

La relation *Ressource - Consommateur*

II - GAUSE

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Interaction Ressource-Consommateur

Ressource : Biotique ou abiotique

$x(t)$ = “quantité” de ressource à l’instant t

Dynamique de la Ressource seule

$$x(t + dt) = x(t) + dt \cdot f(x(t))$$

- $x(t + dt) = x(t) + dt \cdot r \cdot x(t)$ Croissance exponentielle
- $x(t + dt) = x(t) + dt \cdot r(x(t)) \cdot x(t)$ “Type logistique”
- $s(t + dt) = s(t) + dt \cdot D \cdot S_{in}$ Apport constant en substrat

Dynamique du consommateur

$$y(t) + dt = y(t) + dt \cdot (+ \text{“natalité”} - \text{“mortalité”})$$

- “natalité” = “taux de natalité” $\cdot y(t)$
- “mortalité” = “taux de mortalité” $\cdot y(t)$
- “taux de natalité” = $\mu(x(t), y(t))$
- “taux de mortalité” = $\nu(y(t))$

Interaction Ressource-Consommateur

Interaction

$$x(t + dt) = x(t) + dt \cdot f(x(t)) - dt \cdot c(x(t), y(t)) \cdot y(t)$$

$$y(t + dt) = y(t) + dt \cdot \mu(x(t), y(t)) \cdot y(t) - dt \cdot \nu(y(t)) \cdot y(t)$$

Une hypothèse forte :

$$\mu(x(t), y(t)) = Y \cdot c(x(t), y(t))$$

Proportionnalité entre ce qui est consommé et
l'accroissement de la population de consommateurs

Interaction Ressource-Consommateur

$$x(t + dt) = x(t) + dt \cdot \left(f(x(t)) - \frac{1}{Y} \mu(x(t), y(t)) \cdot y(t) \right)$$

$$y(t + dt) = y(t) + dt \cdot (\mu(x(t), y(t)) \cdot y(t) - \nu(y(t)) \cdot y(t))$$

$$\frac{dx(t)}{dt} = f(x(t)) - \frac{1}{Y} \mu(x(t), y(t)) \cdot y(t)$$

$$\frac{dy(t)}{dt} = \mu(x(t), y(t)) \cdot y(t) - \nu(y(t)) \cdot y(t)$$

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

Interaction Ressource-Consommateur

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

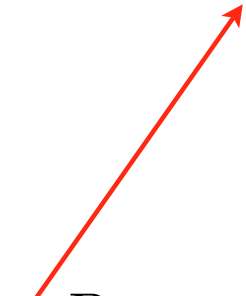
Modèle canonique

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

Interaction Ressource-Consommateur

$$\dot{x} = f(x)$$



- Dynamique de la ressource en l'absence de consommateur

$$\dot{x} = f(x) - \frac{1}{Y}\mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

Interaction Ressource-Consommateur

$$\dot{y} = -\nu(y) \cdot y$$

- Dynamique du consommateur en l'absence de ressource

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

Interaction Ressource-Consommateur

$$\dot{x} = -\frac{1}{Y}\mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y$$

- “Réponse fonctionnelle”
- “Réponse numérique”

$$\dot{x} = f(x) - \frac{1}{Y}\mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

Le modèle Proie-Prédateur de Lotka-Volterra

$$\dot{x} = f(x) - \frac{1}{Y}\mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

Le plus simple possible

$$f(x) = a \cdot x$$

$$\frac{1}{Y}\mu(x, y) = b \cdot x \cdot y$$

$$\mu(x, y) = c \cdot x \cdot y$$

$$\nu(x, y) = c \cdot y$$

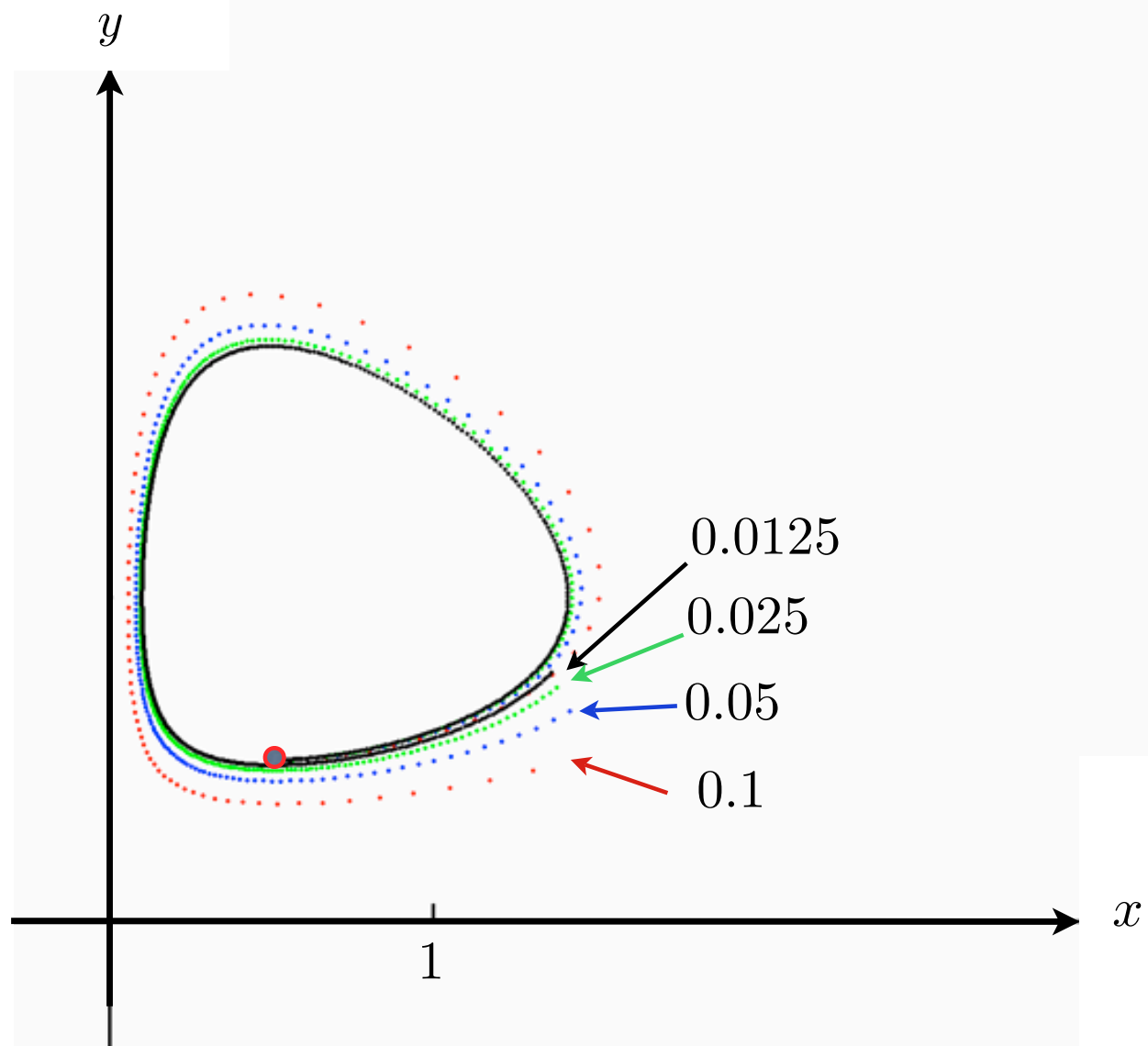
$$\dot{x} = a \cdot x - b \cdot x \cdot y$$

$$\dot{y} = c \cdot x \cdot y - d \cdot y$$

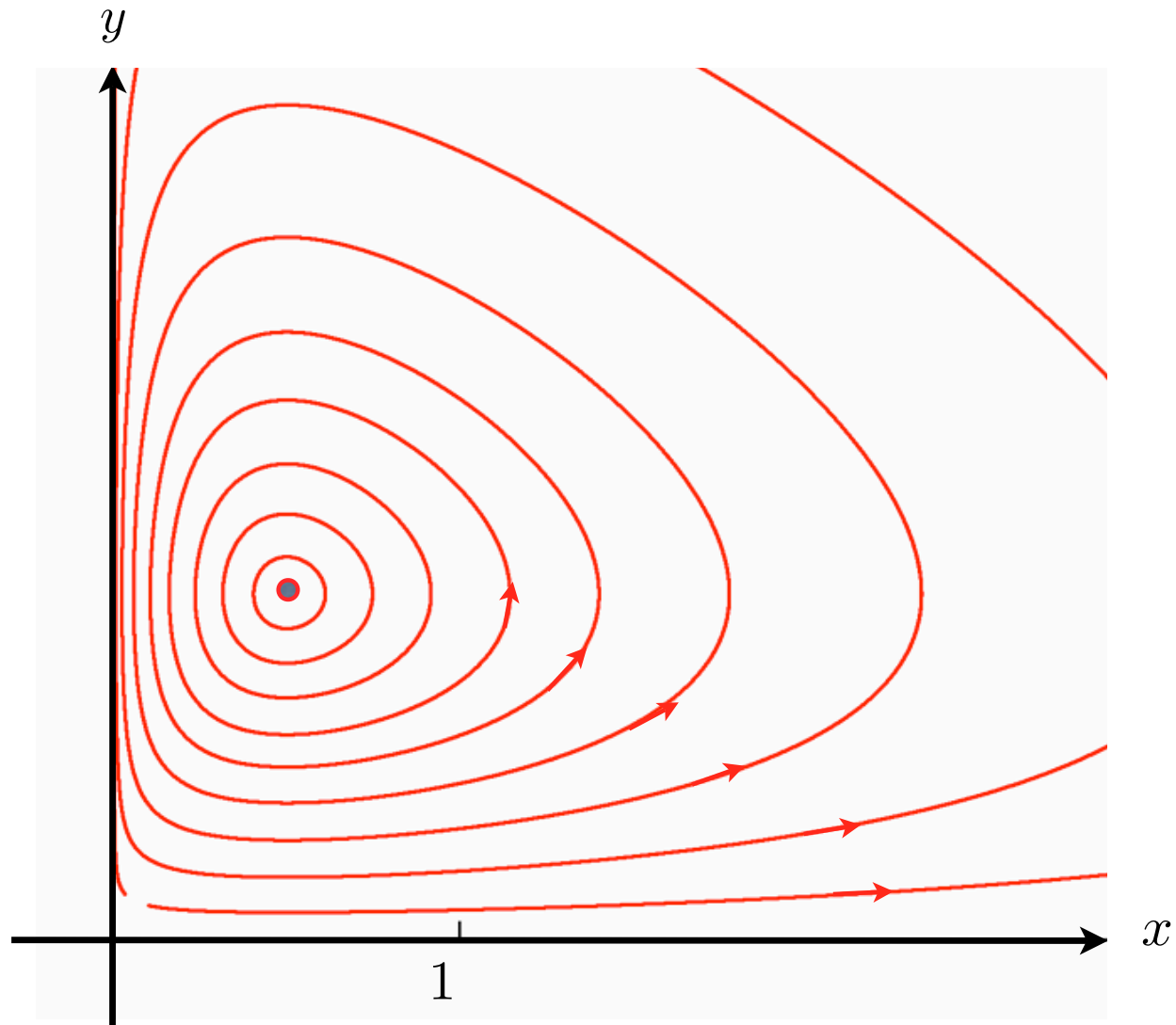
$$\dot{x} = ax - bxy = x(a - by)$$

$$\dot{y} = cxy - dy = y(c - dx)$$

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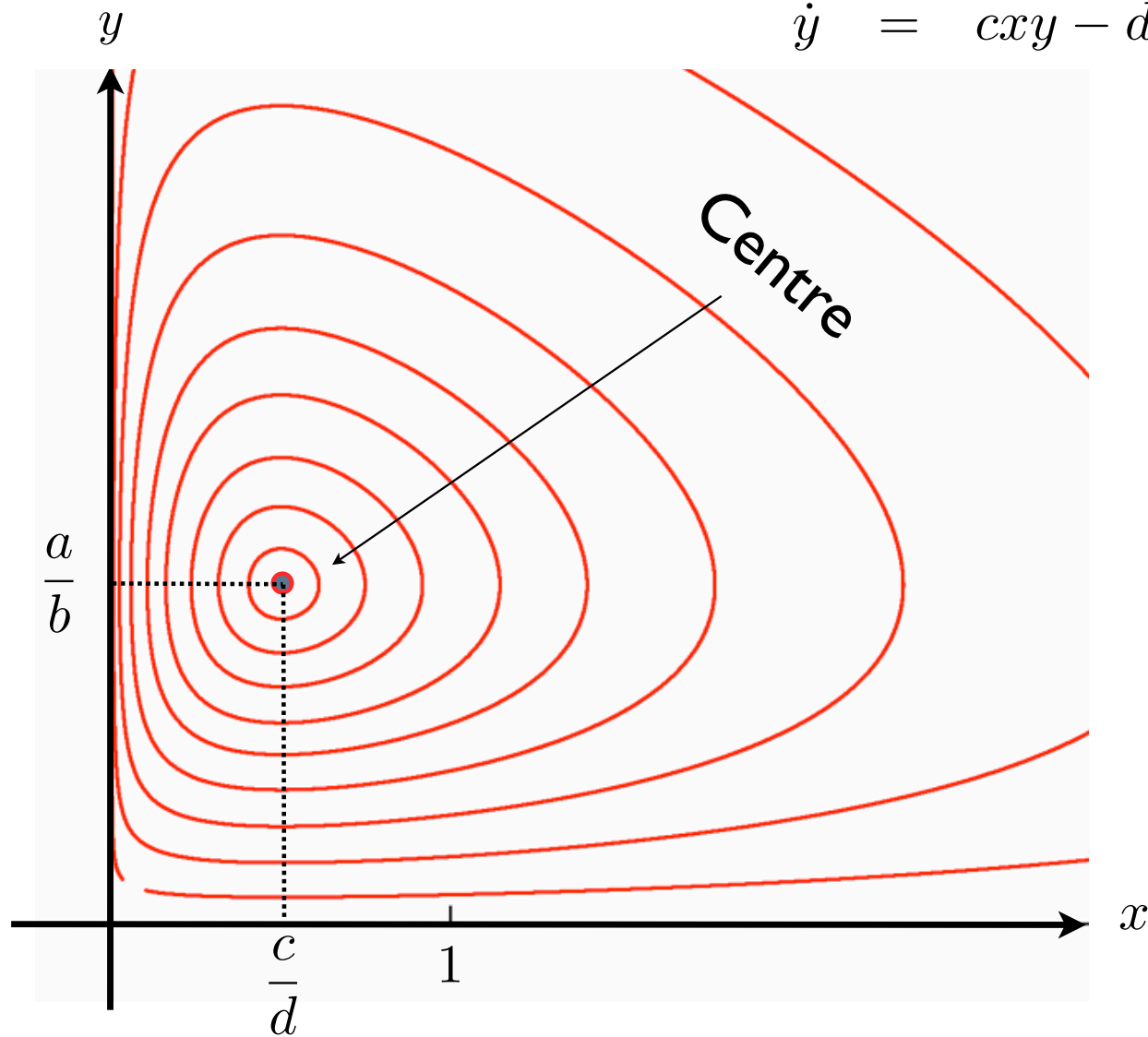
Le modèle Proie-Prédateur de Lotka-Volterra



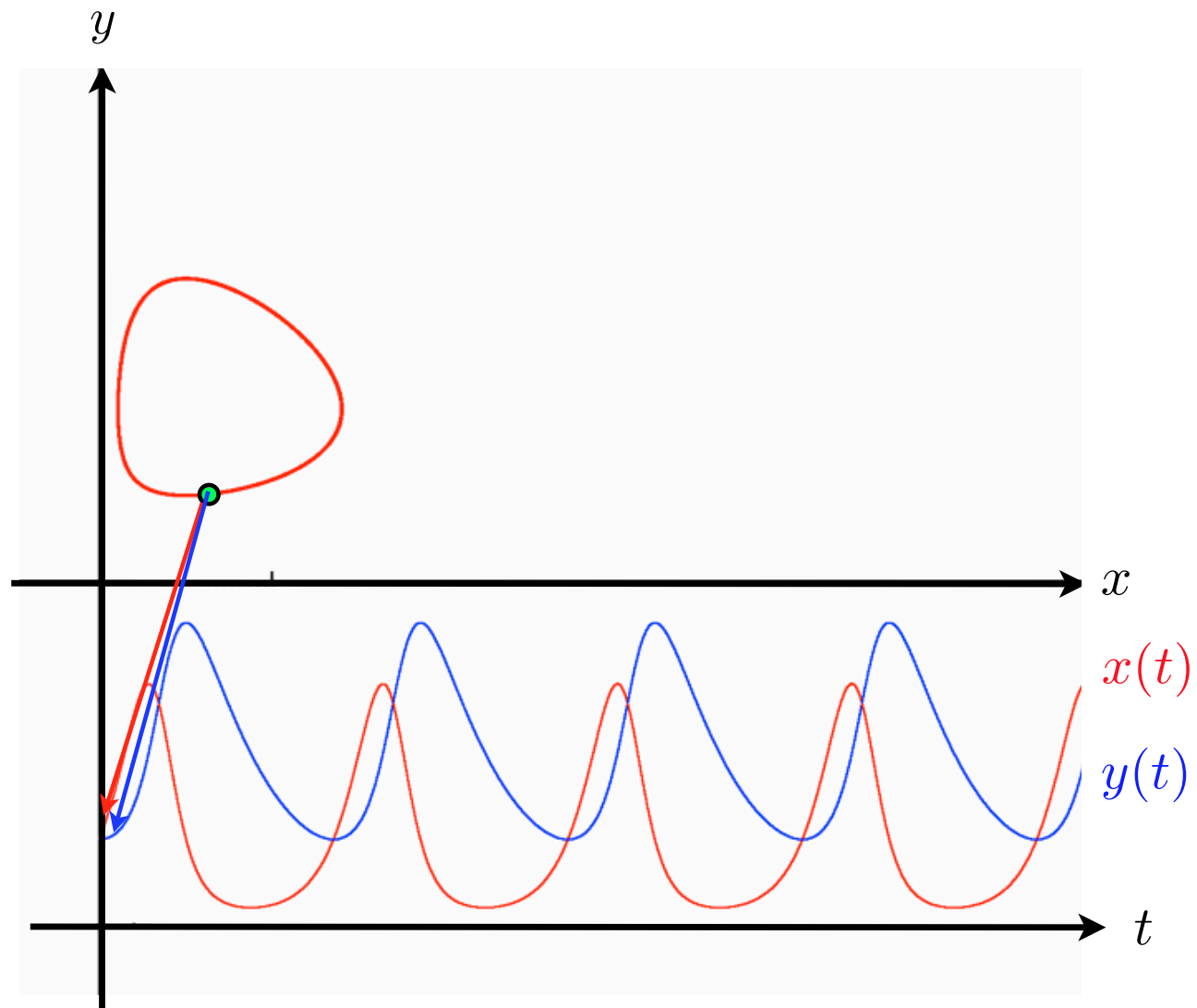
Le modèle Proie-Prédateur de Lotka-Volterra

