

Introduction to Evolutionary Games - 2

Escuela de Bioestocástica

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The simplest model consider two species A and B that reproduces at rates a and b respectively (and no death is included).

Here we have

$$\dot{x} = ax$$

$$\dot{y} = ay$$



$$x(t) = x_0 e^{at}$$

$$y(t) = y_0 e^{bt}$$

$$\dot{x} = ax$$

$$\dot{y} = by$$

$$\Rightarrow$$

$$x(t) = x_0 e^{at}$$

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Therefore,

$$\frac{x(t)}{y(t)} = \frac{x_0}{y_0} e^{(a-b)t}$$

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Therefore,

$$\frac{x(t)}{y(t)} = \frac{x_0}{y_0} e^{(a-b)t}$$

- ▶ if $a = b$ then the quotient is constant: the size of the population are in the same proportion
- ▶ if $a > b$ then $\lim_{t \rightarrow \infty} \frac{x(t)}{y(t)} \rightarrow \infty$: Population A outcompete population B
- ▶ if $a < b$ then $\lim_{t \rightarrow \infty} \frac{x(t)}{y(t)} \rightarrow 0$: Population B outcompete population A

Selection

A much more interesting case is when the total abundance is constant, i.e. we set $x(t) + y(t) = 1$. In this setting the simplest model is

$$\dot{x}(t) = (a - \phi(t))x(t)$$

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$$(a - \phi(t))x(t) + (b - \phi(t))y(t) = 0 \rightarrow ax + by = \phi(x + y) \rightarrow \phi = (ax + by)$$

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$$\dot{x} = x(1 - x)(a - b) \Rightarrow \begin{cases} x(t) = 0 & \text{if } x(0) = 0 \\ x(t) = 1 & \text{if } x(0) = 1 \\ x(t) = \frac{x_0 e^{(a-b)t}}{1 - x_0 + x_0 e^{(a-b)t}} & \text{if } x(0) \in (0, 1) \end{cases}$$

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Exercise

If $x(0) \in (0, 1)$, show that $\lim_{t \rightarrow \infty} x(t) \rightarrow 1$ if $a > b$, and $\lim_{t \rightarrow \infty} x(t) \rightarrow 0$ if $b < a$

We can have more than two species, e.g. A , B , and C

$$\dot{x}(t) = (a - \phi(t))x(t)$$

$$\dot{y}(t) = (b - \phi(t))y(t)$$

$$\dot{z}(t) = (c - \phi(t))z(t)$$

with $x(t) + y(t) + z(t) = 1$. In this case $\phi(t) = ax(t) + by(t) + cz(t)$ which is, again, the average fitness. However, solving this equation is much harder.

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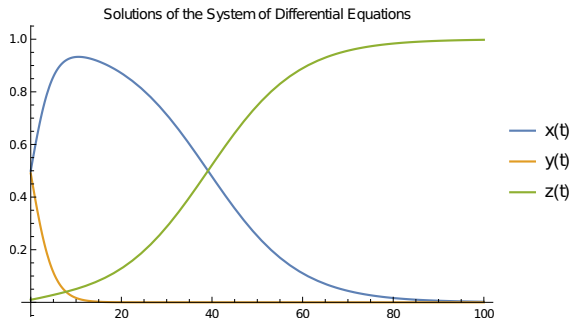
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But.... Computers!

Mathematica is my to-go software for solving stuff. Other alternatives like Matlab or several libraries in python (scipy, numpy, etc)

```
a = 1.9; b = 1.5; c = 2; (*fitness value*)
phi[t_] := a*x[t] + b*y[t] + c*z[t]; (*average fitness*)
eq1 = (x'[t] == (a - phi[t])*x[t]); (*the three equations and initial conditions*)
eq2 = (y'[t] == (b - phi[t])*y[t]);
eq3 = (z'[t] == (c - phi[t])*z[t]);
initialConditions = {x[0] == 50/100, y[0] == 49/100, z[0] == 1/100};
solution = NDSolve[{eq1, eq2, eq3, initialConditions},
{x[t], y[t], z[t]}, {t, 0, 100}]; (*solver for ODE*)
{xSol, ySol, zSol} = {x[t], y[t], z[t]} /.
  solution[[1]]; (*extract the solutions*)
Plot[{xSol, ySol, zSol}, {t, 0, 100}, PlotLegends-> {"x(t)", "y(t)", "z(t)"},
  FrameLabel -> {"t", "Values"}, PlotLabel-> "Solutions of the System of Differential
```


