

INVESTMENTS IN EDUCATION DEVELOPMENT

# Deterministic models of natural selection and their relation to ecology

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# **Theoretical background**





### Newton law of motion

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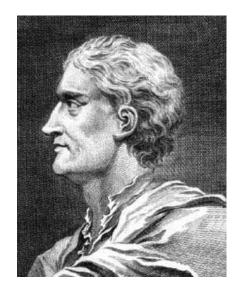
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$$p = mx',$$
  
 $F = mx''$ 







### Newton law of motion

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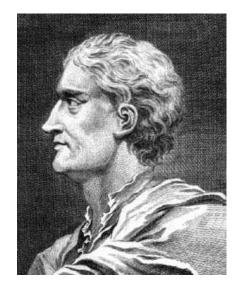
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$$p = mx',$$
  
 $F = mx''$ 

Simple rearrangement:

$$\boldsymbol{x}' = \frac{1}{m}\boldsymbol{p}$$
$$\boldsymbol{F} = m\boldsymbol{x}'' = m (\boldsymbol{x}')' = m \left(\frac{\boldsymbol{p}}{m}\right)' = \boldsymbol{p}'$$







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$$egin{aligned} m{p} &= m m{x}', \ m{F} &= m m{x}'' \end{aligned}$$

Simple rearrangement:

Hence

$$\boldsymbol{x}' = \frac{1}{m}\boldsymbol{p}$$
$$\boldsymbol{F} = m\boldsymbol{x}'' = m (\boldsymbol{x}')' = m \left(\frac{\boldsymbol{p}}{m}\right)' = \boldsymbol{p}'$$

$$oldsymbol{x}' = rac{1}{m} oldsymbol{p}$$
 $oldsymbol{p}' = oldsymbol{F}(oldsymbol{x})$ 





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### **Bipartite system**

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$$oldsymbol{x}' = rac{1}{m} oldsymbol{p}$$
  
 $oldsymbol{p}' = oldsymbol{F}(oldsymbol{x})$ 

$$\boldsymbol{F}(\boldsymbol{x}) = \frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x}$$





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$$oldsymbol{x}' = rac{1}{m} oldsymbol{p}$$
 $oldsymbol{p}' = oldsymbol{F}(oldsymbol{x})$ 

$$\boldsymbol{F}(\boldsymbol{x}) = \frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x}$$

Consequently, the system is of the form

Central force

$$\boldsymbol{x}' = \frac{1}{m} \boldsymbol{p}$$
$$\boldsymbol{p}' = \frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x}$$





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$$\boldsymbol{x}' = \frac{1}{m} \boldsymbol{p}$$
$$\boldsymbol{p}' = \frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x}$$





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$$\boldsymbol{x} = -\frac{m}{m}\boldsymbol{p}$$

$$\boldsymbol{p}' = \frac{cm}{\|\boldsymbol{x}\|^3}\boldsymbol{x}$$
Kinetic energy:  $\frac{1}{2}m\|\boldsymbol{x}'\|^2 = \frac{1}{2m}\|\boldsymbol{p}\|^2$ 
Potential energy:  $\frac{cm}{\|\boldsymbol{x}\|}$ 
Total energy (Hamiltonian):

$$H(\boldsymbol{x},\boldsymbol{p}) = \frac{1}{2m} \|\boldsymbol{p}\|^2 + \frac{cm}{\|\boldsymbol{x}\|}$$

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The following holds:

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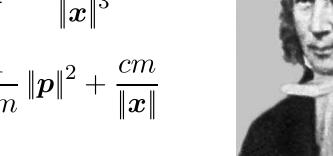
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 $\boldsymbol{x}' = \frac{1}{m} \boldsymbol{p}$  $\boldsymbol{p}' = \frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x}$ Hamiltonian:  $H(\boldsymbol{x}, \boldsymbol{p}) = \frac{1}{2m} \|\boldsymbol{p}\|^2 + \frac{cm}{\|\boldsymbol{x}\|}$ 



$$abla_{\boldsymbol{x}} H(\boldsymbol{x}, \boldsymbol{p}) = \frac{\partial H}{\partial \boldsymbol{x}} = -\frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x} = -\boldsymbol{p}'$$

$$abla_{\boldsymbol{p}}H(\boldsymbol{x},\boldsymbol{p}) = rac{\partial H}{\partial \boldsymbol{p}} = rac{1}{m}\boldsymbol{p} = \boldsymbol{x}'$$





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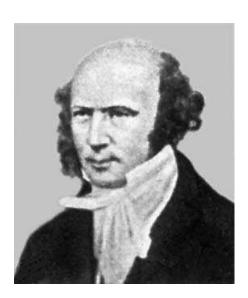
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Alternative approaches  $\boldsymbol{x}' = \frac{1}{m} \boldsymbol{p}$  $\boldsymbol{p}' = \frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x}$ 

Hamiltonian: 
$$H(oldsymbol{x},oldsymbol{p}) = rac{1}{2m} \|oldsymbol{p}\|^2 + rac{cm}{\|oldsymbol{x}\|}$$



$$oldsymbol{x}'= egin{array}{c} rac{\partial H}{\partial oldsymbol{p}} \end{array}$$

$$p' = -rac{\partial H}{\partial x}$$



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Alternative approaches  $\boldsymbol{x}' = \frac{1}{m} \boldsymbol{p}$  $\boldsymbol{p}' = \frac{cm}{\|\boldsymbol{x}\|^3} \boldsymbol{x}$ 

Hamiltonian: 
$$H(\boldsymbol{x},\boldsymbol{p}) = \frac{1}{2m} \|\boldsymbol{p}\|^2 + \frac{cm}{\|\boldsymbol{x}\|}$$

$$\begin{pmatrix} \boldsymbol{x} \\ \boldsymbol{p} \end{pmatrix}' = \begin{pmatrix} \mathsf{O} & \mathsf{E} \\ -\mathsf{E} & \mathsf{O} \end{pmatrix} \begin{pmatrix} \nabla_{\boldsymbol{x}} H(\boldsymbol{x}, \boldsymbol{p}) \\ \nabla_{\boldsymbol{p}} H(\boldsymbol{x}, \boldsymbol{p}) \end{pmatrix}.$$

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 $oldsymbol{x}' = rac{1}{m} oldsymbol{p}$   $oldsymbol{p}' = rac{cm}{\|oldsymbol{x}\|^3} oldsymbol{x}$ 

Hamiltonian: 
$$H(\boldsymbol{x},\boldsymbol{p}) = \frac{1}{2m} \|\boldsymbol{p}\|^2 + \frac{cm}{\|\boldsymbol{x}\|}$$

$$\begin{pmatrix} \boldsymbol{x} \\ \boldsymbol{p} \end{pmatrix}' = \begin{pmatrix} \mathbf{O} & \mathbf{E} \\ -\mathbf{E} & \mathbf{O} \end{pmatrix} \begin{pmatrix} \nabla_{\boldsymbol{x}} H(\boldsymbol{x}, \boldsymbol{p}) \\ \nabla_{\boldsymbol{p}} H(\boldsymbol{x}, \boldsymbol{p}) \end{pmatrix}.$$
  
Moreover:  $\frac{\partial}{\partial t} H(\boldsymbol{x}, \boldsymbol{p}) = \left(\frac{\partial H}{\partial \boldsymbol{x}}\right)^{\mathsf{T}} \boldsymbol{x}' + \left(\frac{\partial H}{\partial \boldsymbol{p}}\right)^{\mathsf{T}} \boldsymbol{p}' = 0$ 





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$$\boldsymbol{x}' = \mathsf{J}(\boldsymbol{x}) \nabla H(\boldsymbol{x})$$
 where  $\mathsf{J}(\boldsymbol{x}) = -\mathsf{J}(\boldsymbol{x})^\mathsf{T}$ 





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$$oldsymbol{x}' = \mathsf{J}(oldsymbol{x}) 
abla H(oldsymbol{x})$$
 where  $\mathsf{J}(oldsymbol{x}) = -\mathsf{J}(oldsymbol{x})^\mathsf{T}$ 

### The following holds:

$$\frac{\partial}{\partial t}H(\boldsymbol{x}) = \left(\nabla H(\boldsymbol{x})\right)^{\mathsf{T}}\boldsymbol{x}' = \left(\nabla H(\boldsymbol{x})\right)^{\mathsf{T}}\mathsf{J}(\boldsymbol{x})\nabla H(\boldsymbol{x}) = 0$$





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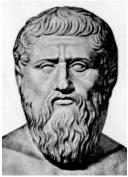
 $\mathbf{x}' = \mathsf{J}(\mathbf{x}) \nabla H(\mathbf{x})$  where  $\mathsf{J}(\mathbf{x}) = -\mathsf{J}(\mathbf{x})^{\mathsf{T}}$ 

### The following holds:

$$\frac{\partial}{\partial t}H(\boldsymbol{x}) = \left(\nabla H(\boldsymbol{x})\right)^{\mathsf{T}}\boldsymbol{x}' = \left(\nabla H(\boldsymbol{x})\right)^{\mathsf{T}}\mathsf{J}(\boldsymbol{x})\nabla H(\boldsymbol{x}) = 0$$

Plato, Timaios 28a: "First then, in my judgment, we must make a distinction and ask,

What is that which always is and has no becoming; and what is that which is always becoming and never is?"