$$\dot{x} = ax - bxy = x(a - by)$$

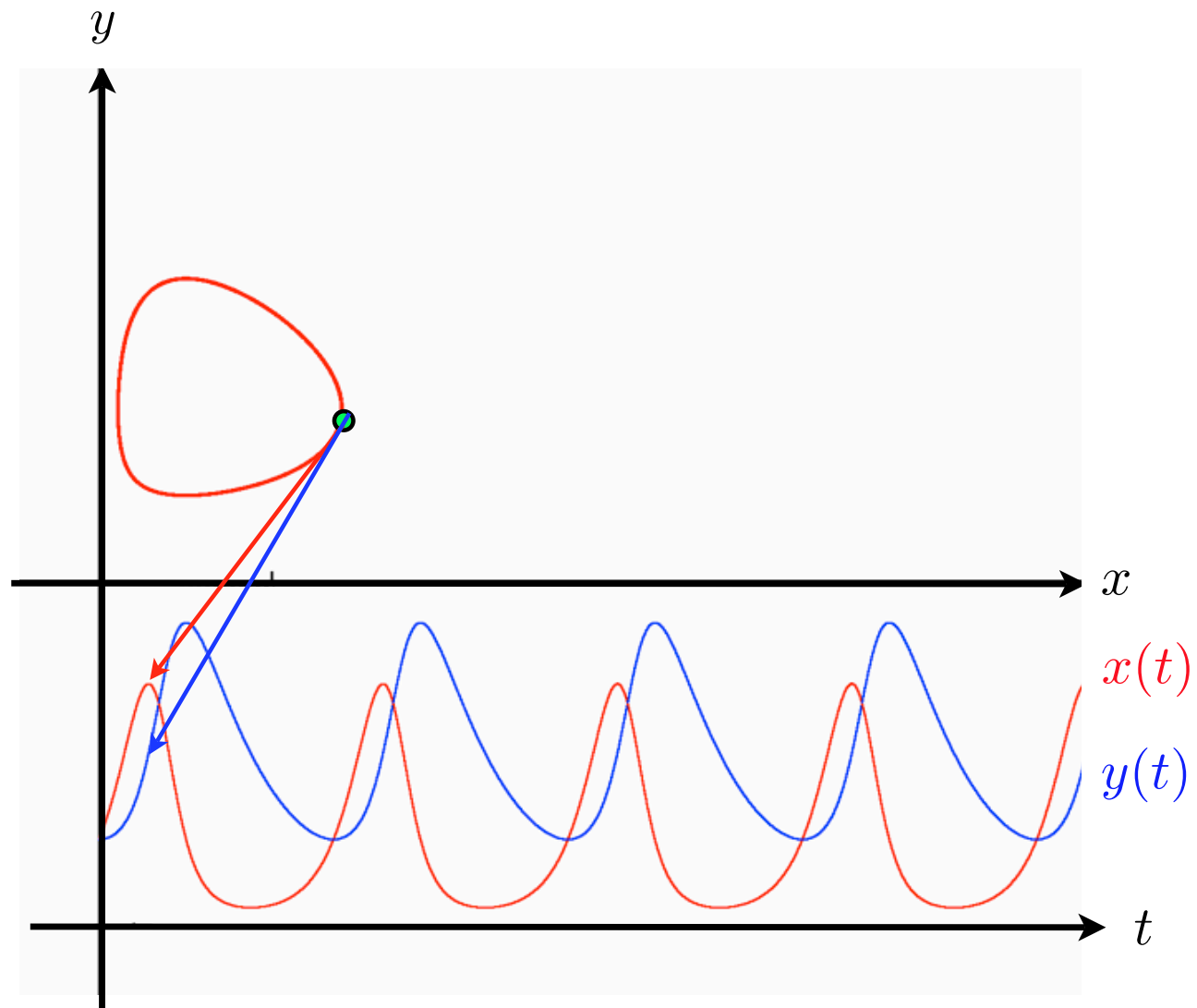
$$\dot{y} = cxy - dy = y(c - dx)$$



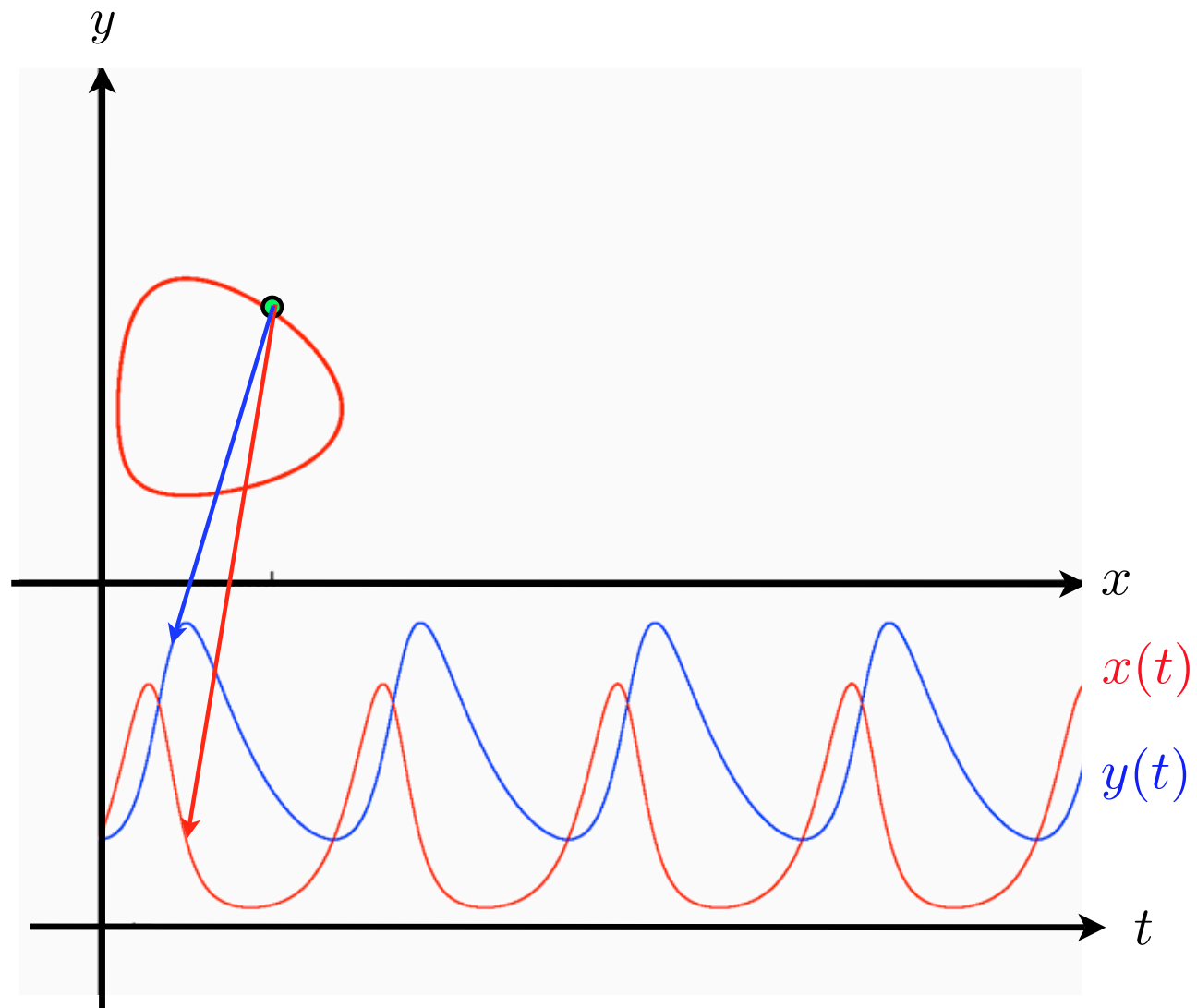
Le modèle Proie-Prédateur de Lotka-Volterra



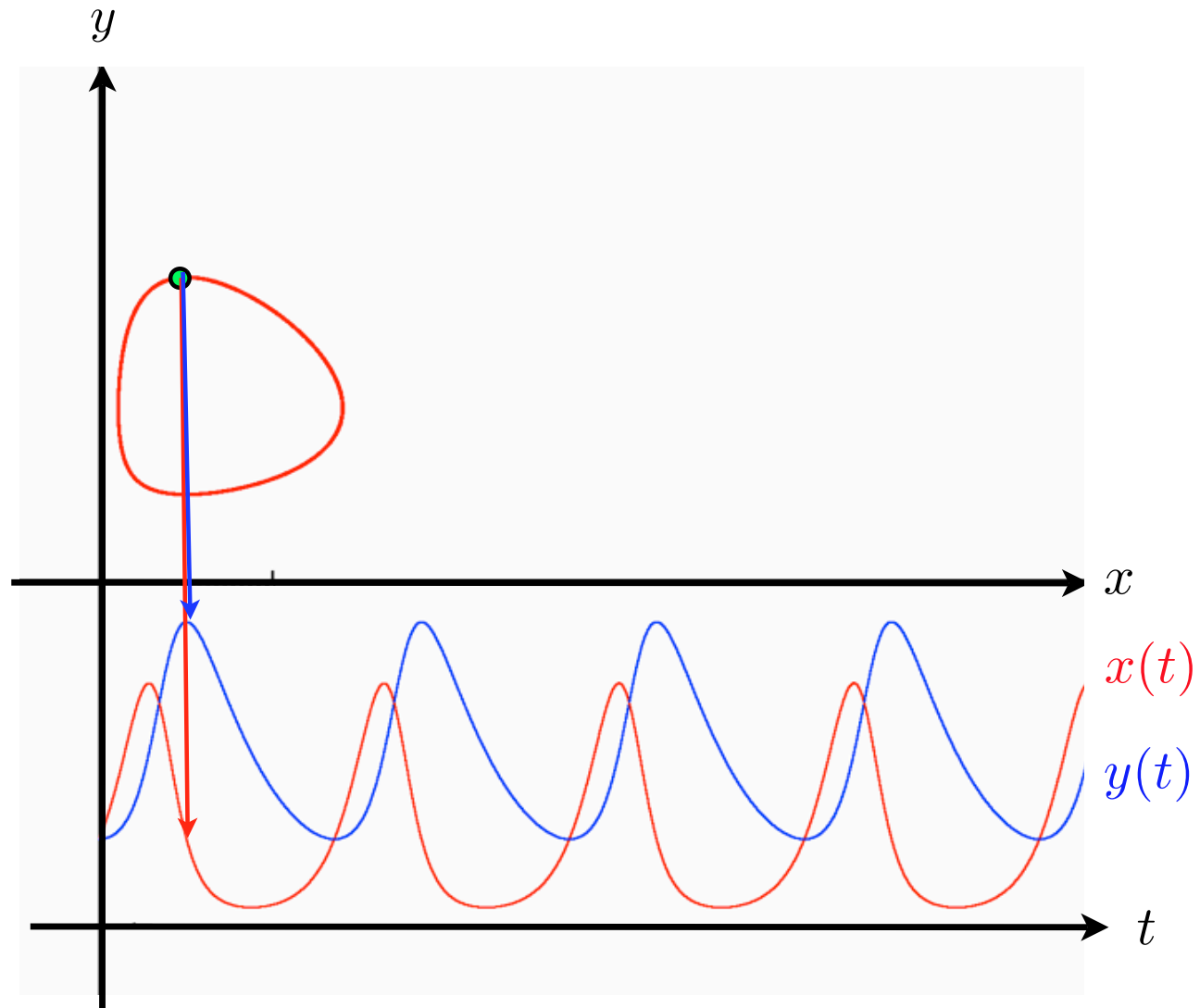
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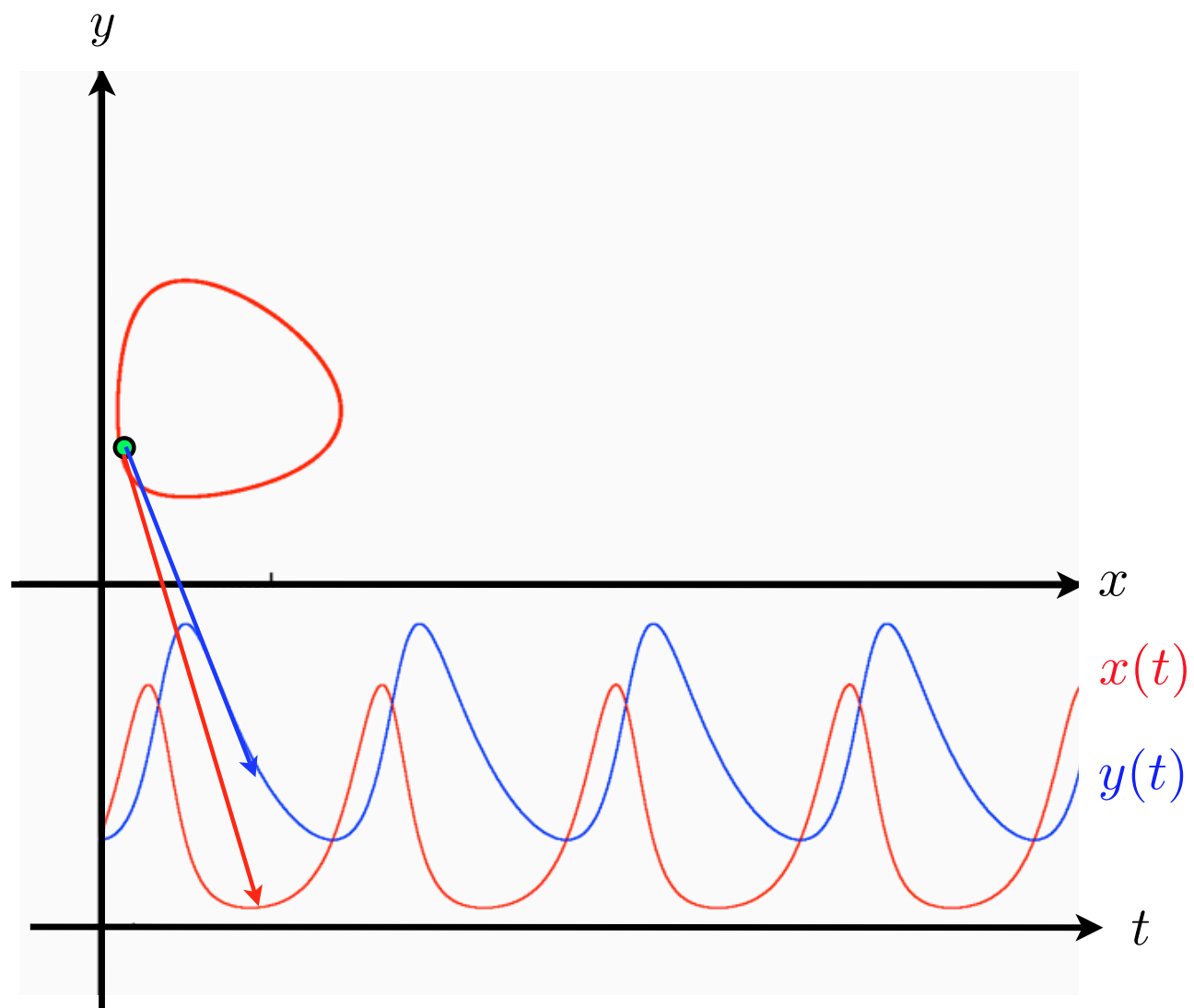
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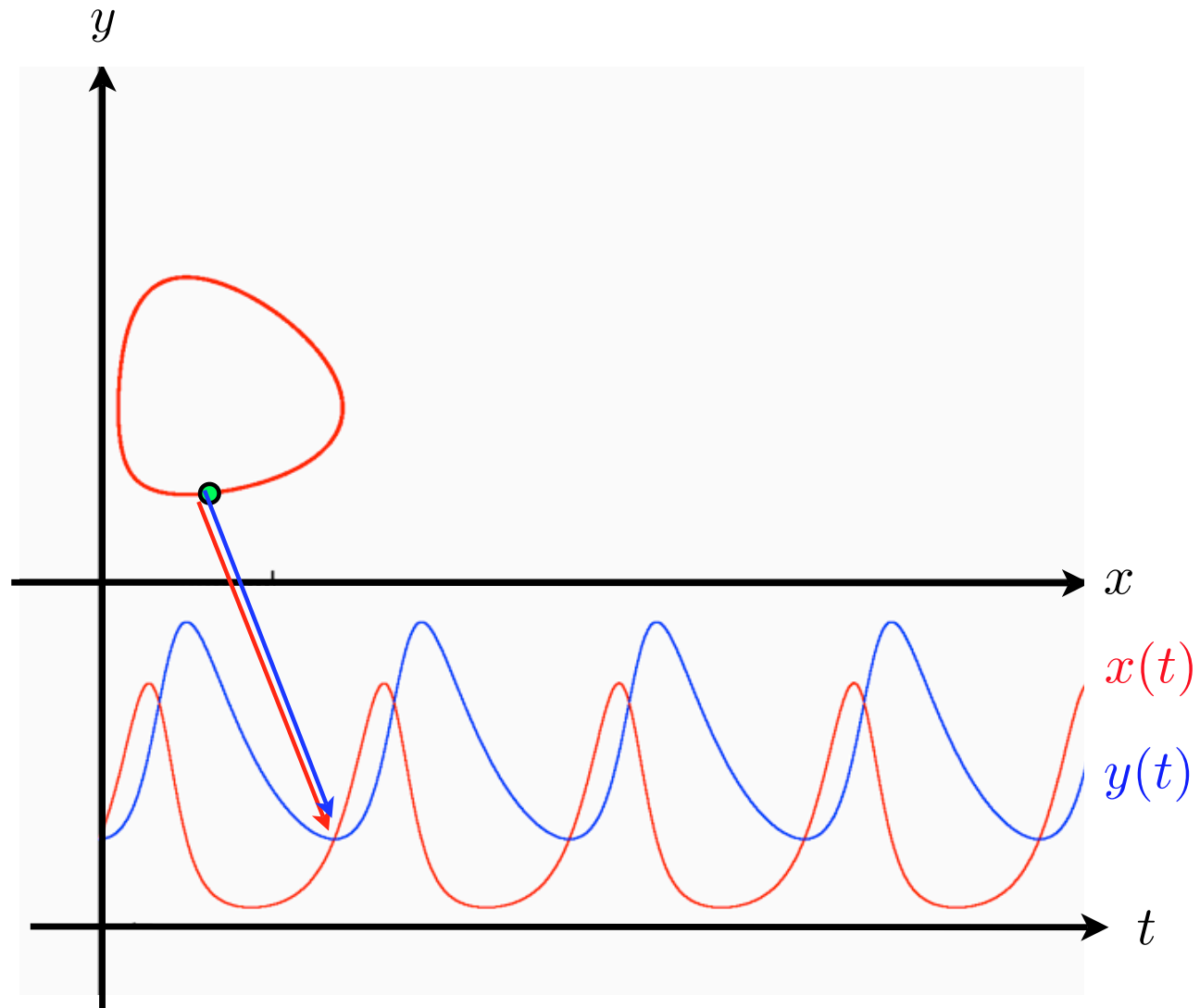
Le modèle Proie-Prédateur de Lotka-Volterra



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ANALYTICAL NOTE ON CERTAIN RHYTHMIC RELATIONS IN ORGANIC SYSTEMS

BY ALFRED J. LOTKA

BROOKLYN, N. Y.