Example with $a = 1.9$, $b = 1.5$, $c = 2$, $x(0) = 50/100$, $y(0) = 49/100$, $z(0) = 1/100$



DETOUR: Simplex and Equilibrium Points

In the previous examples, we had that the total abundance was constant.

The collection of points (x_1, \dots, x_n) such that $x_i \geq 0$ and $\sum_{i=1}^n x_i = 1$ are called the simplex S_n .

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The collection of points (x_1, \dots, x_n) such that $x_i \geq 0$ and $\sum_{i=1}^n x_i = 1$ are called the simplex S_n .

- ▶ Each point of the simplex represents the abundance of the population.
- ▶ If we keep the total abundance fixed at 1, then any evolutionary dynamics will be a dynamic on the simplex.

A bit on equilibrium Points

When we have a system of differential equations

$$\dot{x} = f(x, y, z)$$

$$\dot{y} = g(x, y, z)$$

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Solutions to such a system are important because they are points of "0" velocity. Those points are called **equilibria points**

No all equilibria are the same

1. **Stable Equilibrium:** the system tends to return to that point after a perturbation
2. **Unstable Equilibrium:** the system moves away after a perturbation
3. **Saddle Point:** the system returns and moves away in different directions after a perturbation
4. **Center:** the system moves around the equilibrium
5. **Others**

END OF DETOUR

An important operator is **mutation**: this means that one species transform into others by different means (pure mutation, but also like eating).

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Let's consider again two species A and B .

- ▶ Let x and y be the abundances of A and B respectively, and assume the dynamic is on the simplex
- ▶ Suppose that A has fitness a , and mutates into B at rate m_{AB} . Similarly
- ▶ Suppose that B has fitness b and mutates into A at rate m_{BA} .
- ▶ We will assume that both $m_{AB} > 0$ and $m_{BA} > 0$

Then, the system of equations is given by

$$\dot{x} = ax - m_{AB}x + m_{BA}y - \phi x$$

$$\dot{y} = by - m_{BA}y + m_{AB}x - \phi y$$

since $x + y = 1$ and $\dot{x} + \dot{y} = 0$, we have $\phi(t) = ax + by$.

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Equilibrium Point? We shall solve $\dot{x} = 0$, $\dot{y} = 0$. Let's solve for x :

$$0 = \dot{x} = ax - m_{AB}x + m_{BA}y - (ax + by)x$$

replacing $y = 1 - x$ yields

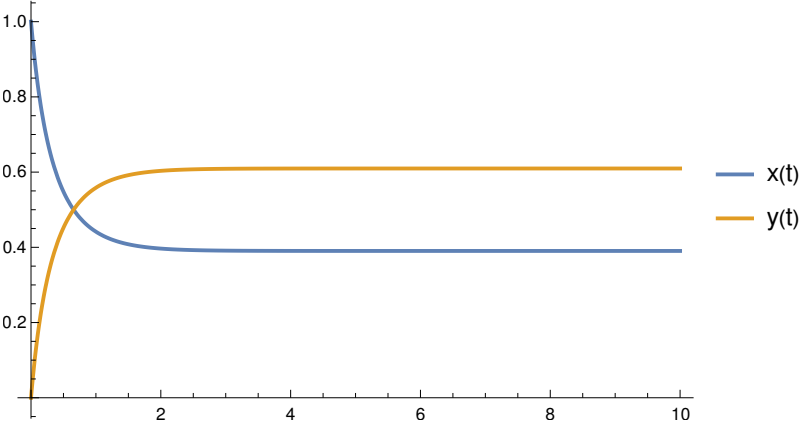
$$(b - a)x^2 + (a - b - (m_{AB} + m_{BA}))x + m_{BA}$$