Nejprve jest podle mého mínění stanoviti tuto rozluku: co jest to, co stále jest, ale vzniku nemá, a co jest to, co stále vzniká, ale nikdy není jsoucí.



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$$\boldsymbol{x}' = \mathsf{J}(\boldsymbol{x}) \nabla H(\boldsymbol{x})$$
 where  $\mathsf{J}(\boldsymbol{x}) = -\mathsf{J}(\boldsymbol{x})^\mathsf{T}$ 

The following holds:

$$\frac{\partial}{\partial t}H(\boldsymbol{x}) = \left(\nabla H(\boldsymbol{x})\right)^{\mathsf{T}}\boldsymbol{x}' = \left(\nabla H(\boldsymbol{x})\right)^{\mathsf{T}}\mathsf{J}(\boldsymbol{x})\nabla H(\boldsymbol{x}) = 0$$

Plato, Timaios 28a: "First then, in my judgment, we must make a distinction and ask,

What is that which always is and has no becoming; (Hamiltonian) and what is that which is always becoming and never is?" (state variables)

Nejprve jest podle mého mínění stanoviti tuto rozluku: co jest to, co stále jest, ale vzniku nemá, a co jest to, co stále vzniká, ale nikdy není jsoucí.





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OP Vzdělávání

time t



x = x(t) ... size of a population at the time t

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• Malthus: x' = rx







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 $\boldsymbol{x} = \boldsymbol{x}(t)$  . . . size of a population at the time t

• Malthus:  $x' = rx \Rightarrow$  exponential growth







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• Malthus:  $x' = rx \Rightarrow$  exponential growth

• Modification: 
$$x' = x(r - f(x))$$





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Alternative approaches  $x = x(t) \dots$  size of a population at the time t

• Malthus:  $x' = rx \Rightarrow$  exponential growth

• Modification: 
$$x' = x(r - f(x))$$

### Models of communities:

 $x_i = x_i(t) \dots$  size of the *i*-th population from community at the time *t*.





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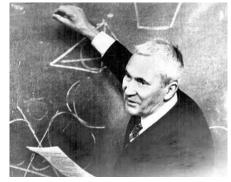
Alternative approaches  $x = x(t) \dots$  size of a population at the time t

• Malthus:  $x' = rx \implies exponential growth$ 

• Modification: 
$$x' = x(r - f(x))$$

### Models of communities: $x_i = x_i(t) \dots$ size of the *i*-th population from community at the time *t*.

Kolmogorov: 
$$x'_{i} = x_{i}(r_{i} - f_{i}(\boldsymbol{x})), \quad i = 1, 2, ..., n$$







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• Malthus:  $x' = rx \Rightarrow$  exponential growth

• Modification: 
$$x' = x(r - f(x))$$

Models of communities:  $x_i = x_i(t) \dots$  size of the *i*-th population from community at the time *t*.

Kolmogorov: 
$$x'_{i} = x_{i}(r_{i} - f_{i}(\boldsymbol{x})), \quad i = 1, 2, ..., n$$

Lotka and Volterra:

the simplest option – all of the functions  $f_i$  are linear.







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Alternative approaches  $x = x(t) \dots$  size of a population at the time t

$$\blacksquare \quad \text{Malthus: } x' = rx \qquad \Rightarrow \text{exponential growth}$$

• Modification: 
$$x' = x(r - f(x))$$

Models of communities:  

$$x_i = x_i(t) \dots$$
 size of the *i*-th population from community  
at the time *t*.

Kolmogorov: 
$$x'_{i} = x_{i}(r_{i} - f_{i}(\boldsymbol{x})), \quad i = 1, 2, ..., n$$

Lotka and Volterra: the simplest option – all of the functions  $f_i$  are linear.  $f_i(\boldsymbol{x}) = f_i(x_1, x_2, \dots, x_n) = \sum_{j=1}^n b_{ij} x_j = (\mathsf{B}\boldsymbol{x})_i$ 



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$$\blacksquare \quad \text{Malthus: } x' = rx \qquad \Rightarrow \text{exponential growth}$$

• Modification: 
$$x' = x(r - f(x))$$

Models of communities:  

$$x_i = x_i(t) \dots$$
 size of the *i*-th population from community  
at the time *t*.

Kolmogorov: 
$$x'_{i} = x_{i}(r_{i} - f_{i}(\boldsymbol{x})), \quad i = 1, 2, ..., n$$

# Lotka and Volterra: the simplest option – all of the functions $f_i$ are linear. $f_i(\boldsymbol{x}) = f_i(x_1, x_2, \dots, x_n) = \sum_{j=1}^n b_{ij} x_j = (\mathsf{B}\boldsymbol{x})_i$

$$x'_i = x_i \big( r_i - (\mathsf{B}\boldsymbol{x})_i \big), \quad i = 1, 2, \dots, n$$





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• Malthus:  $x' = rx \Rightarrow$  exponential growth

• Modification: 
$$x' = x(r - f(x))$$

Models of communities:  $x_i = x_i(t) \dots$  size of the *i*-th population from community at the time *t*.

Kolmogorov: 
$$x'_{i} = x_{i}(r_{i} - f_{i}(\boldsymbol{x})), \quad i = 1, 2, ..., n$$

Lotka and Volterra: the simplest option – all of the functions  $f_i$  are linear.  $f_i(\boldsymbol{x}) = f_i(x_1, x_2, \dots, x_n) = \sum_{j=1}^n b_{ij} x_j = (\mathsf{B}\boldsymbol{x})_i$ 

$$oldsymbol{x}' = oldsymbol{x} \circ (oldsymbol{r} - {\sf B}oldsymbol{x})$$





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$$x' = x(r - by),$$
  
$$y' = y(-s + cx).$$





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$$x' = x(r - by),$$
  
$$y' = y(-s + cx).$$

Transformation 
$$\xi = \ln x$$
,  $\eta = \ln y$ 

$$\begin{aligned} \xi' &= r - b \mathrm{e}^{\eta}, \\ \eta' &= -s + c \mathrm{e}^{\xi}. \end{aligned}$$





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### **Bipartite system**

$$x' = x(r - by),$$
  
$$y' = y(-s + cx).$$

Transformation 
$$\xi = \ln x$$
,  $\eta = \ln y$ .

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$$\xi' = r - b e^{\eta},$$
  
$$\eta' = -s + c e^{\xi}.$$



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$$\begin{aligned} x' &= x(r - by), \\ y' &= y(-s + cx). \end{aligned}$$

### **Bipartite system**

$$H(x,y) = cx + by - \ln x^{s}y^{r}$$
$$\frac{\partial}{\partial x}H(x,y) = c - \frac{s}{x} \qquad \frac{\partial}{\partial y}H(x,y) = b - \frac{r}{y}$$

$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} -xy \left( b - \frac{r}{y} \right) \\ xy \left( c - \frac{s}{x} \right) \end{pmatrix} = \begin{pmatrix} 0 & -xy \\ xy & 0 \end{pmatrix} \begin{pmatrix} \frac{\partial}{\partial x} H(x, y) \\ \frac{\partial}{\partial y} H(x, y) \end{pmatrix}$$



### **Example: classical predator-prey model**

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$$x' = x(r - by),$$
  
$$y' = y(-s + cx).$$

#### **Bipartite system**

$$H(x,y) = cx + by - \ln x^{s}y^{r}$$
$$\frac{\partial}{\partial x}H(x,y) = c - \frac{s}{x} \qquad \frac{\partial}{\partial y}H(x,y) = b - \frac{r}{y}$$

$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} -xy \left( b - \frac{r}{y} \right) \\ xy \left( c - \frac{s}{x} \right) \end{pmatrix} = \begin{pmatrix} 0 & -xy \\ xy & 0 \end{pmatrix} \begin{pmatrix} \frac{\partial}{\partial x} H(x, y) \\ \frac{\partial}{\partial y} H(x, y) \end{pmatrix}$$

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The fitest species survives and propagates.