Communicated by R. Pearl, May 20, 1920

Le modèle Proie-Prédateur de Lotka-Volterra

ANALYTICAL NOTE ON CERTAIN RHYTHMIC RELATIONS IN ORGANIC SYSTEMS

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We now proceed to consider a simple special case, as follows:

The system comprises

1. A species of organism S_1 , a plant species, say, deriving its nourishment from a source presented in such large excess that the mass of the source may be considered constant during the period of time with which we are concerned.

2. A species S_2 , for example a herbivorous animal species, feeding on S_1 .

In this case we have the following obvious relations

$$\left. \begin{array}{l} \text{Rate of in-} \\ \text{crease of } X_1 \\ \text{per unit of} \\ \text{time} \end{array} \right\} = \left. \begin{array}{l} \text{Mass of newly} \\ \text{formed } S_1 \text{ per} \\ \text{unit of time} \end{array} \right\} - \left. \begin{array}{l} \text{Mass of } S_1 \\ \text{destroyed by} \\ S_2 \text{ per unit of} \\ \text{time} \end{array} \right\} - \left. \begin{array}{l} \text{Other dead} \\ \text{or excretory} \\ \text{matter elimi-} \\ \text{nated from } S_1 \\ \text{per unit of} \\ \text{time} \end{array} \right\} \quad (3)$$

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$$\left. \begin{array}{l} \text{Rate of in-} \\ \text{crease of } X_2 \\ \text{per unit of} \\ \text{time} \end{array} \right\} = \left. \begin{array}{l} \text{Mass of newly} \\ \text{formed } S_2 \text{ per} \\ \text{unit of time} \\ \text{(derived from} \\ S_1 \text{ as food in-} \\ \text{gested)} \end{array} \right\} - \left. \begin{array}{l} \text{Mass of } S_2 \\ \text{destroyed or} \\ \text{eliminated per} \\ \text{unit of time} \end{array} \right\}$$

Or, in analytical symbols,

$$\begin{aligned} \frac{dX_1}{dt} &= A'_1 X_1 - B_1 X_1 X_2 - A''_1 X_1 \\ &= (A'_1 - A''_1) X_1 - B_1 X_1 X_2 \\ &= A_1 X_1 - B_1 X_1 X_2 \\ &= X_1 (A_1 - B_1 X_2) \\ \frac{dX_2}{dt} &= A_2 X_1 X_2 - B_2 X_2 \\ &= X_2 (A_2 X_1 - B_2) \end{aligned}$$

Le modèle Proie-Prédateur de Lotka-Volterra

Variations and Fluctuations of the Number of Individuals in Animal Species living together.

By

Professor **Vito Volterra**, Rome.

Translated by Miss Mary Evelyn Wells, Doctor of Mathematics.

¹) The complete work has been published by me in "Memorie della R. Accademia Nazionale dei Lincei", division on mathematical, physical and natural sciences, Series VI, vol. II, and in Memoria CXXXI, of R. Comitato Talassografico Italiano, with the title: *Variazioni e fluttuazioni del numero d'individui in specie animali conviventi*. After the publication of this note I received word that in the study of parasites relative to malaria there existed the equations of Ross, and I learned that in the volume: *Elements of physical Biology*, New York 1925, Doctor Lotka had considered the case of two species developed by me in § 3 of part 1, arriving by other methods at the integral, to his diagram, and to the period of small oscillations. However the general laws obtained by me in this same section, the various cases developed in the other sections of the first part, as likewise all the other three parts of my Memoir, in which I consider the applications of the aforesaid laws and the cohabitation of n species in the hypothesis of conservative and dissipative associations, are new and treated for the first time.

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§ 3. Association of two Species one of which feeds upon the other.

1. Let N_1 and N_2 be the numbers of individuals of the two species. Let $\epsilon_1 > 0$ represent the coefficient of increase which the first would have if the other did not exist. Let us suppose that the second would die out because of lack of food if it were alone; therefore let its coefficient of increase be negative and equal to $-\epsilon_2$ (ϵ_2 can be considered as a coefficient of decrease). If each of the two species were alone we should have

$$[7_1] \quad \frac{dN_1}{dt} = \epsilon_1 N_1,$$

$$[7_2] \quad \frac{dN_2}{dt} = -\epsilon_2 N_2.$$

$$(A_1) \quad \frac{dN_1}{dt} = (\epsilon_1 - \gamma_1 N_2) N_1,$$

$$(A_2) \quad \frac{dN_2}{dt} = (-\epsilon_2 + \gamma_2 N_1) N_2.$$

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$$r_1 = \frac{e_1}{K_2}, \quad r_2 = \frac{e_2}{K_1}.$$

Now let us pass to the integration of equations (A_1) and (A_2) .

From (A_1) and (A_2) it follows that

$$[9] \quad \frac{d \frac{N_1}{K_1}}{dt} = e_1 \left(1 - \frac{N_2}{K_2}\right) \frac{N_1}{K_1}, \quad \frac{d \frac{N_2}{K_2}}{dt} = -e_2 \left(1 - \frac{N_1}{K_1}\right) \frac{N_2}{K_2},$$

whence, by placing

$$[10] \quad N_1 = K_1 n_1, \quad N_2 = K_2 n_2,$$

the preceding equations may be written

$$(A'_1) \quad \frac{dn_1}{dt} = e_1 (1 - n_2) n_1, \quad (A'_2) \quad \frac{dn_2}{dt} = -e_2 (1 - n_1) n_2.$$

Multiplying these equations respectively by e_2 and e_1 and adding we have

$$[11] \quad \frac{d}{dt} (e_2 n_1 + e_1 n_2) = e_1 e_2 (n_1 - n_2).$$

Multiplying them respectively by $\frac{e_2}{n_1}$ and $\frac{e_1}{n_2}$, and adding, we find

$$\frac{e_2}{n_1} \frac{dn_1}{dt} + \frac{e_1}{n_2} \frac{dn_2}{dt} = e_1 e_2 (n_1 - n_2),$$

that is to say

$$[12] \quad \frac{d}{dt} (\log n_1^{e_2} + \log n_2^{e_1}) = e_1 e_2 (n_1 - n_2).$$

Equating the first members of [11] and [12] there follows

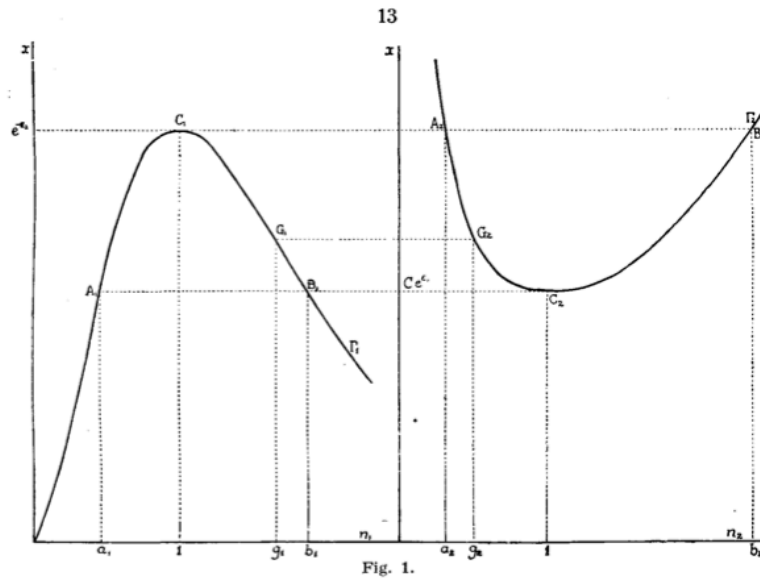
$$\frac{d}{dt} (e_2 n_1 + e_1 n_2) = \frac{d}{dt} (\log n_1^{e_2} + \log n_2^{e_1}),$$

and integrating and passing from logarithms to numbers

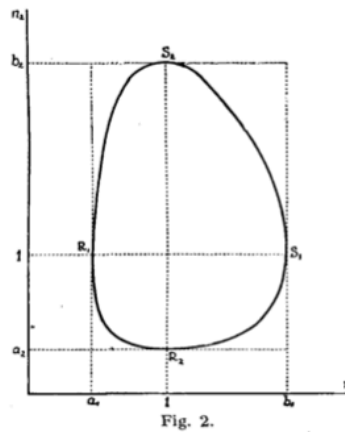
$$n_1^{e_2} n_2^{e_1} = C e^{e_2 n_1 + e_1 n_2}$$

where C is a positive constant. Whence

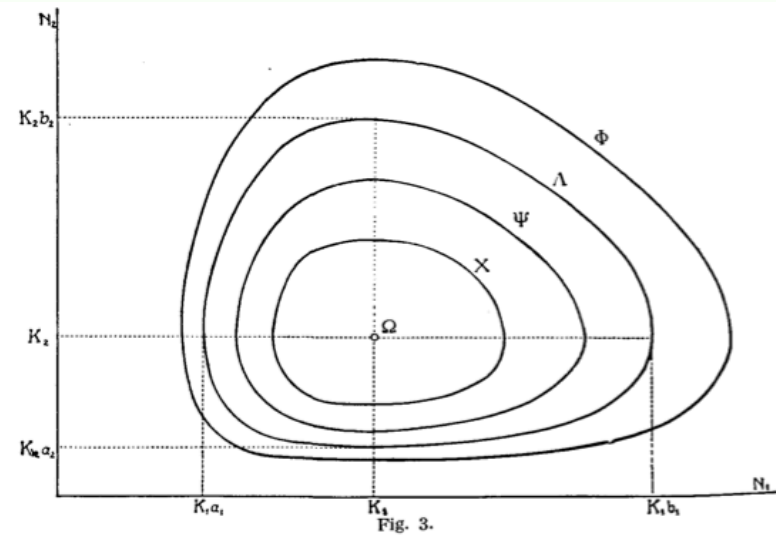
Le modèle Proie-Prédateur de Lotka-Volterra



arranged the two curves as in fig. 1, with one axis of abscissas the continuation of the other, let us draw the normals to x from the vertices C_1 and C_2 and consider the sections $A_1C_1B_1$, $A_2C_2B_2$ of the two curves lying between these two parallels. Let $a_1 < 1$ and $b_1 > 1$ be the abscissas of A_1 and B_1 , $a_2 < 1$, $b_2 > 1$ the abscissas of A_2 and B_2 .



Then let us try to construct the curve λ having n_1 for abscissa and n_2 for ordinate. First let us make the point A_2 correspond to the point C_1 and trace the arc C_1B_1 with the point G_1 . Then in the curve Γ_2 let us trace the arc A_2C_2 , and, corresponding to G_1 on Γ_1 we shall have G_2 on Γ_2 , on the same perpendicular to x . Then the value $n_2 = g_2$ will correspond to $n_1 = g_1$, g_1 and g_2 being respectively the abscissas of G_1 and G_2 . Then while n_1 increases from 1 to b_1 , n_2 will increase from a_2



Le modèle Proie-Prédateur de Lotka-Volterra

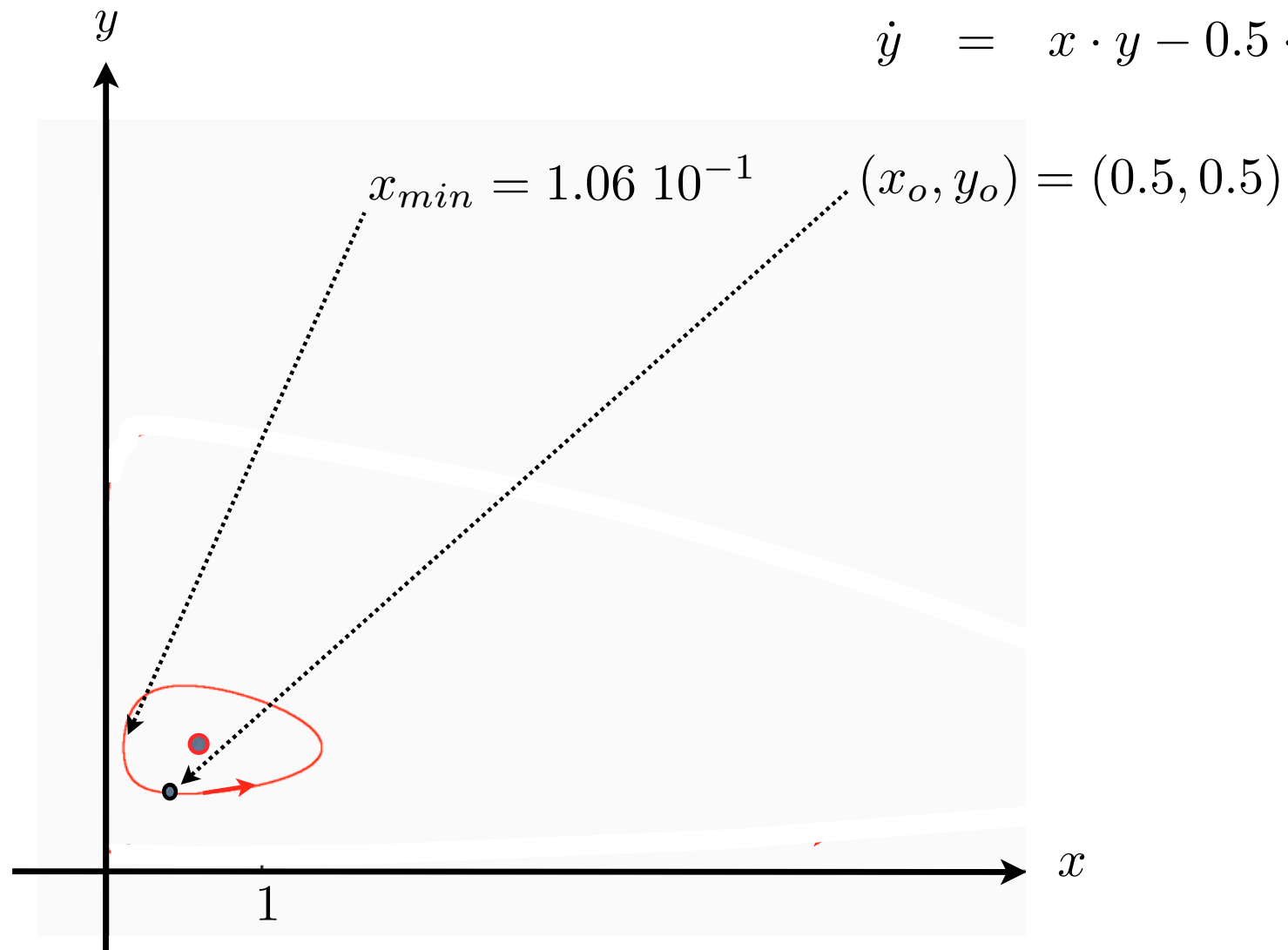
Evidences expérimentales et critique du modèle.