- ▶ if $a = b$, then $(m_{AB} + m_{BA})x + m_{BA}$
- ▶ if $a \neq b$, then we have a quadratic equation. The analysis of equilibrium points is harder here.

$$x \rightarrow \frac{b - a + m_{AB} + m_{BA} \pm \sqrt{(b - a + m_{AB} + m_{BA})^2 - 4(b - a)m_{BA}}}{2(b - a)}$$

A system with $a = 5$, $b = 3$, $m_AB = 2$, $m_{BA} = 0.5$

System with Mutation



Mutation Matrix

Let's have a look again at our system of differential equations:

$$\dot{x} = ax - m_{AB}x + m_{BA}y - \phi x$$

$$\dot{y} = by - m_{BA}y + m_{AB}x - \phi y$$

Now consider another species, C, then we would have a system like

$$\dot{x} = ax - (m_{AB} + m_{AC})x + (m_{BA}y + m_{CA}z) - \phi x$$

$$\dot{y} = by - (m_{BA} + m_{BC})y + (m_{AB}x + m_{CA}z) - \phi y$$

$$\dot{z} = cz - (m_{CA} + m_{CB})z + (m_{AC}x + m_{BC}y) - \phi z$$

Then, we can write

$$Q = \begin{pmatrix} -(m_{AB} + m_{AC}) & m_{AB} & m_{AC} \\ m_{BA} & -(m_{BA} + m_{BC}) & m_{BC} \\ m_{CA} & m_{CB} & -(m_{CA} + m_{CB}) \end{pmatrix}$$

then, by using the notation $\vec{x} = (x, y, z)$, the mutation part can be written as

$$Q^T \vec{x}$$

In general, any mutation matrix Q is such that

1. For diagonal entries: $Q_{ii} \leq 0$
2. For off-diagonal entries $Q_{ij} \geq 0$
3. The sum of the entries of each column is 0.

Summary

Reproduction:

- ▶ Reproduction can be model as ax with $a > 0$ being the reproduction rate, meaning that each individual reproduces at rate a
- ▶ Dead can be model as $-dx$ meaning that each individual dies at rate d
- ▶ the simplest model is then $\dot{x} = (a - d)x$. We can allow $a \in \mathbb{R}$ and encode reproduction and death in the variable a

Selection and Competition:

- ▶ We allow more than one species, we can model the abundance of two species with two variables x and y
- ▶ If we fix the total abundance $x + y = 1$, then we introduce competence
- ▶ Average fitness *balance* the equations

$$\dot{x} = ax - \phi x$$

$$\dot{y} = by - \phi y$$

with $\phi(t) = ax(t) + by(t)$.

Mutation

- ▶ models the rate that one species transform into another one via a mutation

$$\dot{x} = ax - m_{AB}x + m_{BA}y - \phi x$$

$$\dot{y} = by - m_{BA}y + m_{AB}x - \phi y$$

- ▶ it can be encoded in a mutation matrix Q

Extra: Modelling Infections - SIR model

Suppose we have an infection in a population of size N .

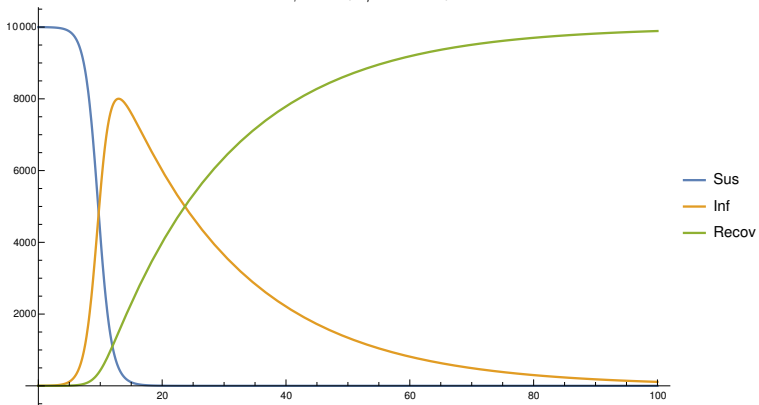
1. There are three type of subjects: **infected**, **susceptible**, and **recovered**
2. **Susceptible** agents can be **infected**
3. **Infected** can infect **susceptible**
4. **Recovered** cannot **infect** nor be **infected** (they are immune or dead)

