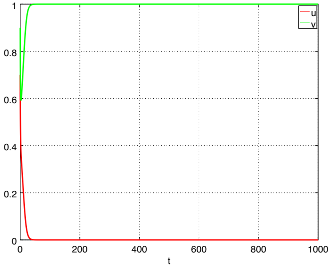

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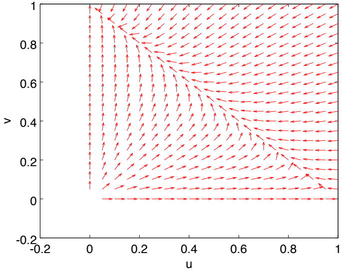

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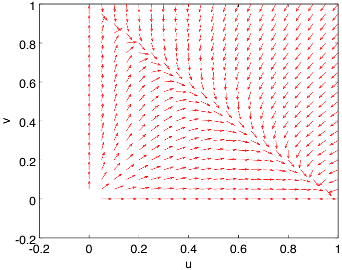

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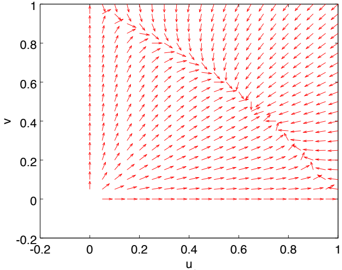

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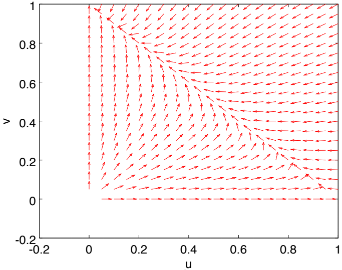

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   However for competitive species occupying the same ecological niche, $ab = \alpha\beta$ must $= 1$, so a and b cannot both be less than 1. Hence this scenario is not possible.

4. $\boxed{a > 1, b > 1}$ 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.

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$\hookrightarrow$ 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