- Remarques de U. d'Ancona sur le rôle de la pêche en Adriatique.
- La série des lièvres et des Lynx du Canada
- Expériences de laboratoire
- synthèse TD Lyon 1 de J-R Lobry

Le modèle Proie-Prédateur de Lotka-Volterra

$$\dot{x} = 4 \cdot x - \frac{1}{0.2} x \cdot y$$

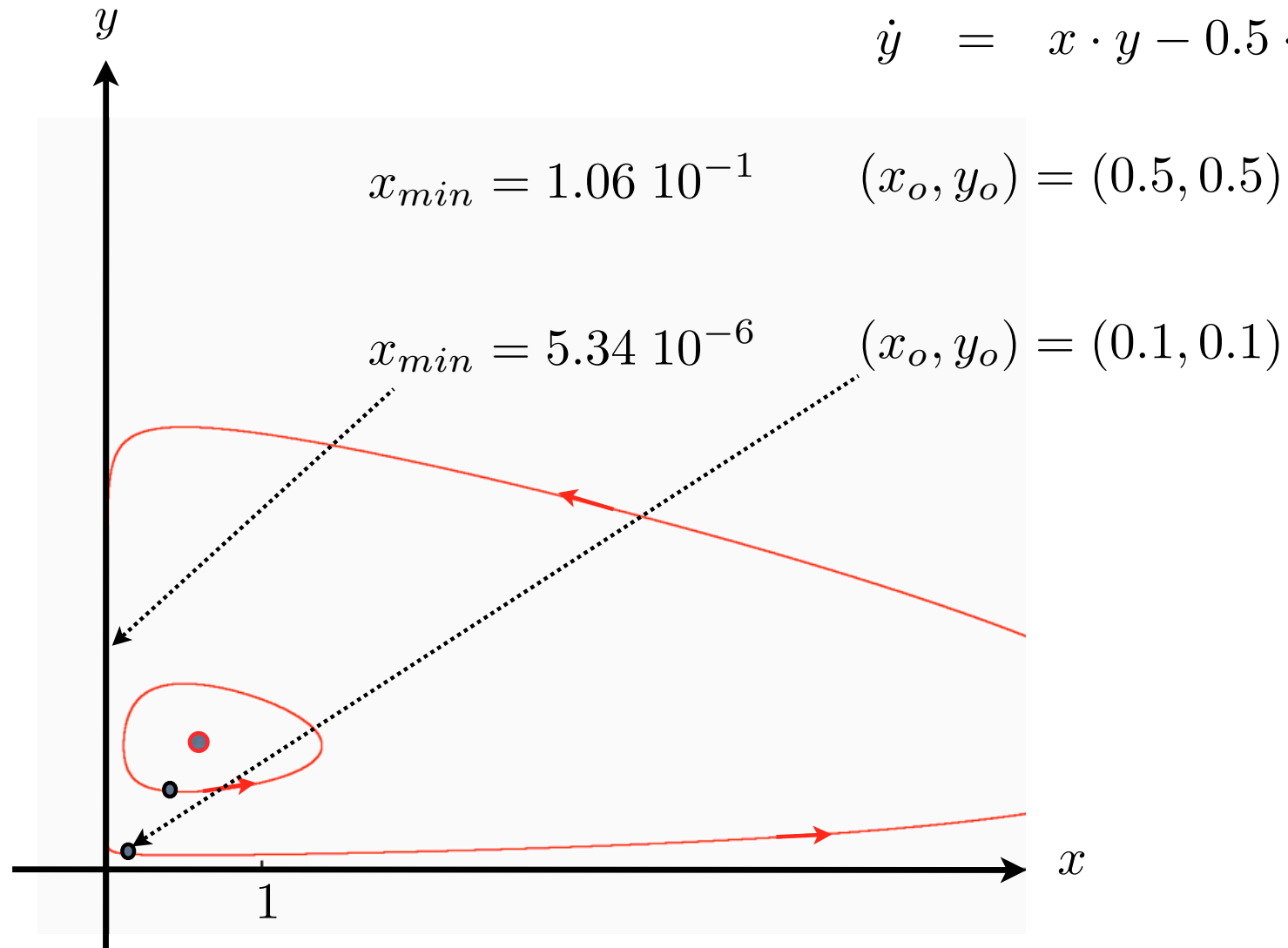
$$\dot{y} = x \cdot y - 0.5 \cdot y$$



Le modèle Proie-Prédateur de Lotka-Volterra

$$\dot{x} = 4 \cdot x - \frac{1}{0.2} x \cdot y$$

$$\dot{y} = x \cdot y - 0.5 \cdot y$$



Evolution de Gause

Gause 1936

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

~~Lotka-Volterra : $\mu(x) = \rho \cdot x$~~

$$\dot{x} = r \cdot x - \frac{1}{Y} \mu(x) \cdot y$$

$$\dot{y} = \mu(x) \cdot y - d \cdot y$$

Seuil

Si $x > \alpha$ alors : $\mu(x) = \frac{\mu \cdot x}{e + x}$
sinon : $\mu(x) = 0$

Evolution de Gause

Gause, G. F., Smaragdova, N. P., Witt, A. A., 1936. Further studies of interaction between predators and prey. *The Journal of Animal Ecology* 5, 1–18.

D'après

On the Gause predator-prey model with a refuge: A fresh look at the history

January 14, 2011

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Evolution de Gause

$$\dot{x} = f(x) - \frac{1}{Y} \mu(x, y) \cdot y$$

$$\dot{y} = \mu(x, y) \cdot y - \nu(y) \cdot y$$

3. INTERACTION BETWEEN *PARAMECIUM* AND YEAST CELLS

The technique of our previous investigations with this biological system has been described in (3) and (4). It can be summarised by stating that we cultivated Paramecia and yeast cells in glass tubes for centrifuging containing 5 c.c. of the liquid (Osterhout's medium as described in (3) buffered with the aid of 3 c.c. $m/20$ KH_2PO_4 per 100 c.c. and $m/20$ KOH to $p\text{H}$ equal to 7.7). These tubes were shaken once a day to avoid the sedimentation of yeast, and kept in a thermostat with a glass wall at 23.5°C . Putting the general equation of interaction between predators (N_2) and prey (N_1) in the form

$$\left. \begin{aligned} \frac{dN_1}{dt} &= b_1 N_1 - N_2 f(N_1), \\ \frac{dN_2}{dt} &= k N_2 f(N_1) - d_2 N_2, \end{aligned} \right\} \dots\dots(1)$$

we can state that the multiplication of prey (yeast cells, *Saccharomyces exiguus*) per unit of time ($b_1 N_1$) as well as the mortality of predators (*Paramecium bursaria*) per unit of time ($d_2 N_2$) were maintained constant by addition of yeast cells and by rarifying Paramecia as described in (3) and (4), in order to measure the movement of the system due to the factors $N_2 f(N_1)$ and $k N_2 f(N_1)$.

Evolution de Gause

8 Studies of Interaction between Predators and Prey

Table 2 (cont.).

Days	<i>A. agilis</i>			<i>Ch. eruditus</i>		
	Larvae			increase of the biomass of the predators.		
	♀	♂	Total	6-pod	8-pod	Image
Wheat flour 50/5						
6	4	4	16	20	44	4
12	12	4	16	36	68	—
18	8	4	76	24	112	—
23	20	8	100	20	148	4
27	8	—	216	—	224	16
32	32	16	448	—	496	—
35	—	—	112	16	128	—
38	—	—	16	—	16	8
41	—	—	—	—	—	4
44	—	—	—	—	—	4
Semoletta 50/5						
7	12	4	26	20	62	—
24	64	32	128	32	256	—
Wheat flour 50/5						
6	—	—	12	12	24	4
12	20	8	—	—	28	4
23	12	8	228	8	256	8
27	24	16	32	336	408	8
32	32	16	336	112	496	—
35	80	16	160	32	288	48
38	8	—	16	8	32	32
41	—	—	—	—	—	8
44	—	—	20	—	20	12
47	—	—	—	—	—	4
Wheat flour 75/5						
12	12	—	—	8	20	—
18	—	—	4	—	4	—
27	4	—	36	4	44	—
32	16	8	32	56	112	—
35	16	32	16	96	160	—
38	40	16	—	—	56	8
41	—	—	—	—	—	8
44	—	—	12	—	12	8
47	—	—	—	—	—	—
Semoletta 100/5						
8	4	4	36	40	84	—
14	—	—	68	20	88	—
20	—	—	8	—	—	24
24	—	—	8	4	12	—
30	—	—	—	—	—	—
Semoletta 125/5						
8	12	4	44	72	132	4
14	—	—	48	16	64	—
20	—	—	8	—	8	—
25	—	—	—	—	—	—
30	—	—	—	—	—	—
Wheat flour 150/5						
7	12	4	24	64	104	—
13	24	24	88	88	224	—
19	64	40	72	112	288	8
24	8	8	160	56	232	16
29	64	24	184	64	336	—
33	—	—	192	—	192	32
36	—	—	16	—	16	—
38	—	—	8	—	8	4
41	—	—	—	—	—	8

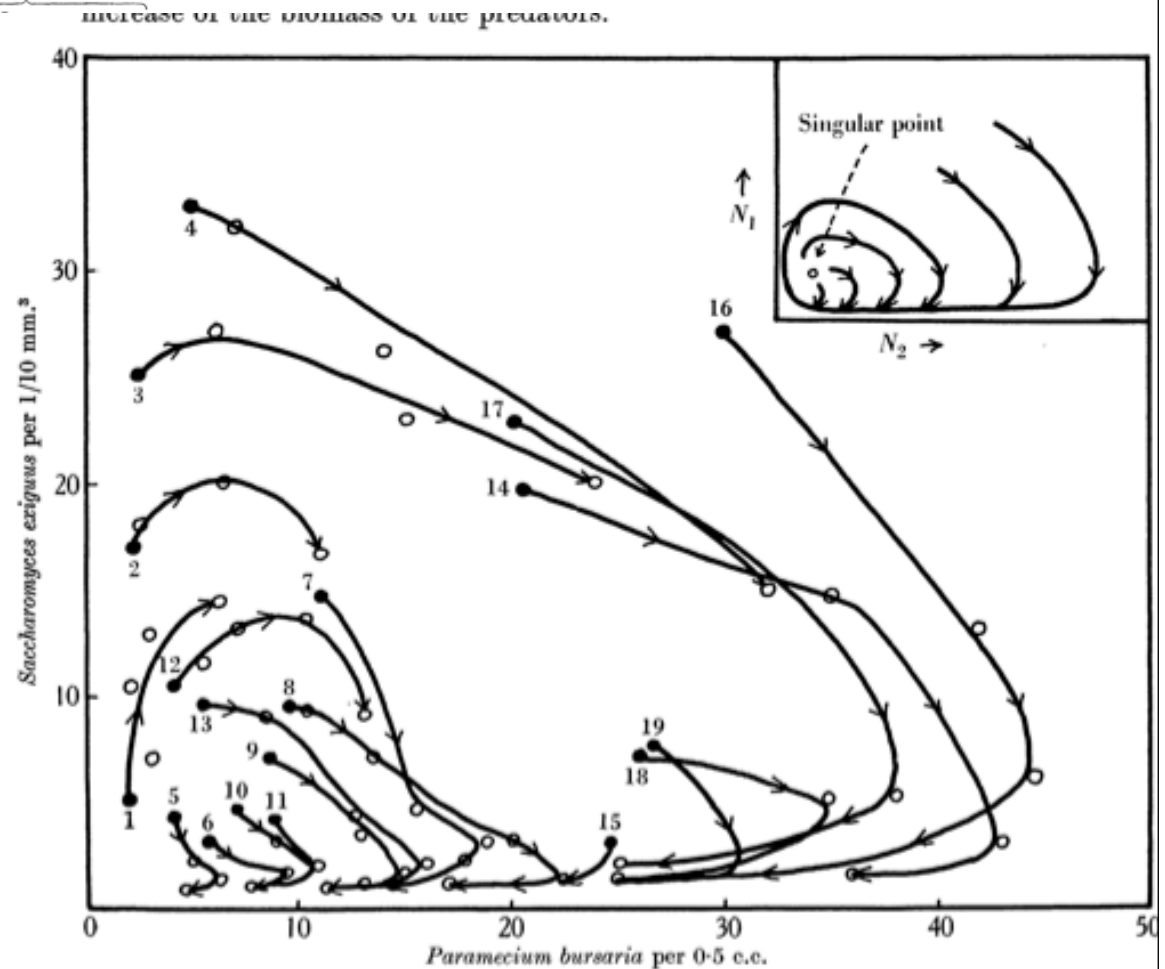


Fig. 4. Interaction between predators (*Paramecium bursaria*) and prey (*Saccharomyces exiguus*).

Evolution de Gause

The conclusion of our previous investigations (3, 4) was that, under the conditions as laid down above, periodic fluctuations are observed in the concentrations of both species. The *P. bursaria* cannot completely destroy the yeast cells and “sterilise” the microcosm, and at the same time do not disappear entirely from the population at the time of food shortage. We have also remarked (3) that these periodic fluctuations do not apparently belong to the “conservative” type. In other words they do not keep the magnitude initially given them but tend towards an inherent magnitude of their own. Let us continue here the analysis of this problem.