We have the following dynamics

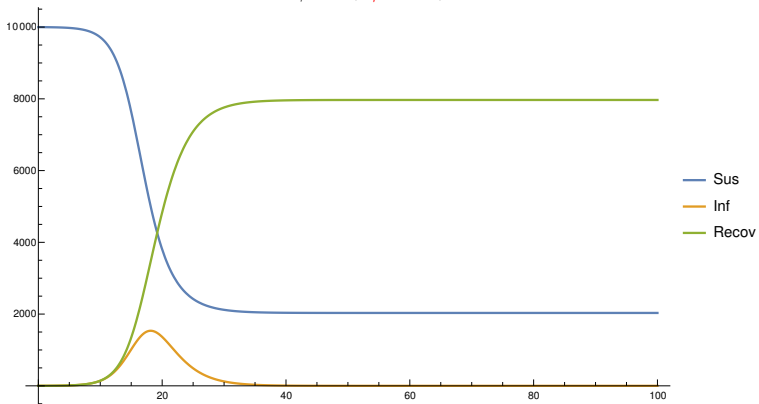
1. An **infected** agent meets a random agent at rate β and infects her
2. **Infected** agents recover at rate γ

Can we write the model?

SIR with $\beta = 1$, $\gamma = 0.05$, $N = 10000$

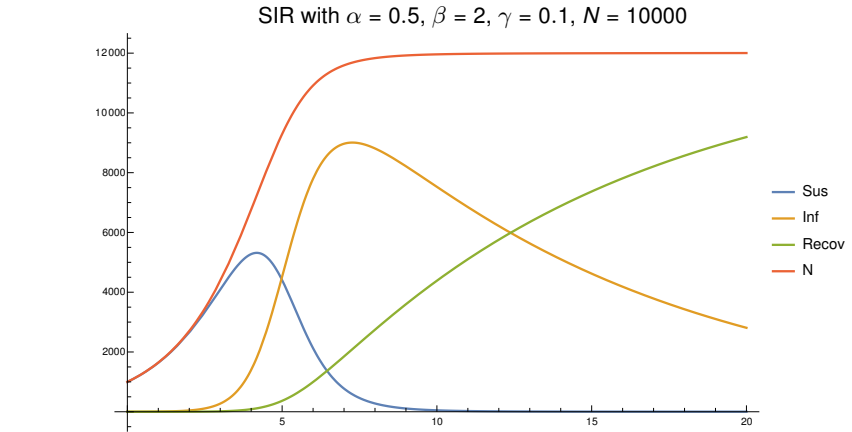


SIR with $\beta = 1$, $\gamma = 0.5$, $N = 10000$



What if we allow the susceptible population to reproduce in our model? e.g. susceptible reproduce at rate α .

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Lecture 3: Evolutionary Games

We already studied three ideas

- ▶ Reproduction
- ▶ Selection
- ▶ Mutation

however, we studied one last example at the end of Lecture 2

$$\dot{S} = -\beta \frac{S}{N} \cdot I$$

$$\dot{I} = \beta \frac{S}{N} \cdot I - \gamma I$$

$$\dot{R} = \gamma I$$

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 1. Each unit of **Infected** attacks at rate β and infects a random agent

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 1. Each unit of **Infected** attacks at rate β and infects a random agent
 2. Each unit of **Infected** attacks at rate 1 a random agent, and gains β units of mass.
- ▶ In this case (due to the interpretation we are making) everything that is loss by the susceptible is adquired by the infected, but this is not always true.