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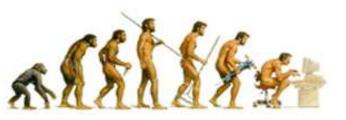
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A change of the relative abundance of species in a community is proportional to difference of its fitness and an overall fitness.







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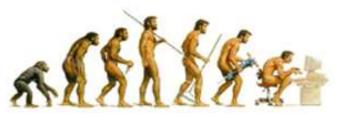
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A change of the relative abundance of species in a community is proportional to difference of its fitness and an overall fitness.

•  $x_i = x_i(t)$  ... frequency of the *i*-th species (alleletype)







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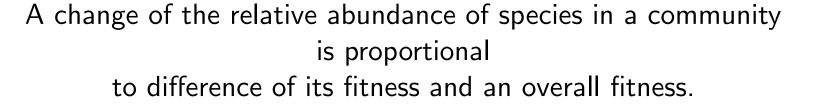
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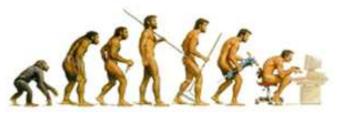
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•  $x_i = x_i(t) \dots$  frequency of the *i*-th species (alleletype)  $\sum_{i=1}^n x_i = 1$ 







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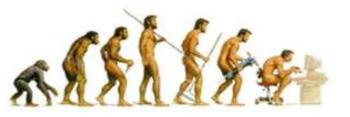
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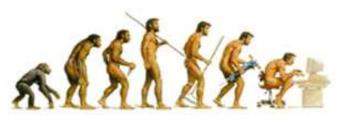
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 $\blacksquare$   $\overline{f}$  ... overall fitness







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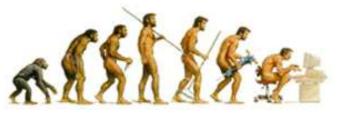
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$$ar{f}$$
 . . . overall fitness,  $ar{f} = \sum\limits_{i=1}^n x_i f_i$ 







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 . . . overall fitness,  $ar{f} = \sum\limits_{i=1}^n x_i f_i$ 

$$f_i = f_i({m x}), \ ar{f} = ar{f}({m x}).$$





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$$f_i = f_i(oldsymbol{x})$$
,  $ar{f} = ar{f}(oldsymbol{x})$ .

time change 
$$x_i \sim f_i(\boldsymbol{x}) - \sum_{j=1}^n x_j f_j(\boldsymbol{x}), \quad i = 1, 2, \dots, n$$



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time change 
$$x_i \sim f_i(\boldsymbol{x}) - \sum_{j=1}^n x_j f_j(\boldsymbol{x}), \quad i = 1, 2, \dots, n$$
$$\frac{x'_i}{x} = c \left( f_i(\boldsymbol{x}) - \sum_{j=1}^n x_j f_j(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$



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time change 
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$$x'_i = cx_i \left( f_i(\boldsymbol{x}) - \sum_{j=1}^n x_j f_j(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$

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time change 
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$$x'_i = x_i \left( f_i(\boldsymbol{x}) - \sum_{j=1}^n x_j f_j(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$

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$$oldsymbol{x}' = oldsymbol{x} \circ ig(\mathsf{E} - oldsymbol{x} \mathbf{1}^\mathsf{T}) oldsymbol{f}(oldsymbol{x})$$



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Community consisting of k populations  $n_i = n_i(t) \dots$  size of the *i*-th population  $r_i = r_i(n) \dots$  growth rate of the *i*-th population

$$n'_i = r_i(\boldsymbol{n})n_i, \quad i = 1, 2, \dots, k$$







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$$n'_i = r_i(\boldsymbol{n})n_i, \quad i = 1, 2, \dots, k$$

 $N = \sum_{j=1}^{\kappa} n_j \dots \text{size of community}$   $x_i = n_i / N \dots \text{ relative abundance of the } i\text{-th population}$  $f_i(\boldsymbol{x}) = r_i(N\boldsymbol{x}) = r_i(\boldsymbol{n})$ 







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 $N = \sum_{j=1}^{\kappa} n_j \dots$  size of community

 $x_i = n_i/N$  ... relative abundance of the *i*-th population  $f_i(\boldsymbol{x}) = r_i(N\boldsymbol{x}) = r_i(\boldsymbol{n})$  $N' = \sum_{j=1}^k n'_j = \sum_{j=1}^k r_j(\boldsymbol{n})n_j = N \sum_{j=1}^k x_j f_j(\boldsymbol{x})$ 







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 $N = \sum_{j=1}^{n} n_j \dots$  size of community  $x_i = n_i/N$  ... relative abundance of the *i*-th population  $f_i(\boldsymbol{x}) = r_i(N\boldsymbol{x}) = r_i(\boldsymbol{n})$  $N' = \sum_{j=1}^{k} n'_{j} = \sum_{j=1}^{k} r_{j}(\boldsymbol{n}) n_{j} = N \sum_{j=1}^{k} x_{j} f_{j}(\boldsymbol{x})$  $x'_{i} = \frac{n'_{i}N - n_{i}N'}{N^{2}} = \frac{r_{i}(n)n_{i} - n_{i}\sum_{j=1}^{n}r_{j}(n)n_{j}}{N^{2}}$  $= x_i \left( f_i(\boldsymbol{x}) - \sum_{j=1}^k x_j f_j(\boldsymbol{x}) \right)$ 



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$$n'_i = r_i(\boldsymbol{n})n_i, \quad i = 1, 2, \dots, k$$

selection system

$$N = \sum_{j=1}^{k} n_j \dots \text{size of community}$$

$$x_i = n_i/N \dots \text{relative abundance of the } i\text{-th population}$$

$$f_i(\boldsymbol{x}) = r_i(N\boldsymbol{x}) = r_i(\boldsymbol{n})$$

$$N' = \sum_{j=1}^{k} n'_j = \sum_{j=1}^{k} r_j(\boldsymbol{n})n_j = N \sum_{j=1}^{k} x_j f_j(\boldsymbol{x})$$

$$x'_i = \frac{n'_i N - n_i N'}{N^2} = \frac{r_i(\boldsymbol{n})n_i - n_i \sum_{j=1}^{k} r_j(\boldsymbol{n})n_j}{N} =$$

$$= x_i \left( f_i(\boldsymbol{x}) - \sum_{j=1}^{k} x_j f_j(\boldsymbol{x}) \right)$$



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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$
 (1)



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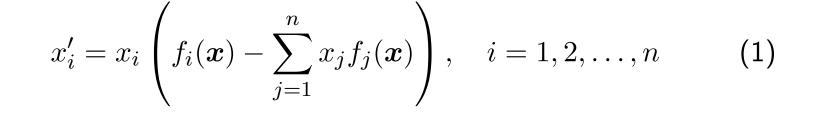
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$$S_n = \left\{ \boldsymbol{x} \in \bar{\mathbb{R}}_+^n : \mathbf{1}^\mathsf{T} \boldsymbol{x} = 1 \right\} \qquad S_n^\circ = \left\{ \boldsymbol{x} \in \mathbb{R}_+^n : \mathbf{1}^\mathsf{T} \boldsymbol{x} = 1 \right\}$$
$$\partial S_n = S_n \smallsetminus S_n^\circ$$

n-dimensional simplex, its interior and its boundary, respectively.





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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$
 (1)

•  $\boldsymbol{x}(0) \in S_n \Rightarrow \boldsymbol{x}(t) \in S_n$  for all  $t \ge 0$ 



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 (1)

 $x(0) \in S_n \Rightarrow x(t) \in S_n \text{ for all } t \ge 0$  $x(0) \in \partial S_n \Rightarrow x(t) \in \partial S_n \text{ for all } t \ge 0$ 



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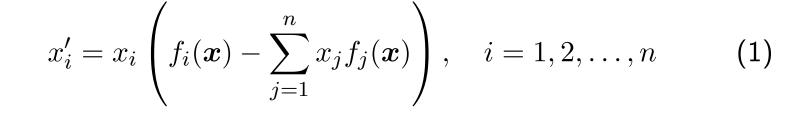
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$$x(0) \in S_n \Rightarrow x(t) \in S_n \text{ for all } t \ge 0$$

$$x(0) \in \partial S_n \Rightarrow x(t) \in \partial S_n \text{ for all } t \ge 0$$

$$x(0) \in S_n^\circ \Rightarrow x(t) \in S_n^\circ \text{ for all } t \ge 0$$

Let  $\Psi: S_n \to \mathbb{R}$  be a continuous function. Put  $g_i = f_i + \Psi$ for all  $i \in \{1, 2, ..., n\}$ . Then x solves the equation (1) if and only if it solves the equation

$$x'_i = x_i \left( g_i(\boldsymbol{x}) - \sum_{j=1}^n x_j g_j(\boldsymbol{x}) \right), \qquad i = 1, 2, \dots, n$$





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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$
 (1)

**Theorem:** Let there is a point  $\hat{x} \in S_n$  and its naighbourhood U such that

$$\sum_{i=1}^n \hat{x}_i f_i(\boldsymbol{x}) > \overline{f}(\boldsymbol{x}) \quad \text{for all } \boldsymbol{x} \in S_n \cap (U \smallsetminus \{\hat{\boldsymbol{x}}\}).$$

Then  $\hat{x}$  is asymptotically stable equilibrium of the equation.