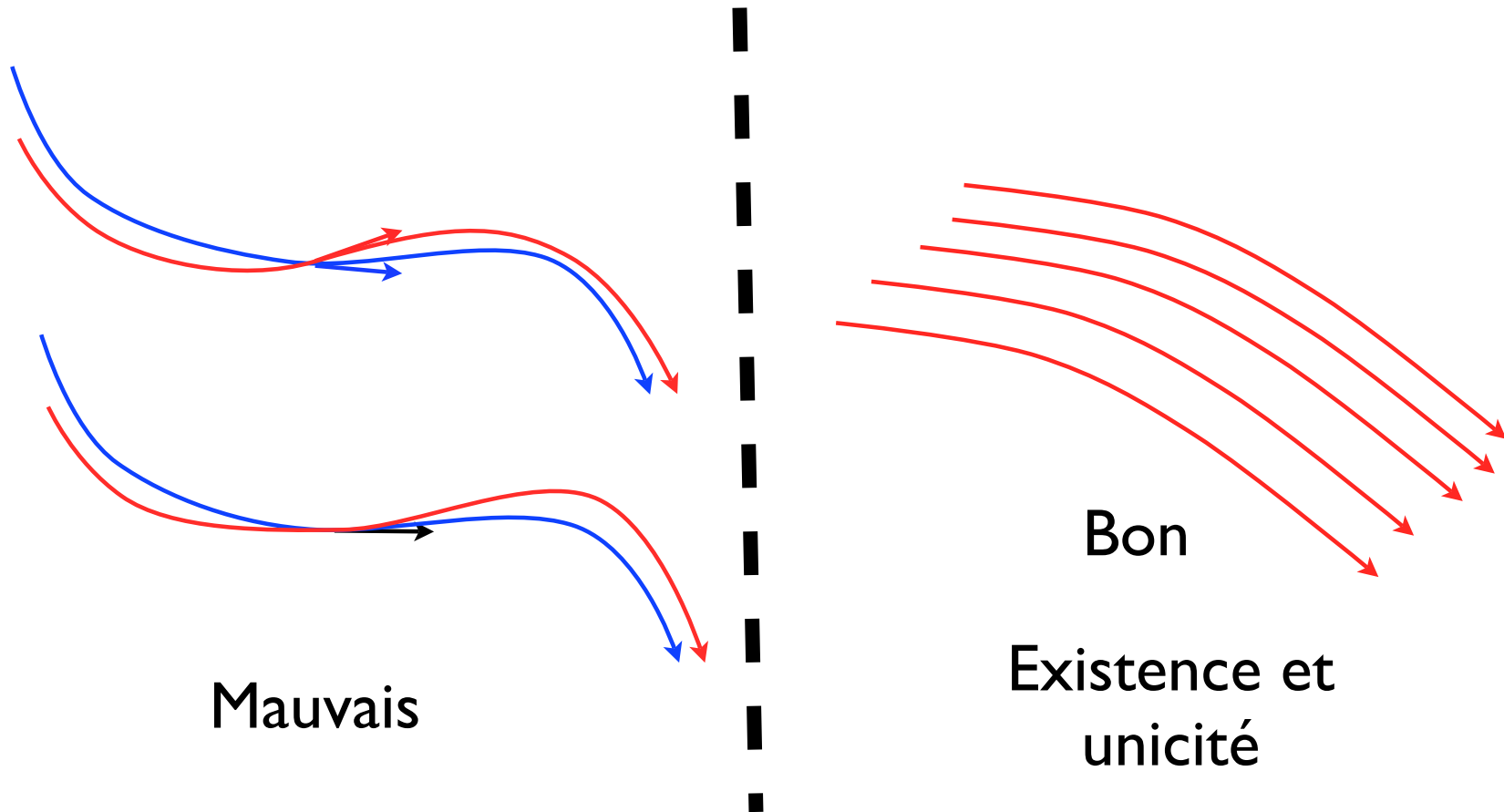
Petit cours de maths

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

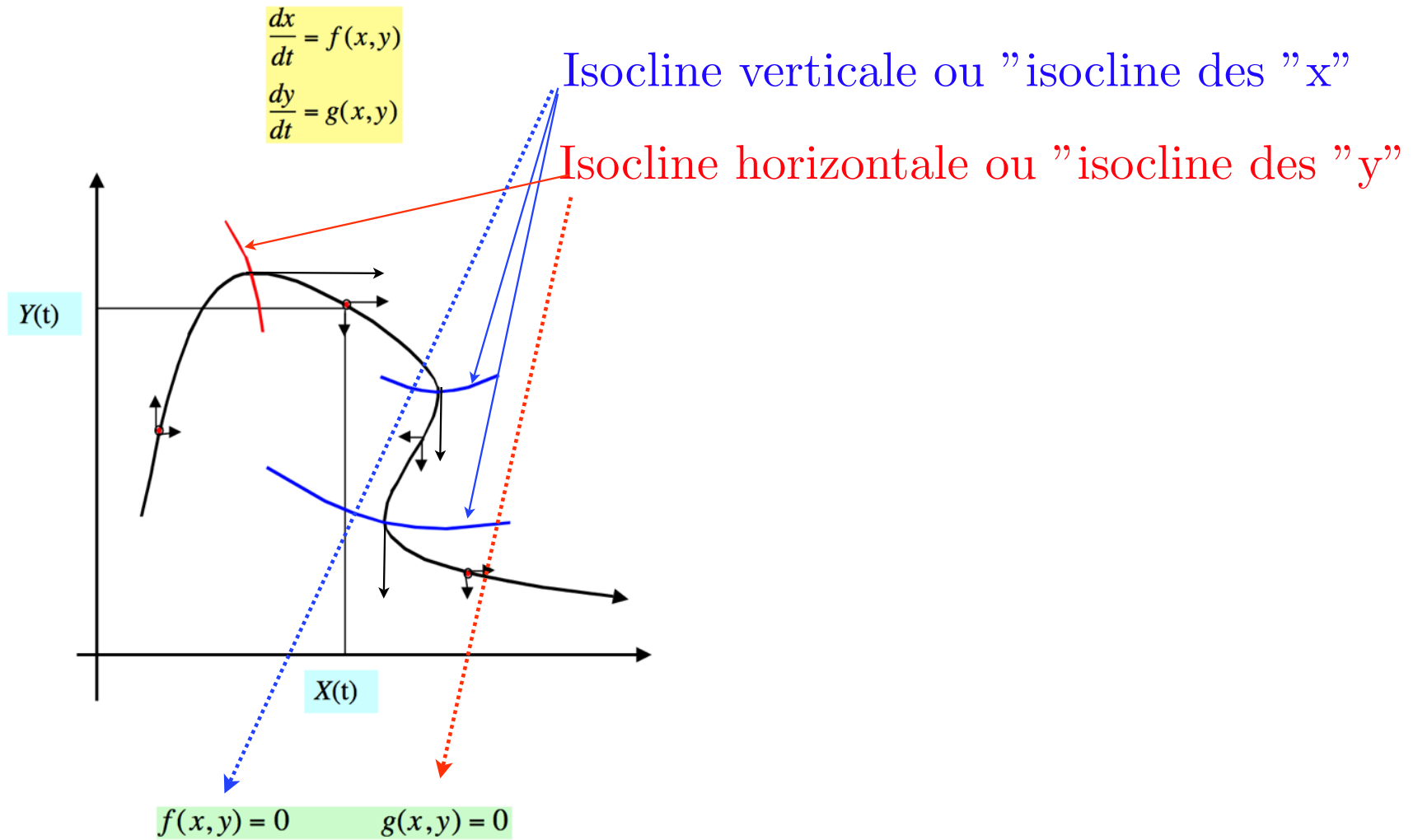
$$\dot{y} = g(x, y)$$

$$x(t + dt) = x(t) + dt \cdot f(x(t), y(t))$$

$$y(t + dt) = y(t) + dt \cdot g(x(t), y(t))$$



Petit cours de maths



Petit cours de maths

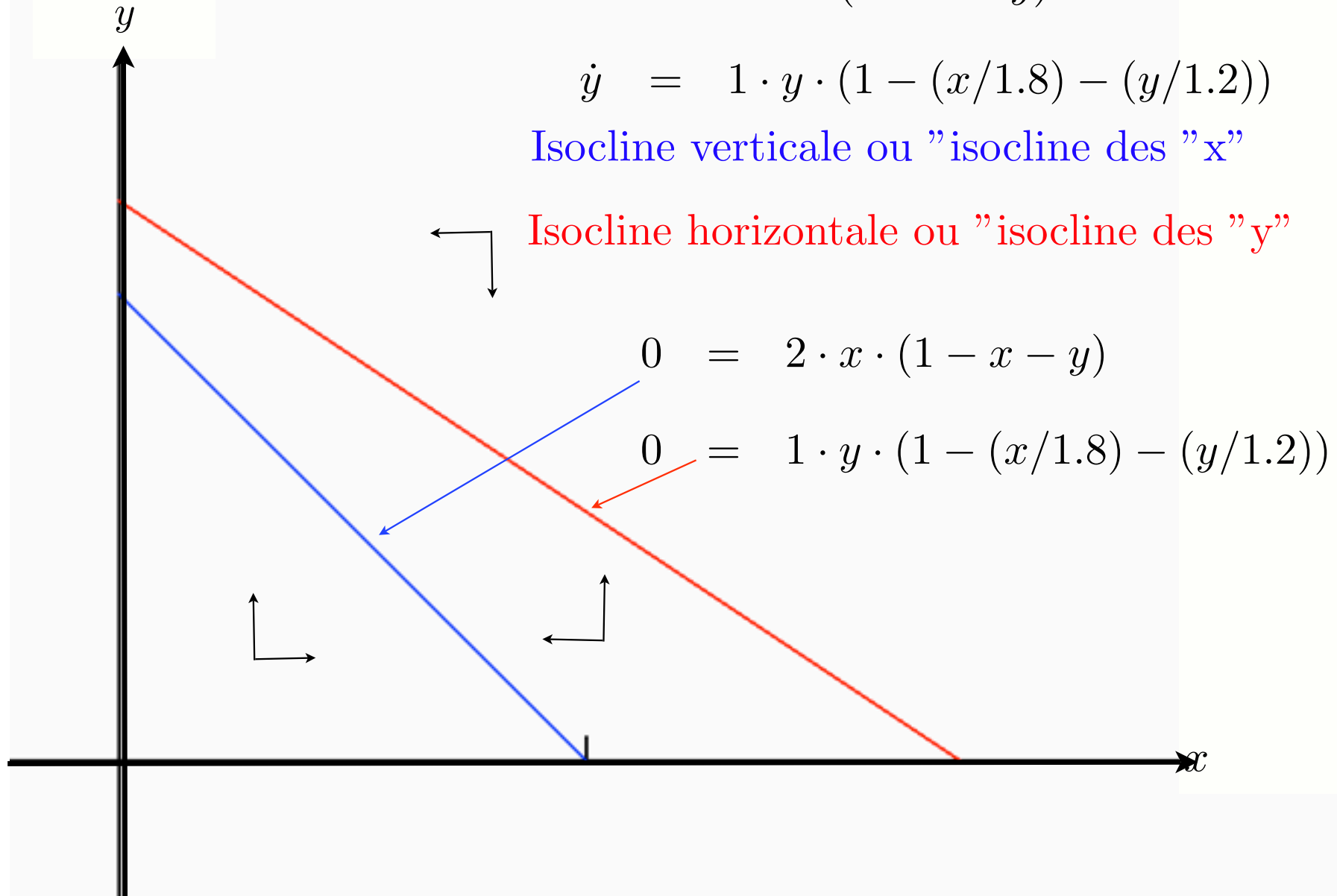
Exemple

$$\dot{x} = 2 \cdot x \cdot (1 - x - y)$$

$$\dot{y} = 1 \cdot y \cdot (1 - (x/1.8) - (y/1.2))$$

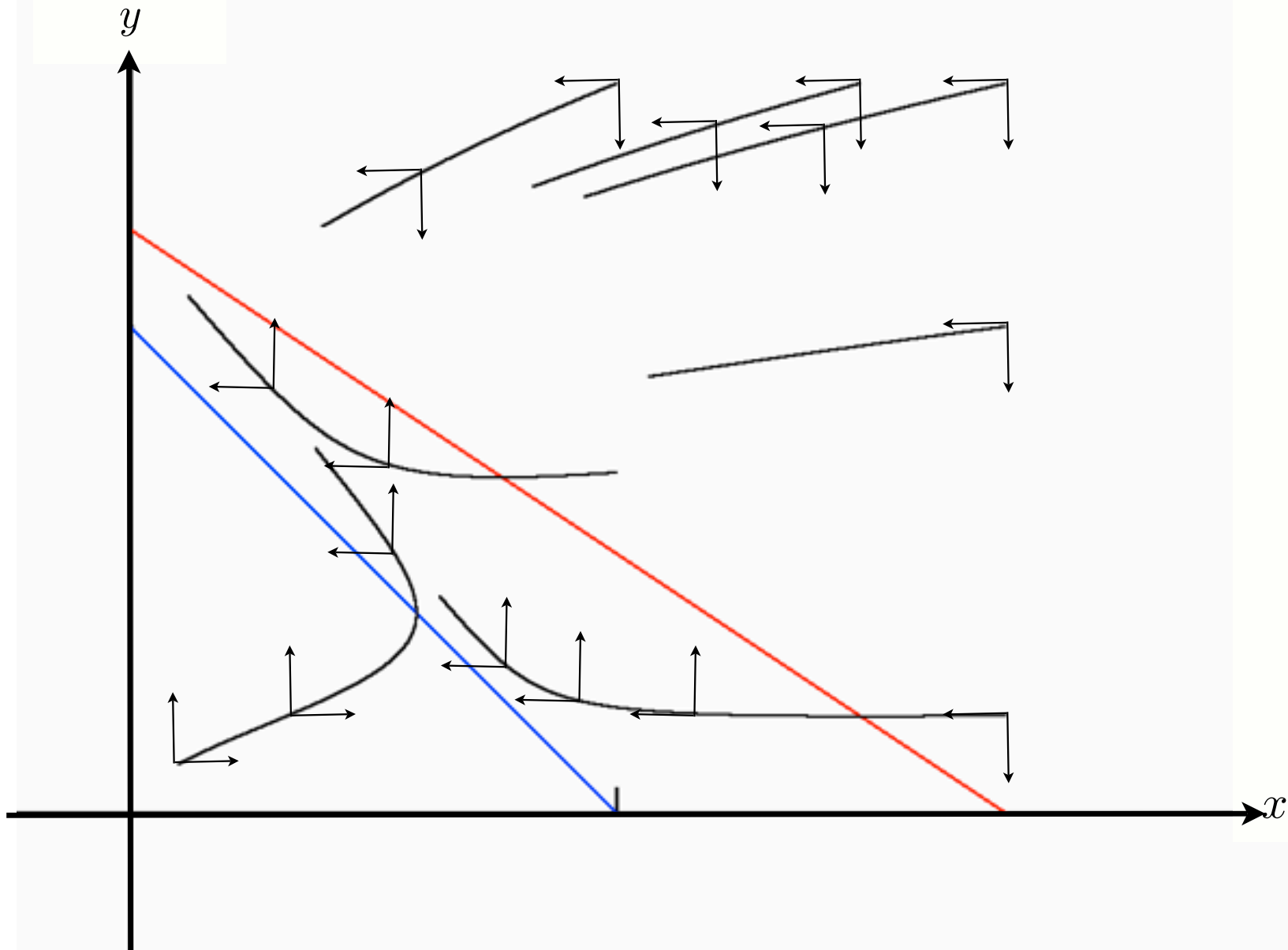
Isocline verticale ou "isocline des "x"

Isocline horizontale ou "isocline des "y"