If a lion eats a zebra, the Zebras lose some mass (say M), but the Lions don't get M extra mass, and some of the mass of the Zebra will go to other animals o the enviroment

Consider two species A and B with abundance $x(t)$ and $y(t)$ with $x + y = 1$.

We will imagine that agents are moving in such a way at rate $1/2$ a pair of agents meet

Competition and Collaboration in the Simplex Consider the following tables of interactions: M_{UV} means what does the agent of type U gets when meeting an agent of type V

	A	B
A	-1	3
B	0.5	1

So our model of competition-collaboration is the following: Each agent starts an interaction with a random agent at rate 1.

1. Call x_A and x_B the abundances of species A and B respectively
2. Since at each 1 a pair of random agents meet we have that:
 - ▶ meeting between two agents of A occurs at rate $x_A^2/2$, and both get -1 of abundance
 - ▶ meeting between two agents of B occurs at rate $x_B^2/2$,
 - ▶ meeting between agents of A and B occurs at rate $x_A x_B$
3. From the point of view of A , we have

$$\dot{x}_A = \frac{x_A^2}{2} \cdot (-1) \cdot 2 + x_A x_B \cdot 3 - \phi(t) x_A$$

	A	B
A	-1	3
B	0.5	1

Miremos la ecuación $\dot{x}_A = \frac{x_A^2}{2} \cdot (-1) \cdot 2 + x_A x_B \cdot 3$

$$\dot{x}_A = \underbrace{\frac{x_A^2}{2}}_{\text{Rate meet AA}} \cdot \overbrace{(-1)}^{\text{outcome}} \cdot \underbrace{2}_{\text{two agents}} + \underbrace{x_A x_B}_{\text{Rate meet AB}} \cdot \underbrace{3}_{\text{outcome}} \cdot \overbrace{1}^{\text{one agent of A}} - \phi(t)x_A$$

and cancelling the terms, we have

$$\dot{x}_A(t) = (-1 \cdot x_A(t) + 3 \cdot x_B(t) - \phi(t))x_A$$

and thus the system

$$\dot{x}_A = (-1 \cdot x_A + 3 \cdot x_B - \phi)x_A$$

$$\dot{x}_B = (0.5 \cdot x_A + x_B - \phi)x_B$$

Payoff matrices

In evolutionary game theory we will assume some sort of interaction between species, and when they meet some reward-loss occurs: this is encoded by the Payoff matrix

		Against	
		A	B
Play	A	M_{AA}	M_{AB}
	B	M_{BA}	M_{BB}

This matrix means

- ▶ If an individual of type A meet another of type A , both get M_{AA}
- ▶ If B meets B , both get M_{BB}
- ▶ if A and B meets, A gets M_{AB} , and B gets M_{BA}

Then, we can define the fitness of both species. Let $x_A(t)$ and $x_B(t)$ be the abundance of each species, then

$$f_A(t) = M_{AA}x_A(t) + M_{AB}x_B(t)$$

$$f_B(t) = M_{BA}x_A(t) + M_{BB}x_B(t)$$

which can also be written in a matrix way as

$$f = M\vec{x}$$

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$$f = M\vec{x}$$

Then, we have

$$\dot{x}_A = (f_A - \phi)x_A$$

$$\dot{x}_B = (f_B - \phi)x_B$$

An interpretation is: the fitness of the species is no longer an intrinsic quantity of the species but something that depends on your interaction with other agents.