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**Theorem:** Let there is a point  $\hat{x} \in S_n$  and its naighbourhood U such that

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Then  $\hat{m{x}}$  is asymptoticaly stable equilibrium of the equation.

 $\hat{x}$  ... evolutionary stable state.



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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$

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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$

$$f_i(x_1, x_2, \dots, x_n) = \sum_{k=1}^n a_{ik} x_k$$



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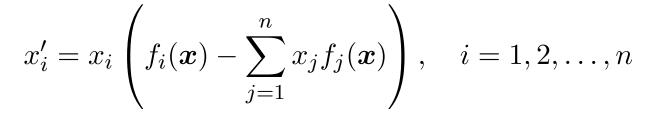
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$$f_i(x_1, x_2, \dots, x_n) = \sum_{k=1}^n a_{ik} x_k$$

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$$x'_{i} = x_{i} \left( \sum_{k=1}^{n} a_{ik} x_{k} - \sum_{j=1}^{n} \sum_{k=1}^{n} x_{j} a_{jk} x_{k} \right), \quad i = 1, 2, \dots, n$$





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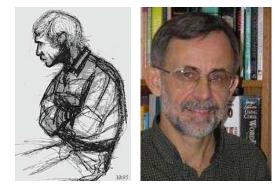
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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$

$$f_i(x_1, x_2, \dots, x_n) = \sum_{k=1}^n a_{ik} x_k$$

$$x'_{i} = x_{i} \left( \sum_{k=1}^{n} a_{ik} x_{k} - \sum_{j=1}^{n} \sum_{k=1}^{n} x_{j} a_{jk} x_{k} \right), \quad i = 1, 2, \dots, n$$







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 $x'_i$ 

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Example: n = 2

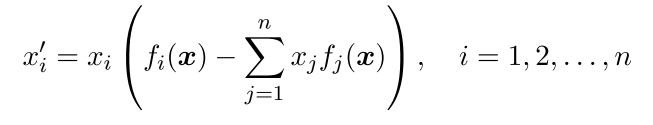
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$$f_i(x_1, x_2, \dots, x_n) = \sum_{k=1}^n a_{ik} x_k$$

$$= x_i \left( \sum_{k=1}^n a_{ik} x_k - \sum_{j=1}^n \sum_{k=1}^n x_j a_{jk} x_k \right), \quad i = 1, 2, \dots, n$$
$$x'_i = x_i \left( (\mathsf{A}\boldsymbol{x})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{x} \right), \quad i = 1, 2, \dots, n$$



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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$

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 $\mathbf{m}$ 

$$x'_{i} = x_{i} \left( \sum_{k=1}^{n} a_{ik} x_{k} - \sum_{j=1}^{n} \sum_{k=1}^{n} x_{j} a_{jk} x_{k} \right), \quad i = 1, 2, \dots, n$$
$$x'_{i} = x_{i} ((\mathsf{A}\boldsymbol{x})_{i} - \boldsymbol{x}^{\mathsf{T}} \mathsf{A}\boldsymbol{x}), \quad i = 1, 2, \dots, n$$
$$x'_{i} = x_{i} (\boldsymbol{e}_{i} - \boldsymbol{x})^{\mathsf{T}} \mathsf{A}\boldsymbol{x}, \quad i = 1, 2, \dots, n$$



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$$x'_{i} = x_{i} \left( f_{i}(\boldsymbol{x}) - \sum_{j=1}^{n} x_{j} f_{j}(\boldsymbol{x}) \right), \quad i = 1, 2, \dots, n$$

$$f_i(x_1, x_2, \dots, x_n) = \sum_{k=1}^n a_{ik} x_k$$

 $\mathbf{m}$ 

$$x'_{i} = x_{i} \left( \sum_{k=1}^{n} a_{ik} x_{k} - \sum_{j=1}^{n} \sum_{k=1}^{n} x_{j} a_{jk} x_{k} \right), \quad i = 1, 2, \dots, n$$
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$$x'_{i} = x_{i} (\boldsymbol{e}_{i} - \boldsymbol{x})^{\mathsf{T}} \mathsf{A}\boldsymbol{x}, \quad i = 1, 2, \dots, n$$
$$\boldsymbol{x}'_{i} = \boldsymbol{x} \circ ((\mathsf{E} - \boldsymbol{x} \mathbf{1}^{\mathsf{T}}) \mathsf{A}\boldsymbol{x})$$





### **Properties of the equation with linear fitnesses**

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$$x'_{i} = x_{i} ((\mathsf{A}\boldsymbol{x})_{i} - \boldsymbol{x}^{\mathsf{T}} \mathsf{A}\boldsymbol{x}), \quad i = 1, 2, \dots, n$$
(2)



# **Properties of the equation with linear fitnesses**

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$$x'_{i} = x_{i} ((\mathsf{A}\boldsymbol{x})_{i} - \boldsymbol{x}^{\mathsf{T}} \mathsf{A}\boldsymbol{x}), \quad i = 1, 2, \dots, n$$
<sup>(2)</sup>

 $\blacksquare$   $S_n$ ,  $\partial S_n$ ,  $S_n^{\circ}$  are positive invariant sets of the equation (2).



### **Properties of the equation with linear fitnesses**

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$$x'_{i} = x_{i} ((\mathsf{A}\boldsymbol{x})_{i} - \boldsymbol{x}^{\mathsf{T}} \mathsf{A}\boldsymbol{x}), \quad i = 1, 2, \dots, n$$
(2)

 $S_n$ ,  $\partial S_n$ ,  $S_n^{\circ}$  are positive invariant sets of the equation (2).

Adding af a diagonal matrix to the matrix A or adding of a constant vector to a row (a column) of the matrix A does not change the solution of the equation (2).



# **Equivalence of the replicator equation** and of the Lotka-Volterra ones

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 $x'_i = x_i ((\mathsf{A}\boldsymbol{x})_i - \boldsymbol{x}^\mathsf{T}\mathsf{A}\boldsymbol{x}), \quad i = 1, 2, \dots, n$ 



# **Equivalence of the replicator equation** and of the Lotka-Volterra ones

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$$x'_i = x_i ((\mathsf{A}\boldsymbol{x})_i - \boldsymbol{x}^\mathsf{T}\mathsf{A}\boldsymbol{x}), \quad i = 1, 2, \dots, n$$

Put  $b_{ij} = a_{nj} - a_{ij}$ ,  $r_i = a_{in} - a_{nn}$  for i, j = 1, 2, ..., n - 1. Transformation both of the independent variable (time) and of the functions  $x_i$  given by the equalities

$$\tau = \int_{0}^{t} x_n(s) ds, \qquad y_j = \frac{x_j}{x_n}, \quad j = 1, 2, \dots, n-1$$

maps the orbits of the replicator equation initialising in the interior of the simplex  $S_n^\circ$  to the orbits of the Lotka-Volterra system

$$\frac{\mathrm{d}y_j}{\mathrm{d}\tau} = y_j \left( r_j - \sum_{k=1}^{n-1} b_{jk} y_k \right), \qquad j = 1, 2, \dots, n-1$$

initialising in the interior of the positive orthant  $\mathbb{R}^{n-1}_+$ .



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$$\mathsf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$



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$$\mathsf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

The corresponding Lotka-Volterra equation is

$$\frac{\mathrm{d}y}{\mathrm{d}\tau} = y \big( a_{12} - a_{22} - (a_{21} - a_{11})y \big)$$



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The corresponding Lotka-Volterra equation is

$$\frac{\mathrm{d}y}{\mathrm{d}\tau} = y \left( a_{12} - a_{22} - (a_{21} - a_{11})y \right)$$

This is the (Verhulst) logistic equation.



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$$\mathsf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

The corresponding Lotka-Volterra equation is

$$\frac{\mathrm{d}y}{\mathrm{d}\tau} = y \left( a_{12} - a_{22} - (a_{21} - a_{11})y \right)$$

This is the (Verhulst) logistic equation.