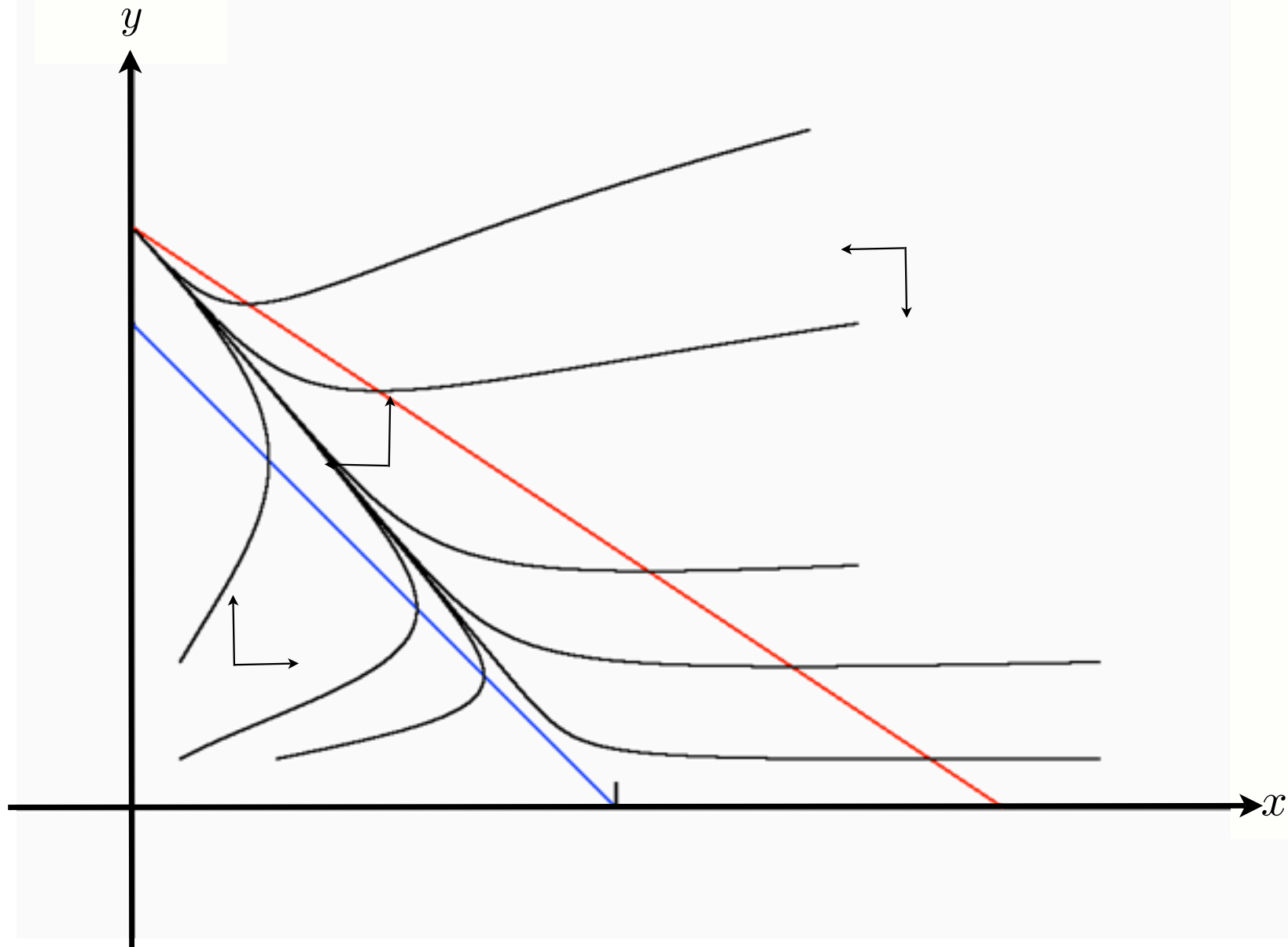
Petit cours de maths

Exemple

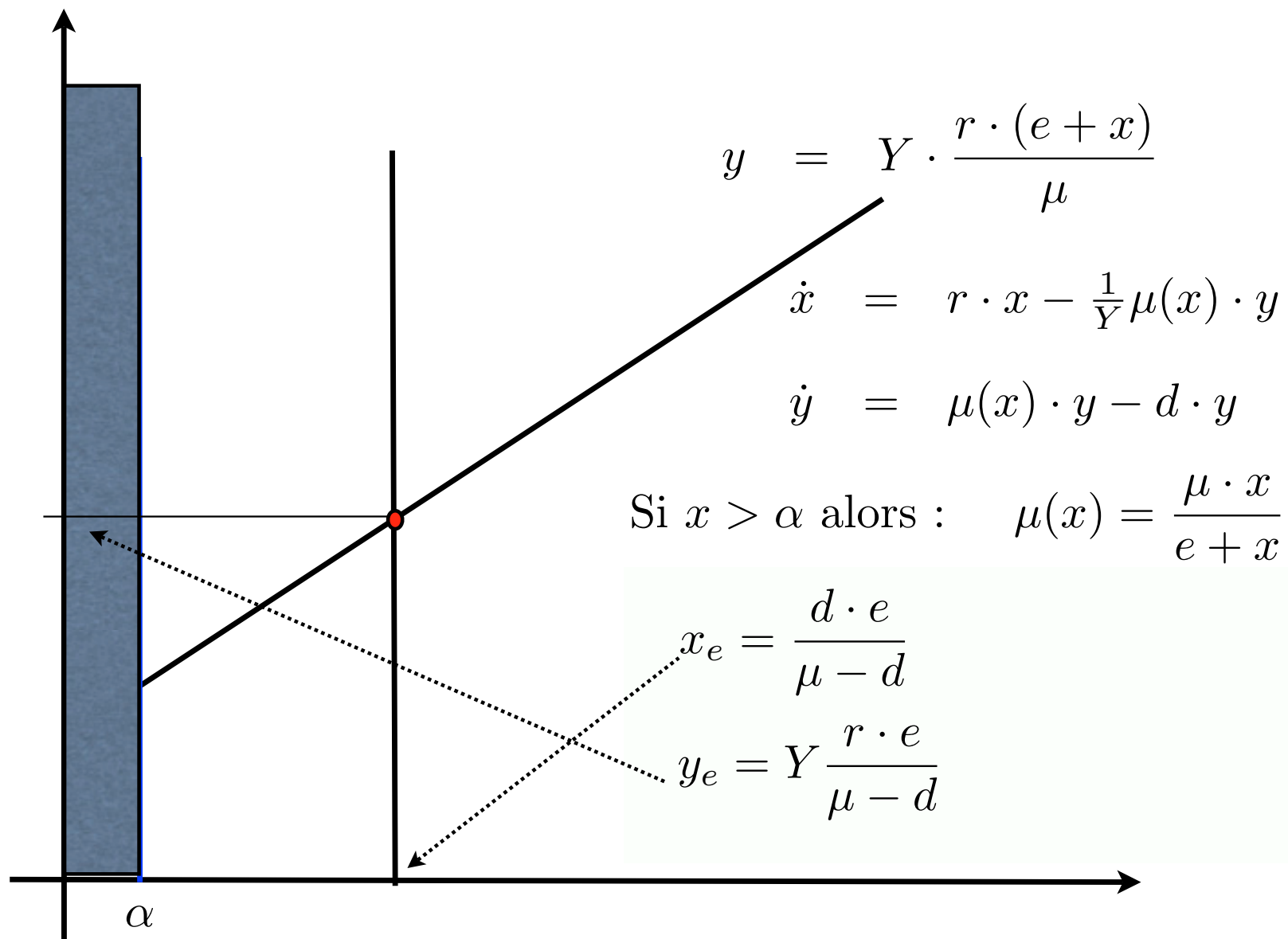


Petit cours de maths

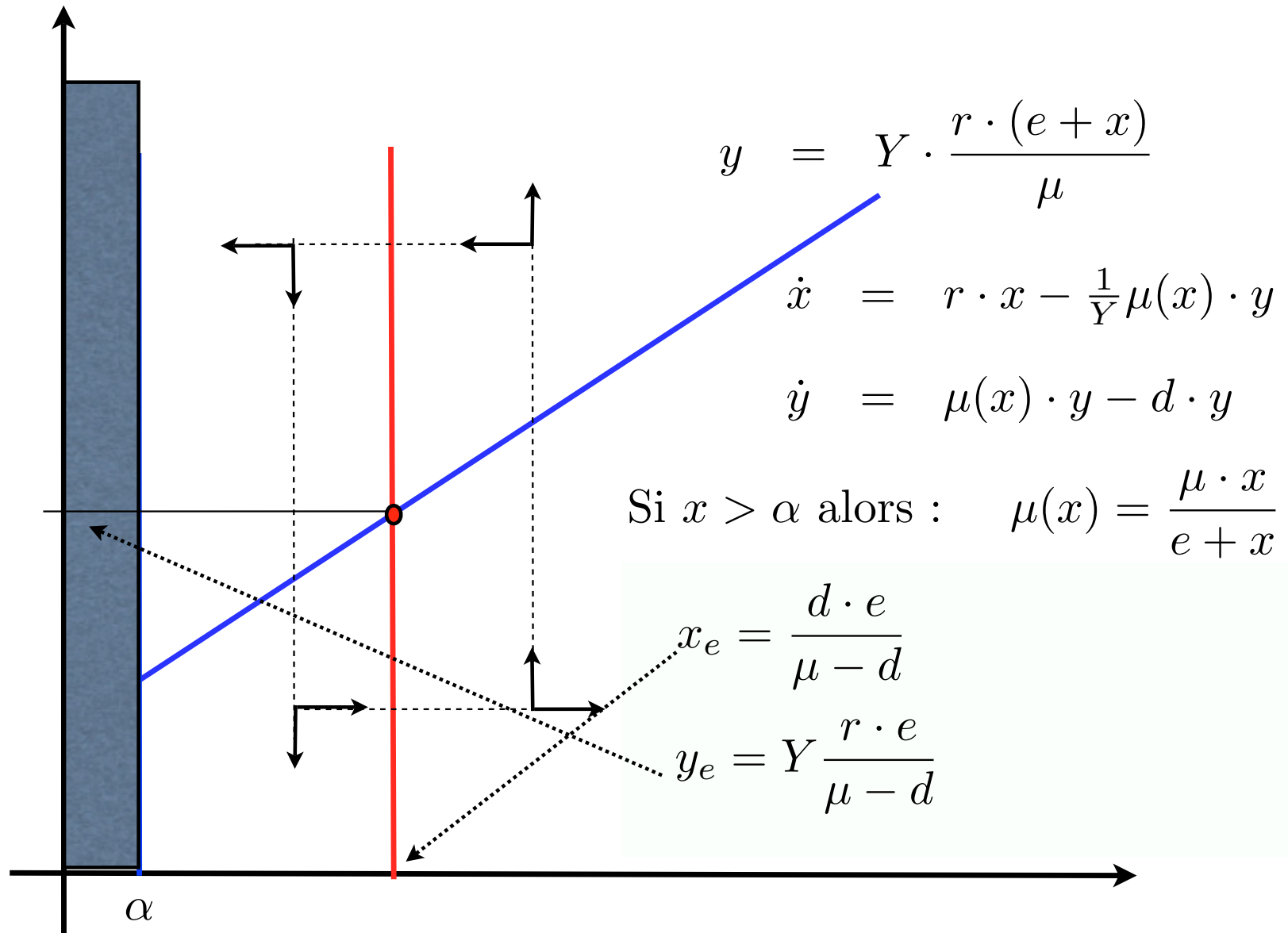
Exemple



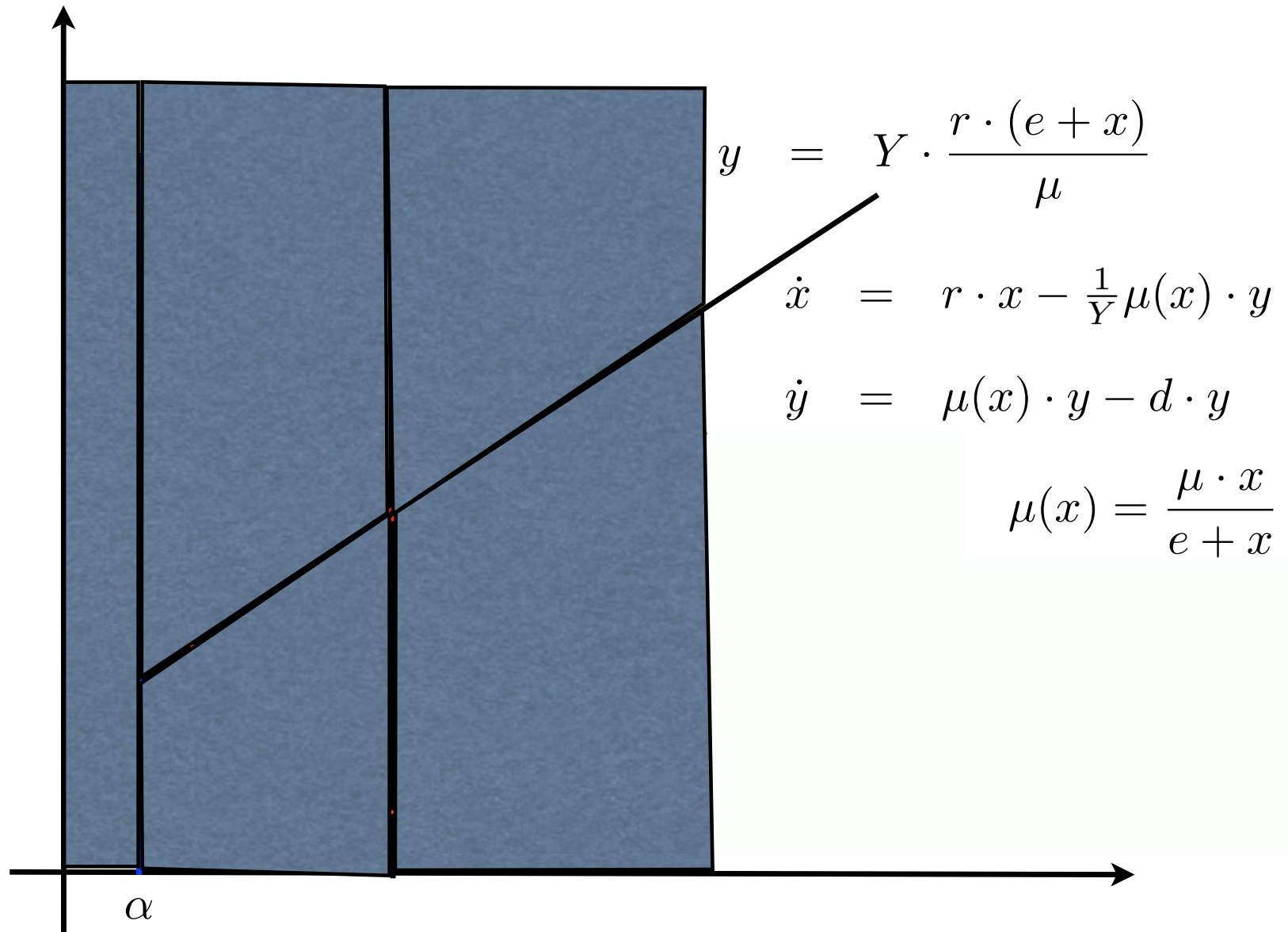
Mathématiques du modèle de Gause



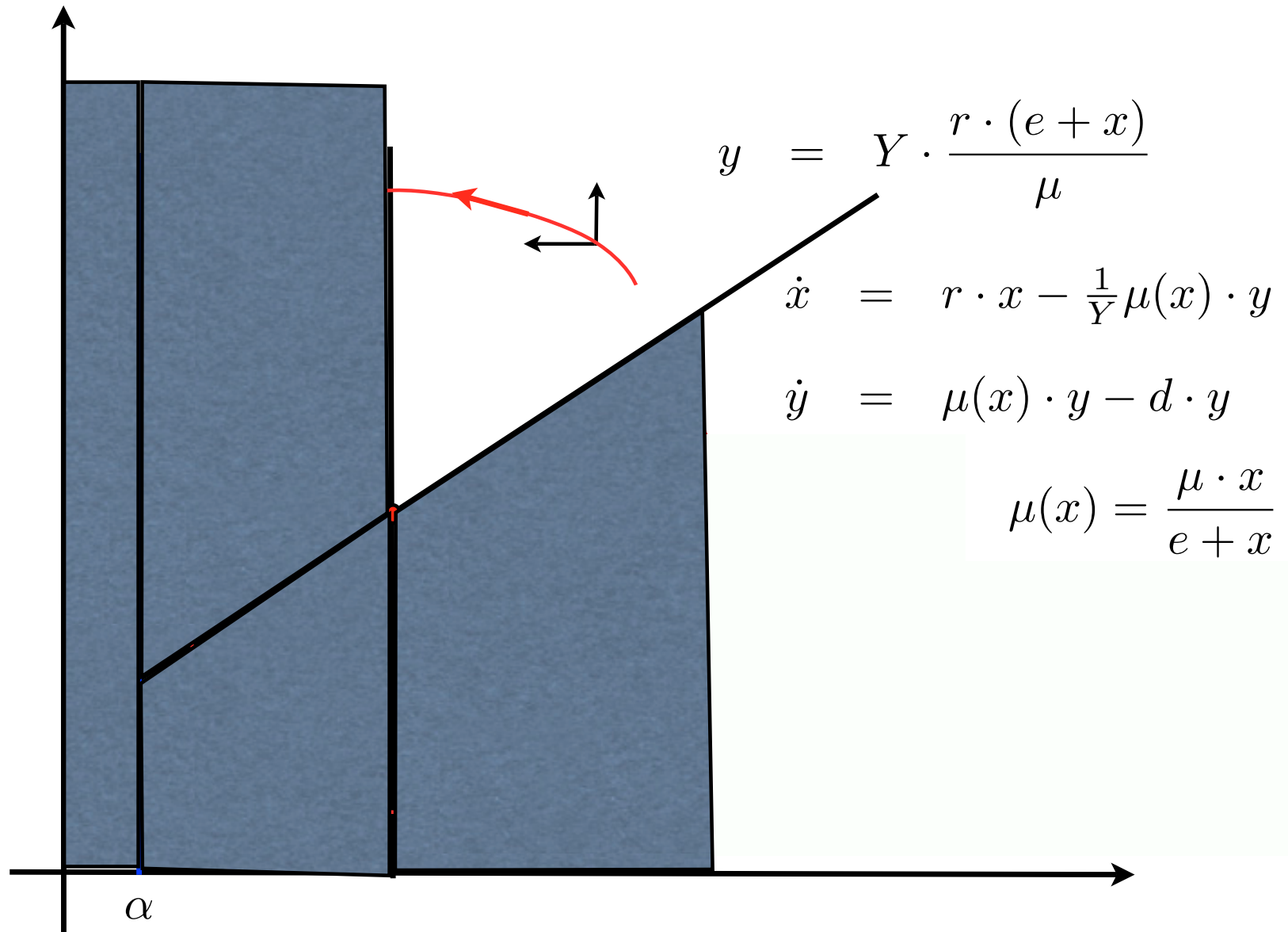
Mathématiques du modèle de Gause



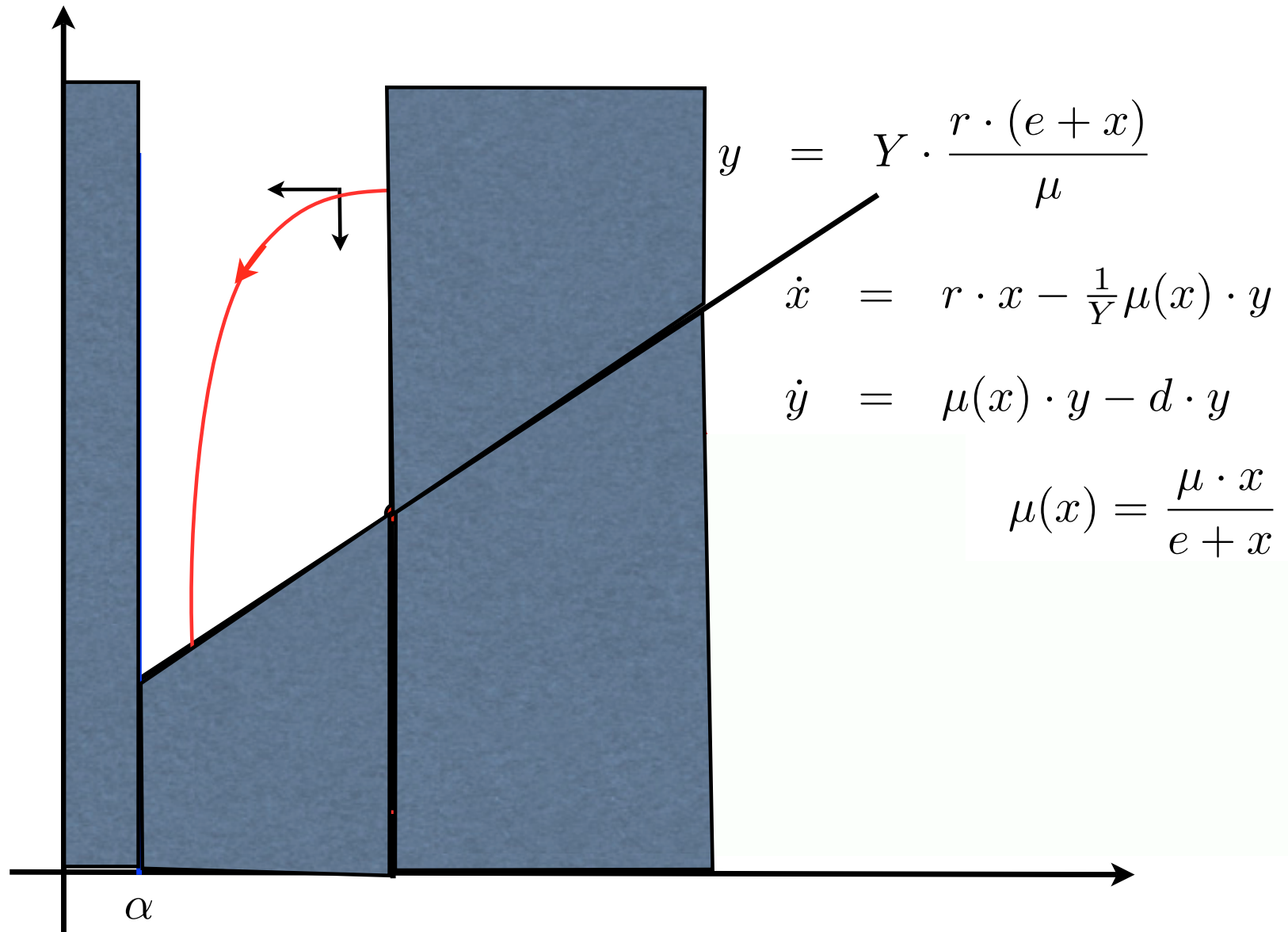
Mathématiques du modèle de Gause