Since we are in the simplex, $x_A + x_B = 1$, then the fitness of a species is the average payoff by interacting with a random agent, assuming that all **interactions are equally likely**

$$f_A(t) = M_{AA}x_A(t) + M_{AB}x_B(t).$$

With this new idea of dynamic fitness we can formulate the evolutionary dynamic in the simplex, without mutation, by

$$\dot{x}_A = x_A(f_A - \phi)$$

$$\dot{x}_B = x_B(f_B - \phi)$$

and since $\dot{x}_A + \dot{x}_B = 0$ we have

$$\phi = x_A f_A + x_B f_B = M_{AA} x_A^2 + M_{AB} x_A x_B + M_{BA} x_B x_A + M_{BB} x_B^2 = x^T M x$$

Games and Dynamics

With this new idea of dynamic fitness we can formulate the evolutionary dynamic in the simplex, without mutation, by

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Using that $x_A = 1 - x_B$, can write

$$\begin{aligned}\dot{x}_A &= x_A(f_A - \phi) = x_A(f_A - x_A f_A - x_B f_B) \\ &= x_A(x_B f_A - x_B f_B) \\ &= x_A x_B (f_A - f_B) \\ &= x_A (1 - x_A) (f_A - f_B)\end{aligned}$$

Therefore, an equilibrium is found when the two fitness are the same (as expected!) or when one of the species disappears

Games and Dynamics: Example 1

Consider a population of Zebras and Lions.

		Against	
		Z	L
Play	Z	3	1
	L	5	0

Suppose that individuals meet in a very random fashion: choose a random individual U and then U meets a random individual V .

- ▶ Think about Zebras and Lions as a sort of citizenship
- ▶ If U is a lion, and V is a lion: U changes, being a Zebra will help him to improve the fitness
- ▶ If U is lion, and V is zebra: U is happy, changing will decrease the fitness
- ▶ if U is zebra and V is lion: U is happy
- ▶ if U is zebra and V is zebra: U changes to lion

Games and Dynamics: Example 1

Consider a population of Zebras and Lions.

		Against	
		Z	L
Play	Z	3	1
	L	5	0

Suppose that individuals meet in a very random fashion: choose a random individual U and then U meets a random individual V .

- ▶ Think about Zebras and Lions as a sort of citizenship
- ▶ If U is a lion, and V is a lion: U changes, being a Zebra will help him to improve the fitness
- ▶ If U is lion, and V is zebra: U is happy, changing will decrease the fitness
- ▶ if U is zebra and V is lion: U is happy
- ▶ if U is zebra and V is zebra: U changes to lion

At the end we find some sort of equilibrium where both populations are more or less the same

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At the end we find some sort of equilibrium where both populations co-exists

Games and Dynamics: Example 2

Consider a population of Zebras and Lions.

		Against	
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Play	Z	5	0
	L	3	1

Exercise: what happen in this case?

Games and Dynamics: Example 2

Consider a population of Zebras and Lions.

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Exercise: what happen in this case?

Answer: Two zebras are happy, two Lions are happy, but when a Zebra meets a Lion both want to change.

Games and Dynamics: Example 2

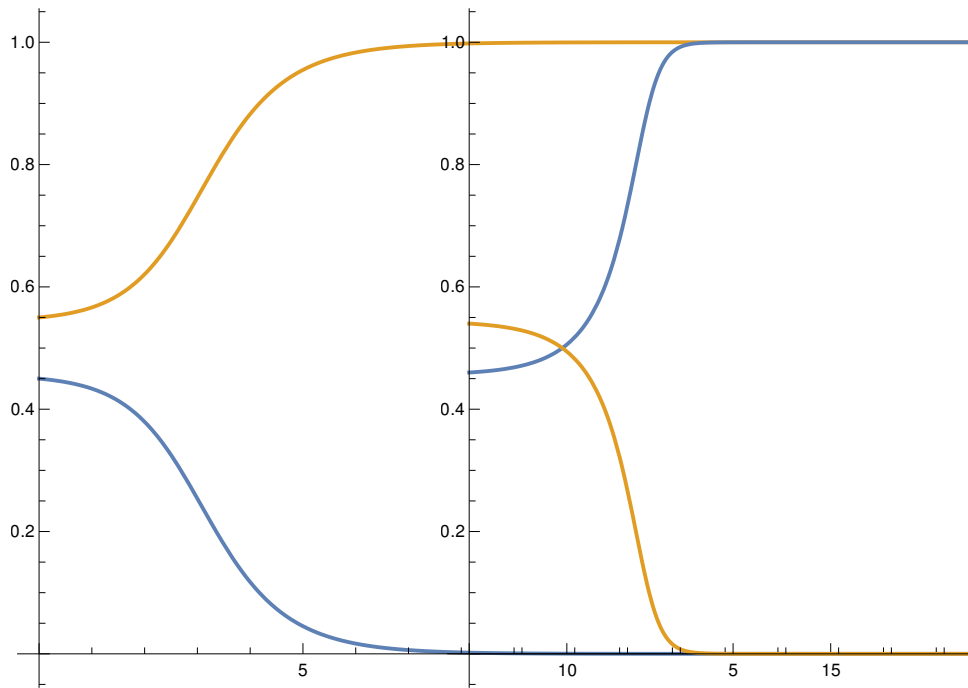
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Exercise: what happen in this case?