Solution with the initial condition  $y(0) = y_0 > 0$  is

$$y(\tau) = \frac{(a_{12} - a_{22})y_0}{(a_{21} - a_{11})y_0 + (a_{12} - a_{22} - (a_{21} - a_{11})y_0)e^{(a_{22} - a_{12})\tau}}$$



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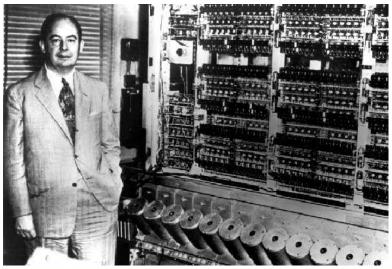
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### Normal form two player game: quadruple $\mathcal{G} = (X, Y, u, v)$ , where X, Y are finite sets and u, v are functions $X \times Y \to \mathbb{R}$ .

Sets X and Y ... sets of strategies of the first and of the second player, respectively.

Functins u and v... payoff function of the first and of the second player, respectively.







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Alternative approaches  $X = \{1, 2, \dots, n\} \quad Y = \{1, 2, \dots, m\}$  $a_{ij} = u(i, j) \quad b_{ji} = v(i, j)$ 

 $\mathsf{A} = \begin{pmatrix} a_{11} & a_{12} & \dots & a_{1m} \\ a_{21} & a_{22} & \dots & a_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nm} \end{pmatrix}, \quad \mathsf{B} = \begin{pmatrix} b_{11} & b_{12} & \dots & b_{1n} \\ b_{21} & b_{22} & \dots & b_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ b_{m1} & b_{m2} & \dots & b_{mn} \end{pmatrix}.$ 





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$$X = \{1, 2, \dots, n\} \quad Y = \{1, 2, \dots, m\}$$
$$a_{ij} = u(i, j) \quad b_{ji} = v(i, j)$$

$$\mathsf{A} = \begin{pmatrix} a_{11} & a_{12} & \dots & a_{1m} \\ a_{21} & a_{22} & \dots & a_{2m} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \dots & a_{nm} \end{pmatrix}, \quad \mathsf{B} = \begin{pmatrix} b_{11} & b_{12} & \dots & b_{1n} \\ b_{21} & b_{22} & \dots & b_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ b_{m1} & b_{m2} & \dots & b_{mn} \end{pmatrix}$$

Using this notation, we have

$$u(i,j) = a_{ij} = e_i^\mathsf{T} \mathsf{A} e_j, \qquad v(i,j) = b_{ji} = e_j^\mathsf{T} \mathsf{B} e_i.$$

Matrix A, B ... payoff matrix.



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$$\mathcal{G} = (X, Y, u, v) = (\mathsf{A}, \mathsf{B})$$

A game can be represented by the table

			player			
		1	2		m	
	1	$b_{11}$	$b_{21}$		$b_{m1}$	
	4	$a_{11}$	$a_{12}$	•••	$a_{1m}$	
player 1	2	$b_{12}$	$b_{22}$		$b_{m2}$	
		$a_{21}$	$a_{22}$	•••	$a_{2m}$	
play 		÷	÷	· · .	÷	
	m	$b_{1n}$	$b_{2n}$		$b_{mn}$	
	n	$a_{n1}$	$a_{n2}$		$a_{nm}$	





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Alternative approaches Probability extension of a bimatrix game  $\mathcal{G} = (X, Y, u, v)$ : quadruple  $\mathcal{G}^* = (X^*, Y^*, u^*, v^*)$ ;

 $X^* = S_n, Y^* = S_m,$  $u^*, v^*$  are functions  $X^* \times Y^* \to \mathbb{R}$ , defined by

$$u^*(\boldsymbol{x}, \boldsymbol{y}) = \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y}, \qquad v^*(\boldsymbol{x}, \boldsymbol{y}) = \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x}.$$

X, Y ... pure strategies

 $X^*$ ,  $Y^*$  ... mixed strategies





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# X, Y ... pure strategies

 $X^*$ ,  $Y^*$  ... mixed strategies  $\mathcal{G}^* = (X^*, Y^*, u^*, v^*) = (\mathsf{A}, \mathsf{B})$ 



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Alternative approaches  $ar{x} \in X^* \dots$  the best reply to the strategy  $oldsymbol{y} \in Y^*$ :  $(\forall oldsymbol{x} \in X^*) \ u^*(oldsymbol{x}, oldsymbol{y}) = oldsymbol{x}^\mathsf{T} \mathsf{A} oldsymbol{y} \ge oldsymbol{x}^\mathsf{T} \mathsf{A} oldsymbol{y} = u^*(oldsymbol{x}, oldsymbol{y})$ 

 $ar{oldsymbol{y}} \in Y^* \dots$  the best reply to the strategy  $oldsymbol{x} \in X^*$ :  $(\forall oldsymbol{y} \in Y^*) \; v^*(oldsymbol{x}, oldsymbol{oldsymbol{y}}) = oldsymbol{oldsymbol{y}}^\mathsf{T}\mathsf{B}oldsymbol{x} \ge oldsymbol{y}^\mathsf{T}\mathsf{B}oldsymbol{x} = v^*(oldsymbol{x}, oldsymbol{y}).$ 





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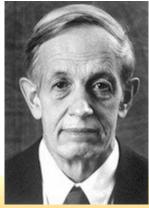
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Alternative approaches  $ar{x} \in X^* \dots$  the best reply to the strategy  $oldsymbol{y} \in Y^*$ :  $(\forall oldsymbol{x} \in X^*) \ u^*(oldsymbol{x}, oldsymbol{y}) = oldsymbol{x}^\mathsf{T} \mathsf{A} oldsymbol{y} \ge oldsymbol{x}^\mathsf{T} \mathsf{A} oldsymbol{y} = u^*(oldsymbol{x}, oldsymbol{y})$ 

 $ar{m{y}} \in Y^* \dots$  the best reply to the strategy  $m{x} \in X^*$ :  $(\forall m{y} \in Y^*) \ v^*(m{x}, ar{m{y}}) = ar{m{y}}^\mathsf{T} \mathsf{B} m{x} \ge m{y}^\mathsf{T} \mathsf{B} m{x} = v^*(m{x}, m{y}).$ 

 $(\bar{\boldsymbol{x}}, \bar{\boldsymbol{y}}) \in X^* \times Y^* \dots$  (Nash) equilibrium:  $\forall (\boldsymbol{x} \in X^*) \forall (\boldsymbol{y} \in Y^*) \ \bar{\boldsymbol{x}}^\mathsf{T} \mathsf{A} \bar{\boldsymbol{y}} \ge \boldsymbol{x}^\mathsf{T} \mathsf{A} \bar{\boldsymbol{y}}, \quad \bar{\boldsymbol{y}}^\mathsf{T} \mathsf{B} \bar{\boldsymbol{x}} \ge \boldsymbol{y}^\mathsf{T} \mathsf{B} \bar{\boldsymbol{x}}$ 

i.e.  $ar{x}$  is the best reply to  $ar{y}$  and at the same time  $ar{y}$  is the best reply to  $ar{x}$ 







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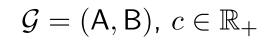
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# $\mathcal{G}=(\mathsf{A},\mathsf{B})$ , $c\in\mathbb{R}_+$

**Partnership** game

### $\mathcal{G}$ is the *c*-partnership game:

$$(\exists \mathsf{D}, \boldsymbol{p}, \boldsymbol{q}) \mathsf{A} = \mathsf{D} + \mathbf{1}\boldsymbol{q}^\mathsf{T}, \quad \mathsf{B} = c\mathsf{D}^\mathsf{T} + \mathbf{1}\boldsymbol{p}^\mathsf{T}$$

i.e. 
$$a_{ij} = d_{ij} + q_j$$
,  $b_{ji} = cd_{ij} + p_i$ 





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# $\mathcal{G}=(\mathsf{A},\mathsf{B})$ , $c\in\mathbb{R}_+$

**Partnership** game

### $\mathcal{G}$ is the *c*-partnership game:

$$(\exists \mathsf{D}, \boldsymbol{p}, \boldsymbol{q}) \mathsf{A} = \mathsf{D} + \mathbf{1}\boldsymbol{q}^\mathsf{T}, \quad \mathsf{B} = c\mathsf{D}^\mathsf{T} + \mathbf{1}\boldsymbol{p}^\mathsf{T}$$
  
.e.  $a_{ij} = d_{ij} + q_j, \quad b_{ji} = cd_{ij} + p_i$ 

 $\mathcal{G}$  is the *identical interest game*:

$$c=1, \quad p=o=q$$

i.e.  $A = B^T$ 

I





 $\mathcal{G} = (\mathsf{A},\mathsf{B})$ 

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$$\mathcal{G} = (\mathsf{A},\mathsf{B})$$