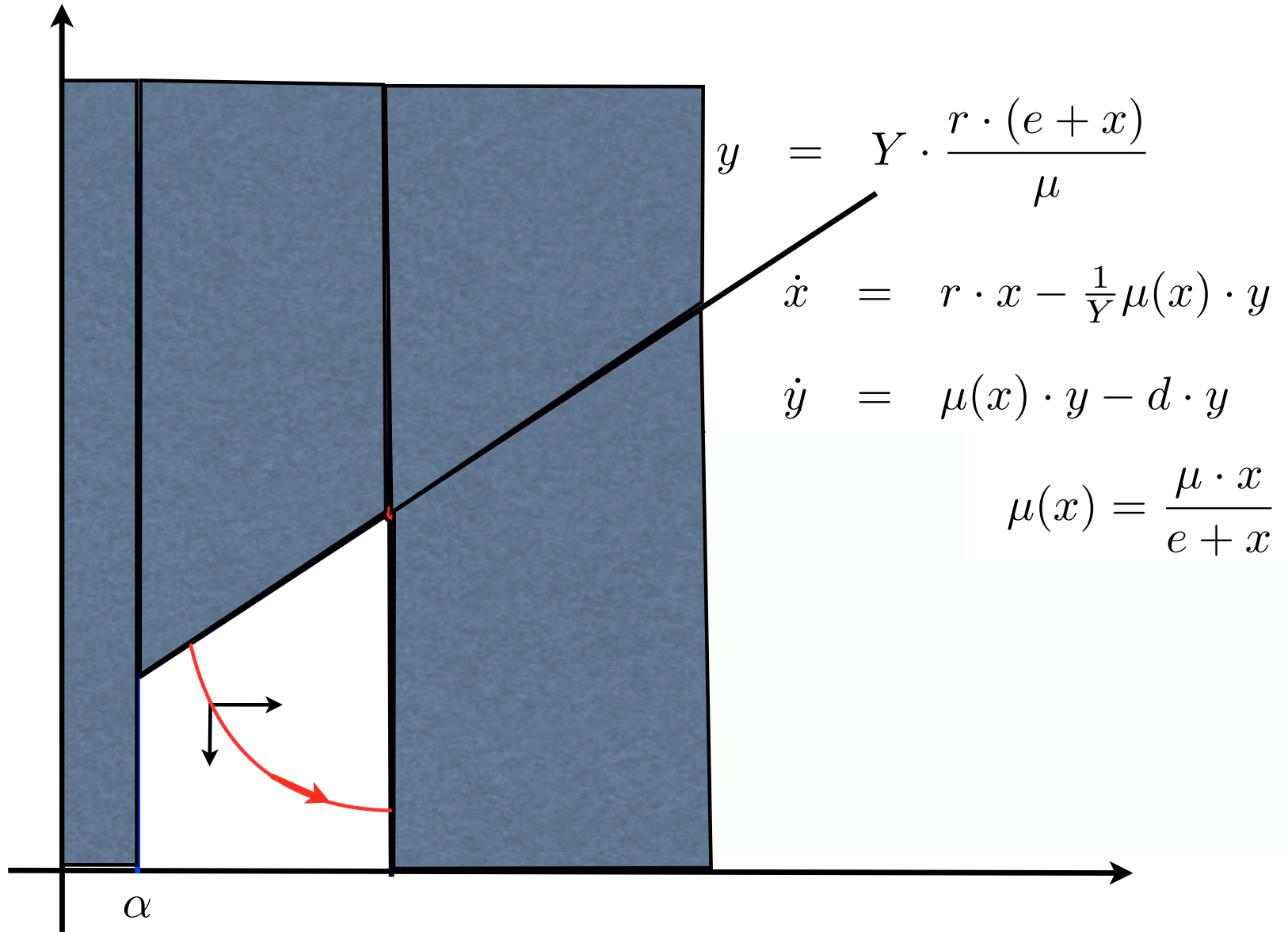
Mathématiques du modèle de Gause



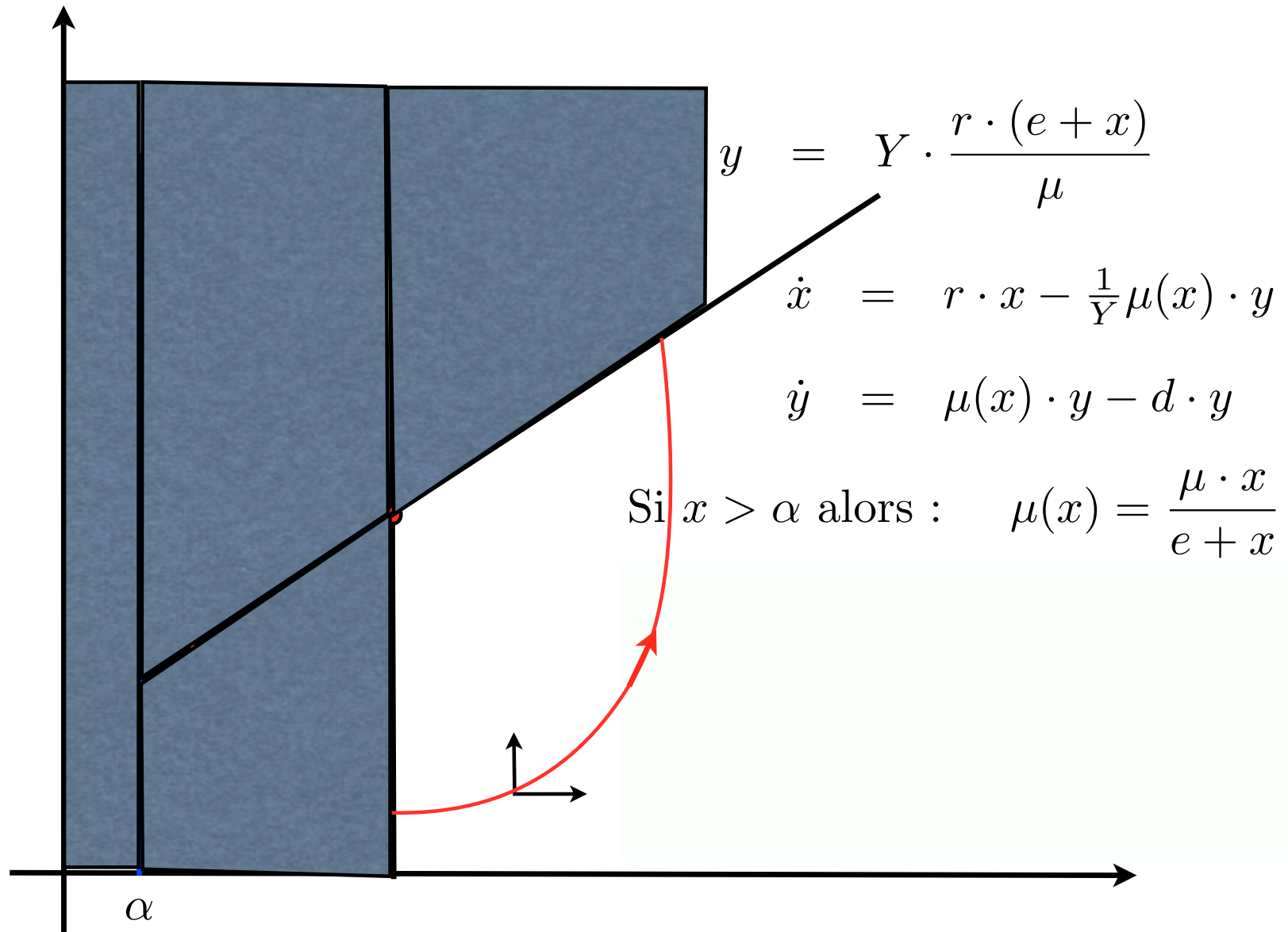
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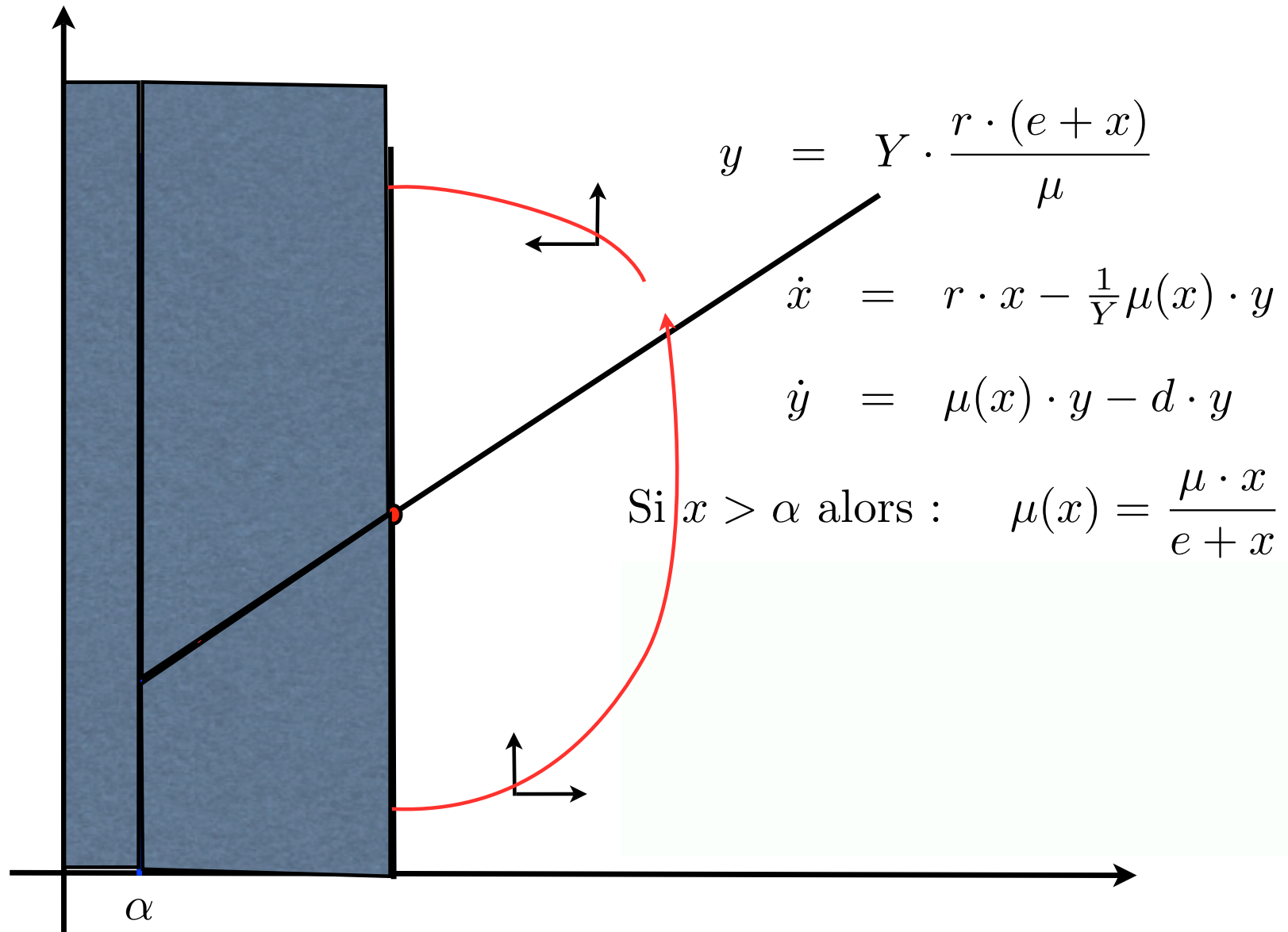
Mathématiques du modèle de Gause



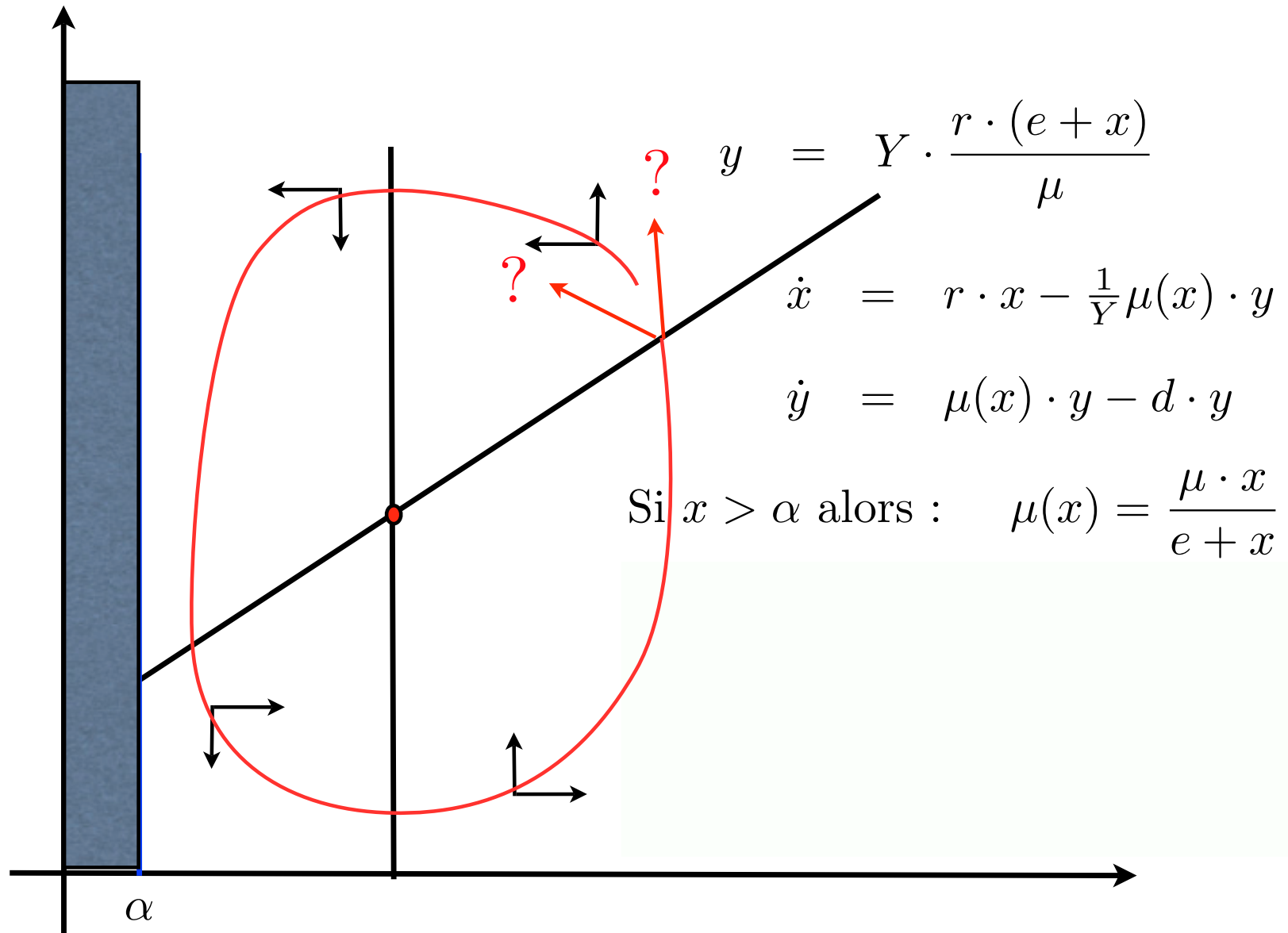
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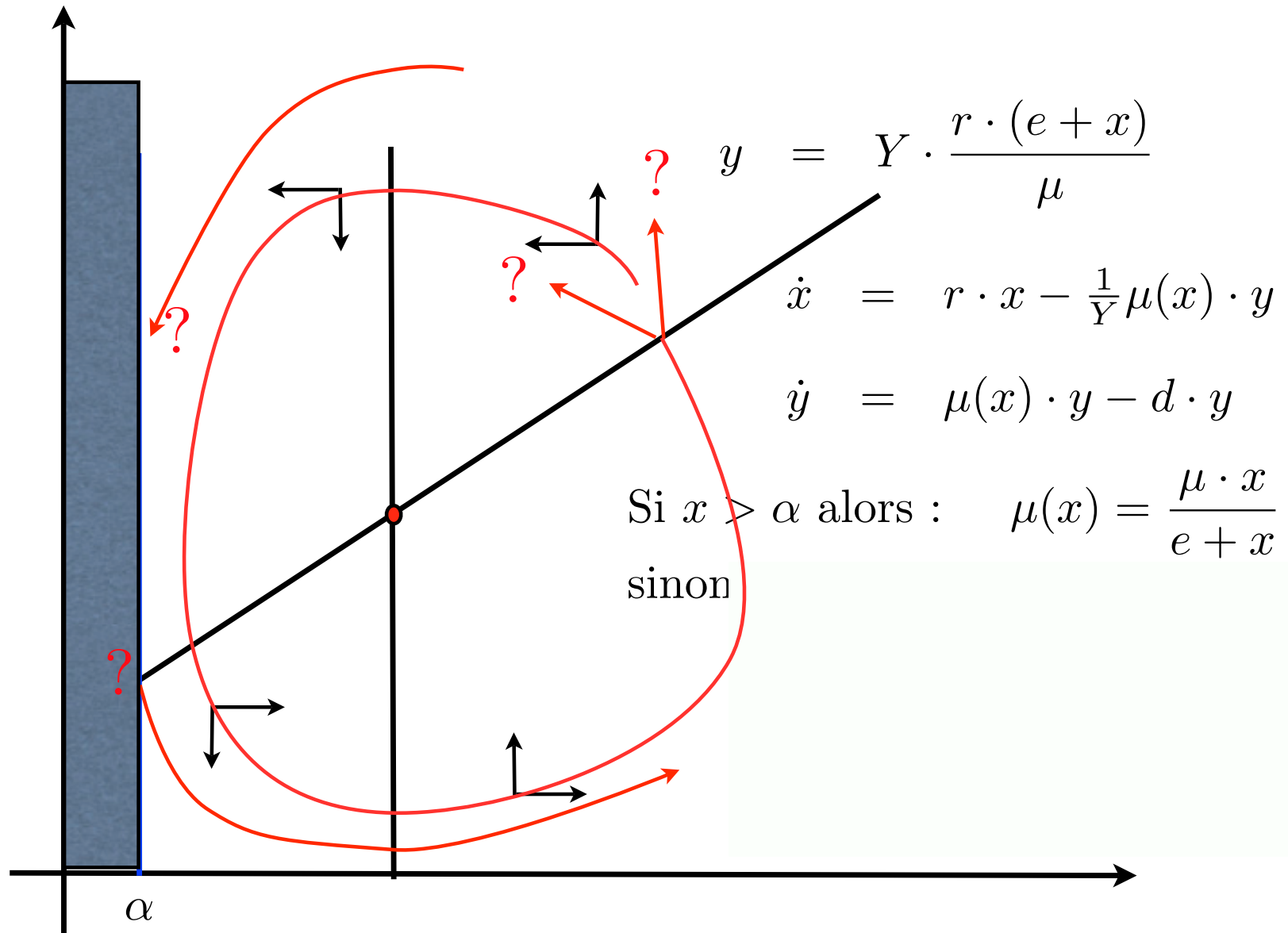
Mathématiques du modèle de Gause