Answer: Two zebras are happy, two Lions are happy, but when a Zebra meets a Lion both want to change.

In terms of dynamics: Both population can survive, but they cannot co-exist. This depends on the initial values



Games and Dynamics: Example 3

We can make our modelling a bit more realistic by adding context to the Payoff matrix.

Example: hawks and doves

Consider a population of hawks and doves engaged in a game over a resource, like territory or food. The prize corresponds to a gain in fitness G , while an injury reduces fitness by C :

- If two doves meet, they divide the good, obtaining in average $G/2$.
- If a dove meets a hawk, it flees with 0, while that of the hawk increases by G .
- If a hawk meets a hawk, they fight. The fitness of the winner is increased by G , that of the loser reduced by C , so that the average increase in fitness is $(G - C)/2$.

This gives us the matrix

	Hawk	Dove
Hawk	$\frac{G-C}{2}$	G
Dove	0	$\frac{G}{2}$

In this case

$$\dot{x}_D = x_D((1 - x_D)f_D - (1 - x_D)f_H) = x_D(1 - x_D) \left(\frac{C - G}{2} - Cx_D/2 \right).$$

Example: hawks and doves

For simplicity, assume the prize $G = 1$. Our payoff-matrix is

	H	D
H	$\frac{1-C}{2}$	1
D	0	$1/2$

We shall analyse different values for C .

1. We first should notice that $\dot{x}_D = 0$ when

$$\frac{C-1}{2} - \frac{Cx_D}{2} = 0, \quad x_D = 0, \quad \text{or } x_D = 1$$

2. $\frac{C-1}{C} \in (0, 1)$ only when $C > 1$, otherwise it is negative or greater than 1

For sake of being interesting, assume that $x_D(0) \in (0, 1)$.

1. Case I: $C > 1$ hawk fights are risky

▶ $DD \rightarrow H$

▶ $DH \rightarrow D$

▶ $HD \rightarrow H$

▶ $HH \rightarrow D$

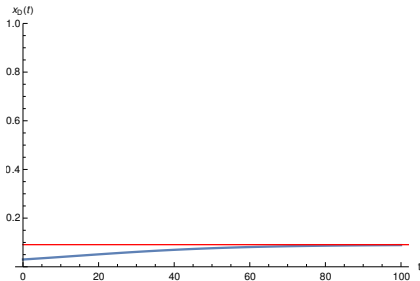
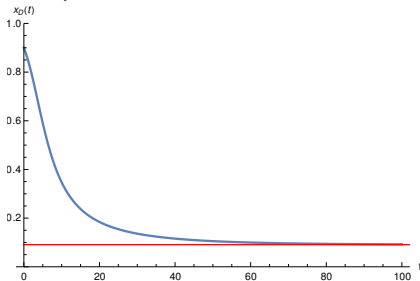
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Examples with $C = 1.1$



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In this case poor Doves will die out. Even when $C = 1$, a hawk has no motive to "change" into a dove.

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Examples with $C = 1$