 $\mathcal{G}$  is a symmetric game :

i.e. 
$$u(i, j) = v(j, i)$$

$$A = B$$





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Alternative approaches  $\mathcal{G} = (\mathsf{A},\mathsf{B})$ 

 $\mathcal{G}$  is a symmetric game (matrix game): A = B i.e. u(i, j) = v(j, i)







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Alternative approaches  $\mathcal{G} = (\mathsf{A},\mathsf{B})$ 

${\cal G}$ is a symmetric ga	ame (matrix game):
	A=B
i.e. $u(i, j) = v(j, i)$	
$() - \pi x^2$	

 $(\bar{\boldsymbol{x}}, \bar{\boldsymbol{y}}) \in X^{*2}$  forms an *equilibrium*:

$$(\forall \boldsymbol{x}, \boldsymbol{y} \in X^*) \ \bar{\boldsymbol{x}}^\mathsf{T} \mathsf{A} \bar{\boldsymbol{y}} \geq \boldsymbol{x}^\mathsf{T} \mathsf{A} \bar{\boldsymbol{y}}, \quad \bar{\boldsymbol{y}}^\mathsf{T} \mathsf{A} \bar{\boldsymbol{x}} \geq \boldsymbol{y}^\mathsf{T} \mathsf{A} \bar{\boldsymbol{x}}$$





 $\mathcal{G} = (\mathsf{A},\mathsf{B})$ 

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Alternative approaches  $\begin{array}{l} \mathcal{G} \text{ is a symmetric game (matrix game):} \\ \mathsf{A} = \mathsf{B} \\ \text{i.e. } u(i,j) = v(j,i) \\ (\bar{\boldsymbol{x}},\bar{\boldsymbol{y}}) \in X^{*2} \text{ forms an equilibrium:} \\ (\forall \boldsymbol{x}, \boldsymbol{y} \in X^{*}) \; \bar{\boldsymbol{x}}^{\mathsf{T}} \mathsf{A} \bar{\boldsymbol{y}} \geq \boldsymbol{x}^{\mathsf{T}} \mathsf{A} \bar{\boldsymbol{y}}, \quad \bar{\boldsymbol{y}}^{\mathsf{T}} \mathsf{A} \bar{\boldsymbol{x}} \geq \boldsymbol{y}^{\mathsf{T}} \mathsf{A} \bar{\boldsymbol{x}} \end{array}$ 

 $ar{x} \in X^*$  is the symmetric (Nash) equilibrium:  $(ar{x}, ar{x})$ , i.e.  $(\forall x \in X^*) \ ar{x}^{\mathsf{T}} \mathsf{A} ar{x} > x^{\mathsf{T}} \mathsf{A} ar{x}$ 







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$$\begin{aligned} x'_i &= x_i \big( (\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y} \big), \qquad i = 1, 2, \dots, n, \\ y'_j &= y_j \big( (\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x} \big), \qquad j = 1, 2, \dots, m, \end{aligned}$$





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$$x'_i = x_i (\boldsymbol{e}_i - \boldsymbol{x})^\mathsf{T} \mathsf{A} \boldsymbol{y}, \qquad i = 1, 2, \dots, n,$$
  
 $y'_j = y_j (\boldsymbol{e}_j - \boldsymbol{y})^\mathsf{T} \mathsf{B} \boldsymbol{x}, \qquad j = 1, 2, \dots, m.$ 





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$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} x \\ y \end{pmatrix} \circ \begin{pmatrix} 0 & (\mathsf{E} - x \mathbf{1}^{\mathsf{T}}) \mathsf{A} \\ (\mathsf{E} - y \mathbf{1}^{\mathsf{T}}) \mathsf{B} & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$





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$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} x \\ y \end{pmatrix} \circ \begin{pmatrix} \mathsf{O} & (\mathsf{E} - x \mathbf{1}^\mathsf{T}) \mathsf{A} \\ (\mathsf{E} - y \mathbf{1}^\mathsf{T}) \mathsf{B} & \mathsf{O} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$

$$\begin{pmatrix} x \\ y \end{pmatrix}' = \begin{pmatrix} x \\ y \end{pmatrix} \circ \begin{bmatrix} \mathsf{E} - \begin{pmatrix} \mathbf{1} x^\mathsf{T} & \mathsf{O} \\ \mathsf{O} & \mathbf{1} y^\mathsf{T} \end{bmatrix} \begin{pmatrix} \mathsf{O} & \mathsf{A} \\ \mathsf{B} & \mathsf{O} \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}$$





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# **Famous conflicts**



### Hawks and doves

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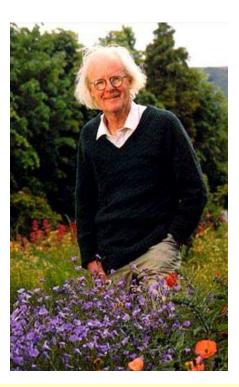
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	Hawk	Dove
Hawk	$\frac{1}{2}V - C$	V
Dove	0	$\frac{1}{2}V$

V - value of the resource C - cost of the contest







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# Mating strategies

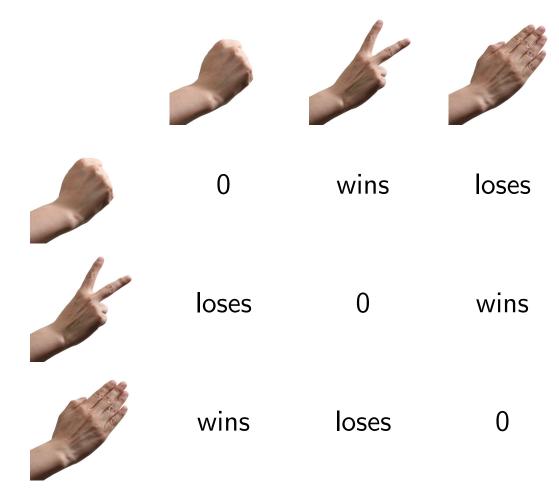
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Replicator equation I			and the second	a Barris	
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Mating strategies Battle of sexes	large teritory, several females	and the second	0	wins	loses
Replicator equation		X			
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approaches	teritory with single female	2000 - C	loses	0	wins
	no teritory		wins	loses	0



# Mating strategies

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### he rock-scissors-paper game







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	Rock	Scissors	Paper
Rock	0	1	-1
Scissors	-1	0	1
Paper	1	-1	0







# **Battle of sexes**

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Entrants	Strategies		
male	faithful	philanderer	
female	соу	fast	

V - value of the offspring2C – parental investment

c - cost of engagement period







# Battle of sexes

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Entrants	Strategies		
male	faithful	philanderer	
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V – value of the offspring 2C – parental investment

c – cost of engagement period



		female		
		соу	fast	
male	faithful	V - C - c $V - C - c$	V - C $V - C$	
ů	philanderer	0	V - 2C $V$	





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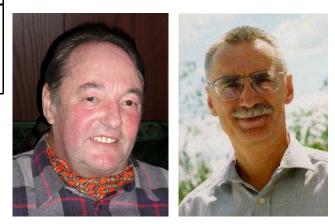
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male	faithful	philanderer	
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V - value of the offspring 2C - parental investment c - cost of engagement period



		female	
		соу	fast
male	faithful	V - C - c $V - C - c$	V - C $V - C$
Ĕ	philanderer	0	V - 2C $V$





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$$\begin{aligned} x'_i &= x_i \big( (\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y} \big), \qquad i = 1, 2, \dots, n \\ y'_j &= y_j \big( (\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x} \big), \qquad j = 1, 2, \dots, m \end{aligned}$$



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$$\begin{aligned} x'_i &= x_i \big( (\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y} \big), \qquad i = 1, 2, \dots, n \\ y'_j &= y_j \big( (\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x} \big), \qquad j = 1, 2, \dots, m \end{aligned}$$

 $\blacksquare S_n \times S_m, \ \partial S_n \times \partial S_m \ S_n^{\circ} \times S_m^{\circ} \text{ are positive invariant sets of}$ the equations





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 $\blacksquare S_n \times S_m, \ \partial S_n \times \partial S_m \ S_n^\circ \times S_m^\circ \text{ are positive invariant sets of the equations,}$ 

consequently, the n + m-dimensional system can be reduced to the n + m - 2-dimensional one:

$$\begin{aligned} x'_i &= x_i (\boldsymbol{e}_i - \boldsymbol{x})^\mathsf{T} \left( \tilde{\mathsf{A}} \boldsymbol{y} - \hat{\boldsymbol{a}} \right), & i = 1, 2, \dots, n-1, \\ y'_j &= y_j (\boldsymbol{e}_j - \boldsymbol{y})^\mathsf{T} \left( \tilde{\mathsf{B}} \boldsymbol{x} - \hat{\boldsymbol{b}} \right), & j = 1, 2, \dots, m-1. \end{aligned}$$

where 
$$\tilde{a}_{ij} = a_{ij} - a_{im} - a_{nj} + a_{nm}$$
,  $\hat{a}_i = a_{nm} - a_{im}$   
 $\tilde{b}_{ij} = b_{ij} - b_{in} - b_{mj} + b_{mn}$ ,  $\hat{b}_j = b_{mn} - b_{jn}$ .





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$$\mathsf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \qquad \mathsf{B} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}.$$





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$$\mathsf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}, \qquad \mathsf{B} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}.$$

#### Reduced system:

$$x' = x(1-x)(\alpha_1 y - \alpha_2)$$
  
$$y' = y(1-y)(\beta_1 x - \beta_2)$$

where 
$$\alpha_1 = a_{11} - a_{12} - a_{21} + a_{22}$$
,  $\alpha_2 = a_{22} - a_{12}$ ,  
 $\beta_1 = b_{11} - b_{12} - b_{21} + b_{22}$ ,  $\beta_2 = b_{22} - b_{12}$ 





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 $\beta_1 = b_{11} - b_{12} - b_{21} + b_{22}$ ,  $\beta_2 = b_{22} - b_{12}$ 

Phase space:  $[0,1] \times [0,1]$ 



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$$\alpha_1 = a_{11} - a_{12} - a_{21} + a_{22}$$
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 $\beta_1 = b_{11} - b_{12} - b_{21} + b_{22}$ ,  $\beta_2 = b_{22} - b_{12}$ 

Phase space:  $[0,1] \times [0,1]$ 

Stationary solutions: (0,0), (0,1), (1,0), (1,1)corresponds to the pure strategies. If  $\alpha_1 \neq 0$ ,  $0 < \frac{\alpha_2}{\alpha_1} < 1$ ,  $\beta_1 \neq 0$ ,  $0 < \frac{\beta_2}{\beta_1} < 1$ , the interior stationary solution:  $\left(\frac{\beta_2}{\beta_1}, \frac{\alpha_2}{\alpha_1}\right)$ corresponds to mixed strategies.



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### Reduced system:

$$x' = x(1-x)(\alpha_1 y - \alpha_2)$$
  

$$y' = y(1-y)(\beta_1 x - \beta_2)$$

The variational matrix of the system:

$$J(0,0) = \begin{pmatrix} -\alpha_2 & 0\\ 0 & -\beta_2 \end{pmatrix}, \quad J(0,1) = \begin{pmatrix} \alpha_1 - \alpha_2 & 0\\ 0 & \beta_2 \end{pmatrix},$$
$$J(1,0) = \begin{pmatrix} \alpha_2 & 0\\ 0 & \beta_1 - \beta_2 \end{pmatrix}, \quad J(1,1) = \begin{pmatrix} \alpha_2 - \alpha_1 & 0\\ 0 & \beta_2 - \beta_1 \end{pmatrix},$$





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$$J(1,0) = \begin{pmatrix} \alpha_2 & 0\\ 0 & \beta_1 - \beta_2 \end{pmatrix}, \quad J(1,1) = \begin{pmatrix} \alpha_2 - \alpha_1 & 0\\ 0 & \beta_2 - \beta_1 \end{pmatrix},$$

$$J\left(\frac{\beta_2}{\beta_1}, \frac{\alpha_2}{\alpha_1}\right) = \begin{pmatrix} 0 & \frac{\alpha_1\beta_2(\beta_1 - \beta_2)}{\beta_1^2} \\ \frac{\alpha_2\beta_1(\alpha_1 - \alpha_2)}{\alpha_1^2} & 0 \end{pmatrix}$$





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 $x' = x(1-x)(\alpha_1 y - \alpha_2)$  $y' = y(1-y)(\beta_1 x - \beta_2)$ 

The stationary points corresponding to the pure strategies are saddle points or nodes, the stationary point corresponding to mixed strategies is saddle point or unstable focus.





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$$\begin{aligned} x'_i &= x_i \big( (\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y} \big), & i = 1, 2, \dots, n \\ y'_j &= y_j \big( (\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x} \big), & j = 1, 2, \dots, m \end{aligned}$$

N ... set of Nash equilibria of bimatrix game  $\mathcal{G}=(\mathsf{A},\mathsf{B})$  E ... set of stationary solutions of the system





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 $N \subseteq E$ 





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Alternative approaches  $\begin{aligned} x'_i &= x_i \big( (\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y} \big), \qquad i = 1, 2, \dots, n \\ y'_j &= y_j \big( (\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x} \big), \qquad j = 1, 2, \dots, m \end{aligned}$ 

 $N \dots$  set of Nash equilibria of bimatrix game  $\mathcal{G} = (\mathsf{A},\mathsf{B})$  $E \dots$  set of stationary solutions of the system

 $N \subseteq E$ 

$$(S_n^\circ \times S_m^\circ) \cap N = E \cap (S_n^\circ \times S_m^\circ)$$





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$$x'_i = x_i ((\mathsf{A}\boldsymbol{x})_i - \boldsymbol{x}^\mathsf{T}\mathsf{A}\boldsymbol{x}), \quad i = 1, 2, \dots, n$$

 $N \dots$  set of symmetric Nash equilibria of matrix game  $\mathcal{G} = \mathsf{A}$  $E \dots$  set of stationary solutions of the equation  $S \dots$  set of stable stationary solutions of the equation





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 $N \dots$  set of symmetric Nash equilibria of matrix game  $\mathcal{G} = \mathsf{A}$  $E \dots$  set of stationary solutions of the equation  $S \dots$  set of stable stationary solutions of the equation

 $S \subseteq N \subseteq E$ 





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 $\begin{array}{l} n=m=2\\ \text{Stationary solutions} \end{array}$ 

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$$\begin{aligned} x'_i &= x_i \big( (\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y} \big), \qquad i = 1, 2, \dots, n \\ y'_j &= y_j \big( (\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x} \big), \qquad j = 1, 2, \dots, m \end{aligned}$$

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Let us consider the system on  $S_n^\circ \times S_m^\circ$ 





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Let us consider the system on  $S_n^\circ \times S_m^\circ$ 

#### Substitution

$$\tilde{a}_{ij} = a_{ij} - a_{nj}, \ \hat{a}_i = a_{im} - a_{nm}, \\ \tilde{b}_{ji} = b_{ji} - b_{mi}, \ \hat{b}_j = b_{jn} - b_{mn},$$
  $\xi_i = \frac{x_i}{x_n}, \ \eta_j = \frac{y_j}{y_m},$ 

$$\xi'_{i} = \xi_{i} \frac{(\tilde{A}\boldsymbol{\eta})_{i} + \hat{a}_{i}}{1 + \mathbf{1}^{\mathsf{T}}\boldsymbol{\eta}}, \qquad i = 1, 2, \dots, n - 1,$$
$$\eta'_{j} = \eta_{j} \frac{(\tilde{B}\boldsymbol{\xi})_{j} + \hat{b}_{j}}{1 + \mathbf{1}^{\mathsf{T}}\boldsymbol{\xi}}, \qquad j = 1, 2, \dots, m - 1.$$





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Let us consider the system on  $S_n^\circ \times S_m^\circ$ 

Further substitution 
$$u_i = \ln \xi_i$$
,  $v_j = \ln \eta_j$   
$$u'_i = \frac{\sum_{k=1}^{m-1} \tilde{a}_{ik} e^{v_k} + \hat{a}_i}{1 + \sum_{k=1}^{m-1} e^{v_k}}, \qquad i = 1, 2, \dots, n-1,$$
$$u'_j = \frac{\sum_{k=1}^{n-1} \tilde{b}_{jk} e^{u_k} + \hat{b}_i}{1 + \sum_{k=1}^{n-1} e^{u_k}}, \qquad j = 1, 2, \dots, m-1.$$





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$$\begin{aligned} x'_i &= x_i \big( (\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y} \big), & i = 1, 2, \dots, n \\ y'_j &= y_j \big( (\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x} \big), & j = 1, 2, \dots, m \end{aligned}$$

Let us consider the system on  $S_n^\circ \times S_m^\circ$ 

Let (A, B) be c-partnership game and  $(\bar{x}, \bar{y}) \in S_n^{\circ} \times S_m^{\circ}$  is the Nash equilibrium. Then the function

$$H(\boldsymbol{x}, \boldsymbol{y}) = c \sum_{i=1}^{n} \bar{x}_i \ln x_i - \sum_{j=1}^{m} \bar{y}_j \ln y_j$$

is the invariant of the system.





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Let (A, B) be c-partnership game and  $(\bar{x}, \bar{y}) \in S_n^{\circ} \times S_m^{\circ}$  is the Nash equilibrium.

Substitution 
$$r_{ij} = a_{ij} - a_{nj} - a_{im} + a_{nm}$$
,  
 $u_i = \ln \frac{x_i}{x_n}$ ,  $v_j = \ln \frac{y_j}{y_m}$ ,  
For  $i = 1, 2, \dots, n-1$ ,  $j = 1, 2, \dots, m-1$ 

transforms the replicator system to the Hamiltonian one:

$$\begin{pmatrix} \boldsymbol{u} \\ \boldsymbol{v} \end{pmatrix}' = \begin{pmatrix} \mathsf{O} & \mathsf{R} \\ -\mathsf{R}^\mathsf{T} & \mathsf{O} \end{pmatrix} \begin{pmatrix} \nabla_{\boldsymbol{u}} H \\ \nabla_{\boldsymbol{v}} H \end{pmatrix}$$





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The types (behaviour patterns, strategies) do not replicate by inheritence but by imitation.





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The types (behaviour patterns, strategies) do not replicate by inheritence but by imitation.

Events:  $S_{ij}$  ... an individual of the type jmeets an individual of the type i

 $C_{ij}$  ... an individual of the type j addopts the type iProbabilities of the events during a time interval of length  $\Delta t$ :  $P(S_{ij}) \sim x_i$ ,  $P(C_{ij}|S_{ij}) \sim \Delta t$ ,  $P(C_{ij}|\neg S_{ij}) = 0$ .



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 $g_{ij}$  ... rate of proportionality

N ... size of population Expected number of individuals of the type i after the time interval  $\Delta t$ :

$$Nx_i(t + \Delta t) = Nx_i(t) + \sum_{j=1}^n \left( Nx_i(t) \right) g_{ij} x_j(t) \Delta t - \sum_{k=1}^n \left( Nx_k(t) \right) g_{ki} x_i(t) \Delta t$$



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$$x'_{i} = x_{i} \sum_{k=1}^{n} (g_{ik} - g_{ki}) x_{k}, \quad i = 1, 2, \dots, n.$$







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$$x'_{i} = x_{i} \sum_{k=1}^{n} (g_{ik} - g_{ki}) x_{k}, \quad i = 1, 2, \dots, n.$$

Probability of transition from the *j*-th type to the *i*-th depends on payoffs  $(Ax)_i$ ,  $(Ax)_j$ :  $g_{ij} = \varphi((Ax)_i, (Ax)_j)$ 



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A rule "imitate the better":  $\varphi(u,v) = \begin{cases} 1, & u > v, \\ 0, & u \leq v \end{cases}$ 



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$$x'_{i} = x_{i} \sum_{k=1}^{n} (g_{ik} - g_{ki}) x_{k}, \quad i = 1, 2, \dots, n.$$

Probability of transition from the *j*-th type to the *i*-th depends on payoffs  $(Ax)_i$ ,  $(Ax)_j$ :  $g_{ij} = \varphi((Ax)_i, (Ax)_j)$ 

A rule "imitate the better with effort which increase with expected gain":

$$\varphi(u,v) = \begin{cases} (u-v)^{\alpha}, & u > v, \\ 0, & u \le v \end{cases} \qquad \alpha > 0$$



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$$x'_{i} = x_{i} \sum_{k=1}^{n} (g_{ik} - g_{ki}) x_{k}, \quad i = 1, 2, \dots, n.$$

Probability of transition from the *j*-th type to the *i*-th depends on payoffs  $(Ax)_i$ ,  $(Ax)_j$ :  $g_{ij} = \varphi((Ax)_i, (Ax)_j)$ 

A rule "imitate the better with effort which increase with expected gain":

$$\varphi(u,v) = \begin{cases} (u-v)^{\alpha}, & u > v, \\ 0, & u \le v \end{cases} \qquad \alpha > 0$$

Replicator equation can be viewed as a particular case of the imitation dynamics equation for  $\alpha = 1$ .



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Growth rate of each subpopulation (behaviour pattern, strategy) is proportional to "the gain":

$$x_i(t+h) = c(t) (\mathsf{A}\boldsymbol{y}(t))_i x_i(t),$$
  
$$y_j(t+h) = d(t) (\mathsf{B}\boldsymbol{x}(t))_j y_j(t)$$





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$$x_i(t+h) = c(t) (\mathbf{A} \mathbf{y}(t))_i x_i(t),$$
  

$$y_j(t+h) = d(t) (\mathbf{B} \mathbf{x}(t))_j y_j(t)$$
  
For  $(\mathbf{x}(t), \mathbf{y}(t)) \in S_n \times S_m \Rightarrow (\mathbf{x}(t), \mathbf{y}(t)) \in S_n \times S_m,$   
the following has to hold  

$$1$$

$$c(t) = \frac{1}{\boldsymbol{x}(t)^{\mathsf{T}} \mathsf{A} \boldsymbol{y}(t)}, \quad d(t) = \frac{1}{\boldsymbol{y}(t)^{\mathsf{T}} \mathsf{B} \boldsymbol{x}(t)}, \quad a_{ij} > 0, \ b_{ij} > 0.$$







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$$\begin{aligned} x_i(t+h) &= c(t) (\mathsf{A} \boldsymbol{y}(t))_i \, x_i(t), \\ y_j(t+h) &= d(t) (\mathsf{B} \boldsymbol{x}(t))_j \, y_j(t) \\ \text{For } (\boldsymbol{x}(t), \boldsymbol{y}(t)) \in S_n \times S_m \Rightarrow (\boldsymbol{x}(t), \boldsymbol{y}(t)) \in S_n \times S_m, \\ \text{the following has to hold} \end{aligned}$$

$$c(t) = \frac{1}{\boldsymbol{x}(t)^{\mathsf{T}} \mathsf{A} \boldsymbol{y}(t)}, \quad d(t) = \frac{1}{\boldsymbol{y}(t)^{\mathsf{T}} \mathsf{B} \boldsymbol{x}(t)}, \quad a_{ij} > 0, \ b_{ij} > 0.$$

Hence

$$x_i(t+h) = x_i(t) \frac{(\mathsf{A}\boldsymbol{y}(t))_i}{\boldsymbol{x}(t)^\mathsf{T} \mathsf{A} \boldsymbol{y}(t)}, \quad y_j(t+h) = y_j(t) \frac{(\mathsf{B}\boldsymbol{x}(t))_j}{\boldsymbol{y}(t)^\mathsf{T} \mathsf{B} \boldsymbol{x}(t)}$$





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$$\Delta x_i(t) = x_i(t) \frac{(\mathsf{A}\boldsymbol{y}(t))_i - \boldsymbol{x}(t)^\mathsf{T} \mathsf{A}\boldsymbol{y}(t)}{\boldsymbol{x}(t)^\mathsf{T} \mathsf{A}\boldsymbol{y}(t)},$$
$$\Delta y_j(t) = y_j(t) \frac{(\mathsf{B}\boldsymbol{x}(t))_j - \boldsymbol{y}(t)^\mathsf{T} \mathsf{B}\boldsymbol{x}(t)}{\boldsymbol{y}(t)^\mathsf{T} \mathsf{B}\boldsymbol{x}(t)}$$







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$$\Delta x_i(t) = x_i(t) \frac{(\mathsf{A}\boldsymbol{y}(t))_i - \boldsymbol{x}(t)^{\mathsf{T}} \mathsf{A}\boldsymbol{y}(t)}{\boldsymbol{x}(t)^{\mathsf{T}} \mathsf{A}\boldsymbol{y}(t)},$$
$$\Delta y_j(t) = y_j(t) \frac{(\mathsf{B}\boldsymbol{x}(t))_j - \boldsymbol{y}(t)^{\mathsf{T}} \mathsf{B}\boldsymbol{x}(t)}{\boldsymbol{y}(t)^{\mathsf{T}} \mathsf{B}\boldsymbol{x}(t)}$$

$$\begin{aligned} x'_i &= x_i \frac{(\mathsf{A} \boldsymbol{y})_i - \boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y}}{\boldsymbol{x}^\mathsf{T} \mathsf{A} \boldsymbol{y}}, \qquad i = 1, 2, \dots, n, \\ y'_j &= y_j \frac{(\mathsf{B} \boldsymbol{x})_j - \boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x}}{\boldsymbol{y}^\mathsf{T} \mathsf{B} \boldsymbol{x}}, \qquad j = 1, 2, \dots, m. \end{aligned}$$

Interpretation of matrices A and B in this case differs from the one for the introduced continuous replicator equation.