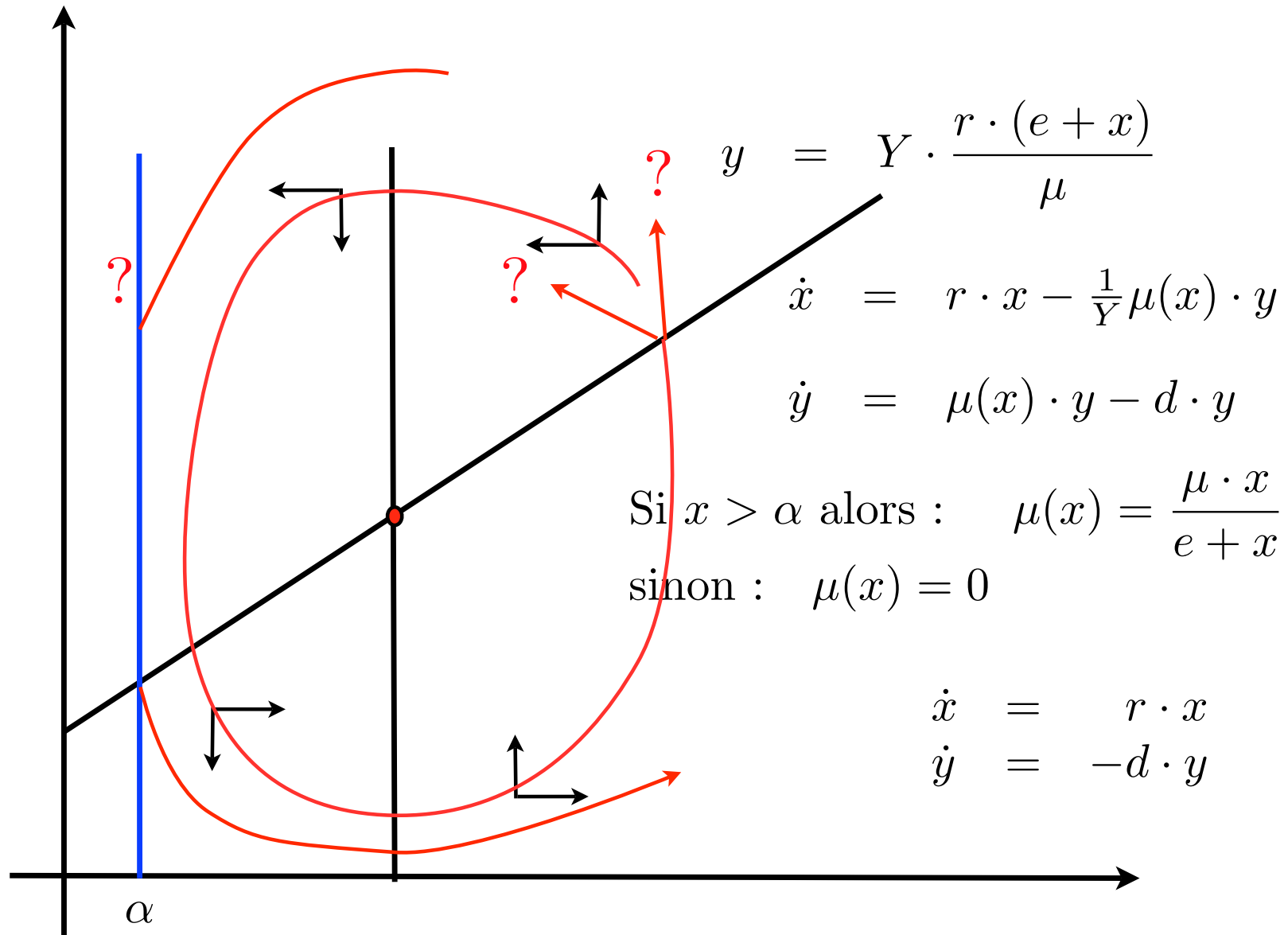
Mathématiques du modèle de Gause



Mathématiques du modèle de Gause



Mathématiques du modèle de Gause



Mathématiques du modèle de Gause

$$\dot{x} = r \cdot x - \frac{1}{Y} \mu(x) \cdot y$$

$$\dot{y} = \mu(x) \cdot y - d \cdot y$$



$$\dot{x} = r \cdot x$$

$$\dot{y} = -d \cdot y$$

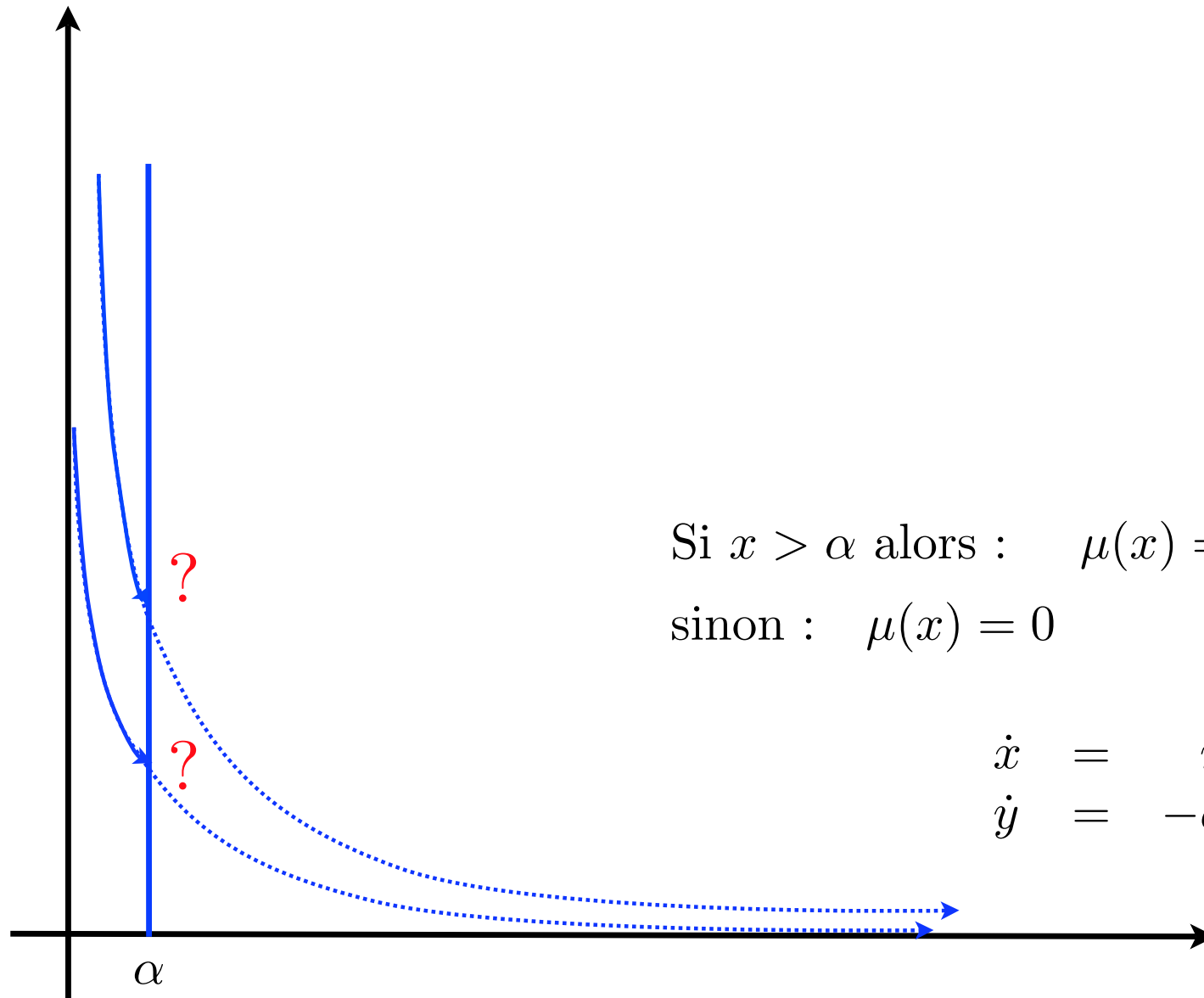
Si $x > \alpha$ alors : $\mu(x) = \frac{\mu \cdot x}{e + x}$

sinon : $\mu(x) = 0$

?

α

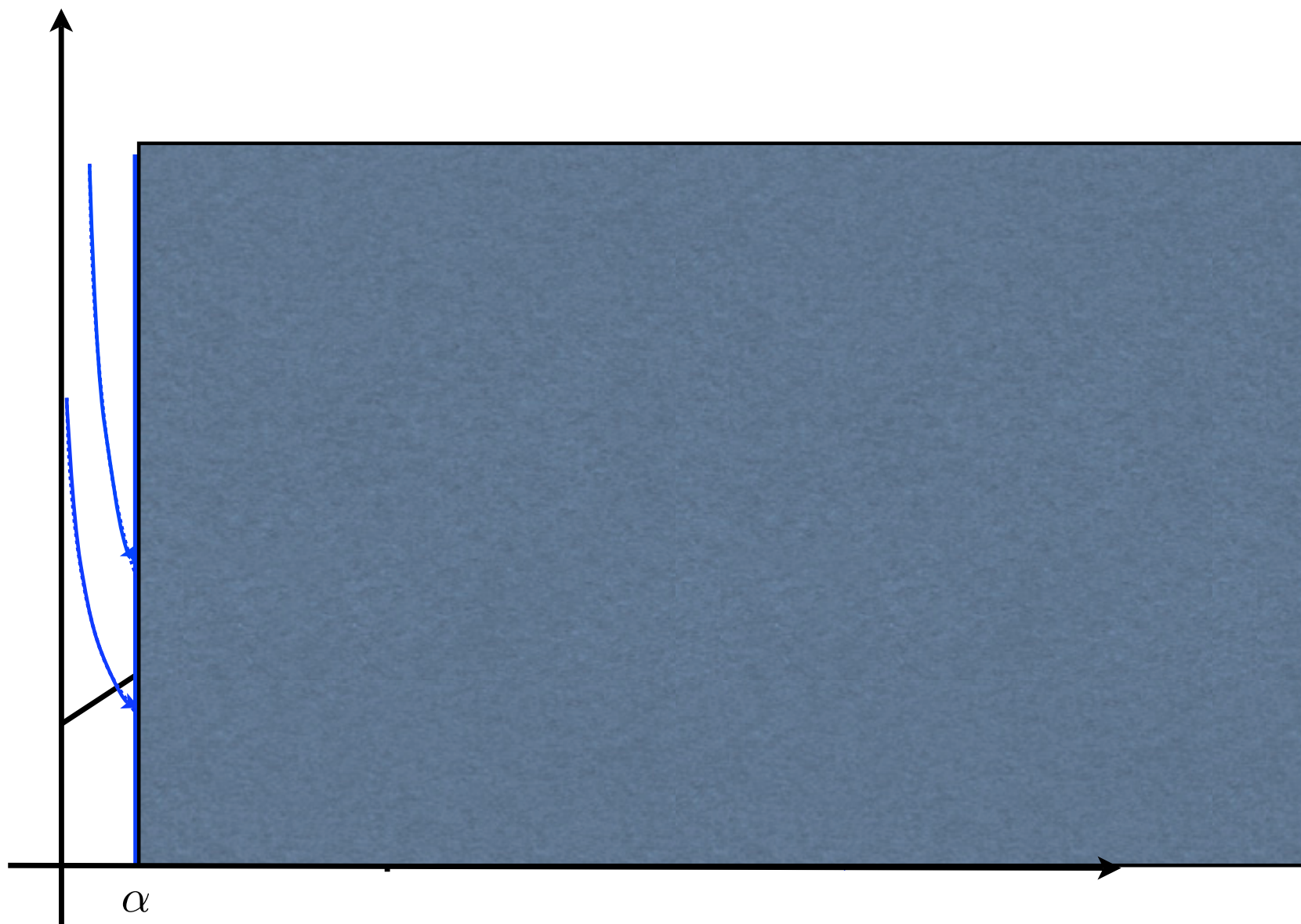
Mathématiques du modèle de Gause



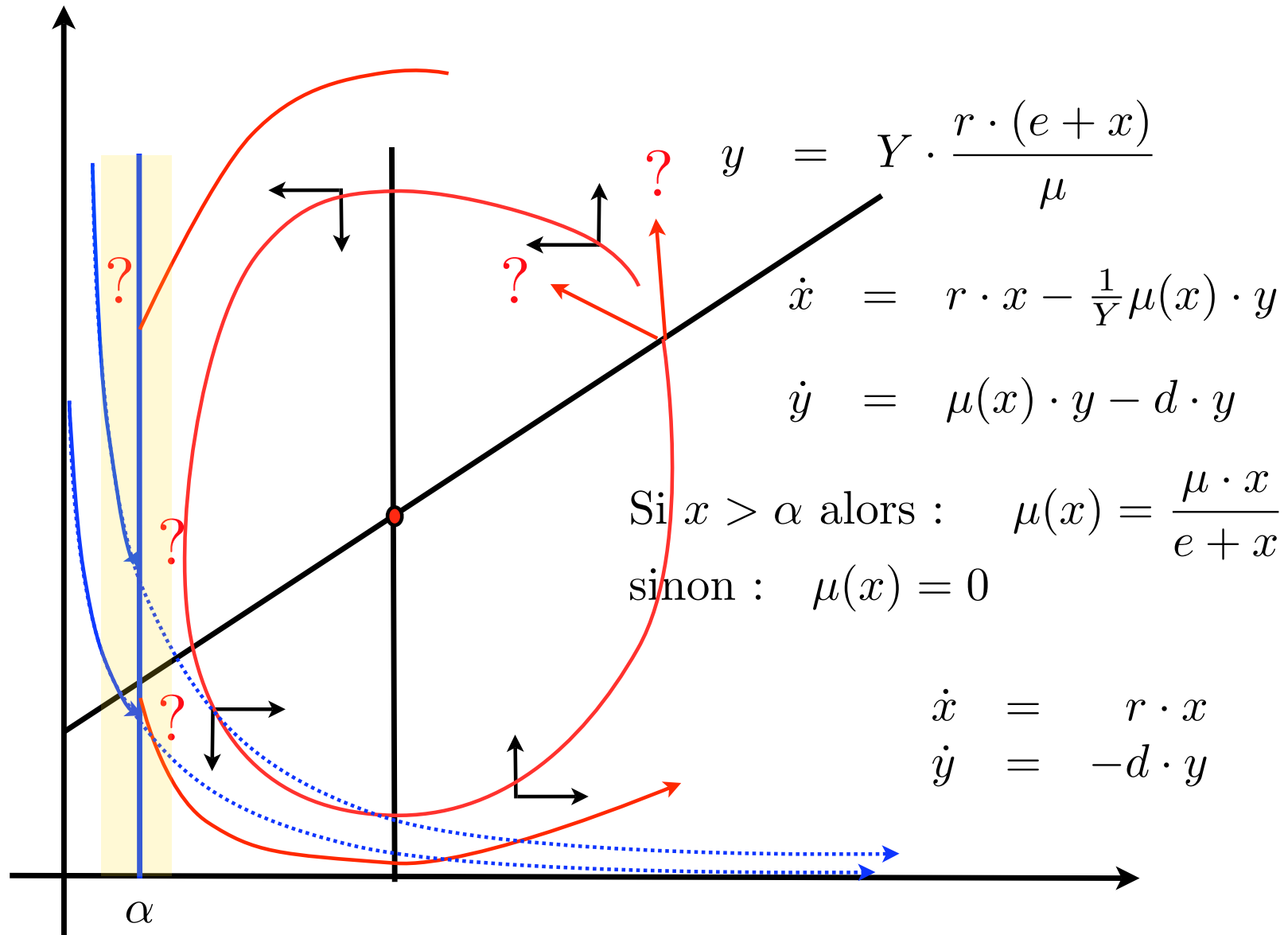
Si $x > \alpha$ alors : $\mu(x) = \frac{\mu \cdot x}{e + x}$
sinon : $\mu(x) = 0$

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

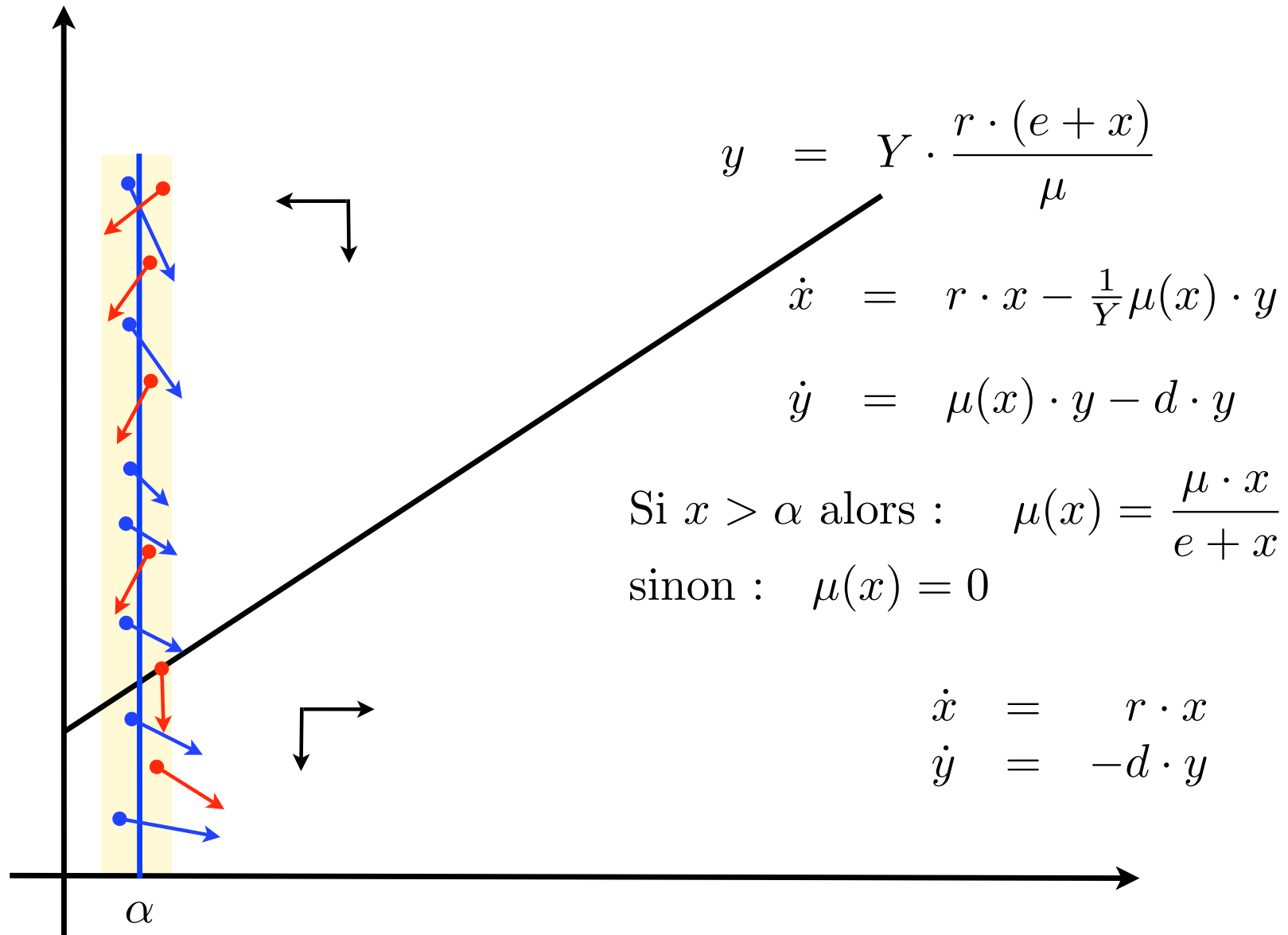
Mathématiques du modèle de Gause



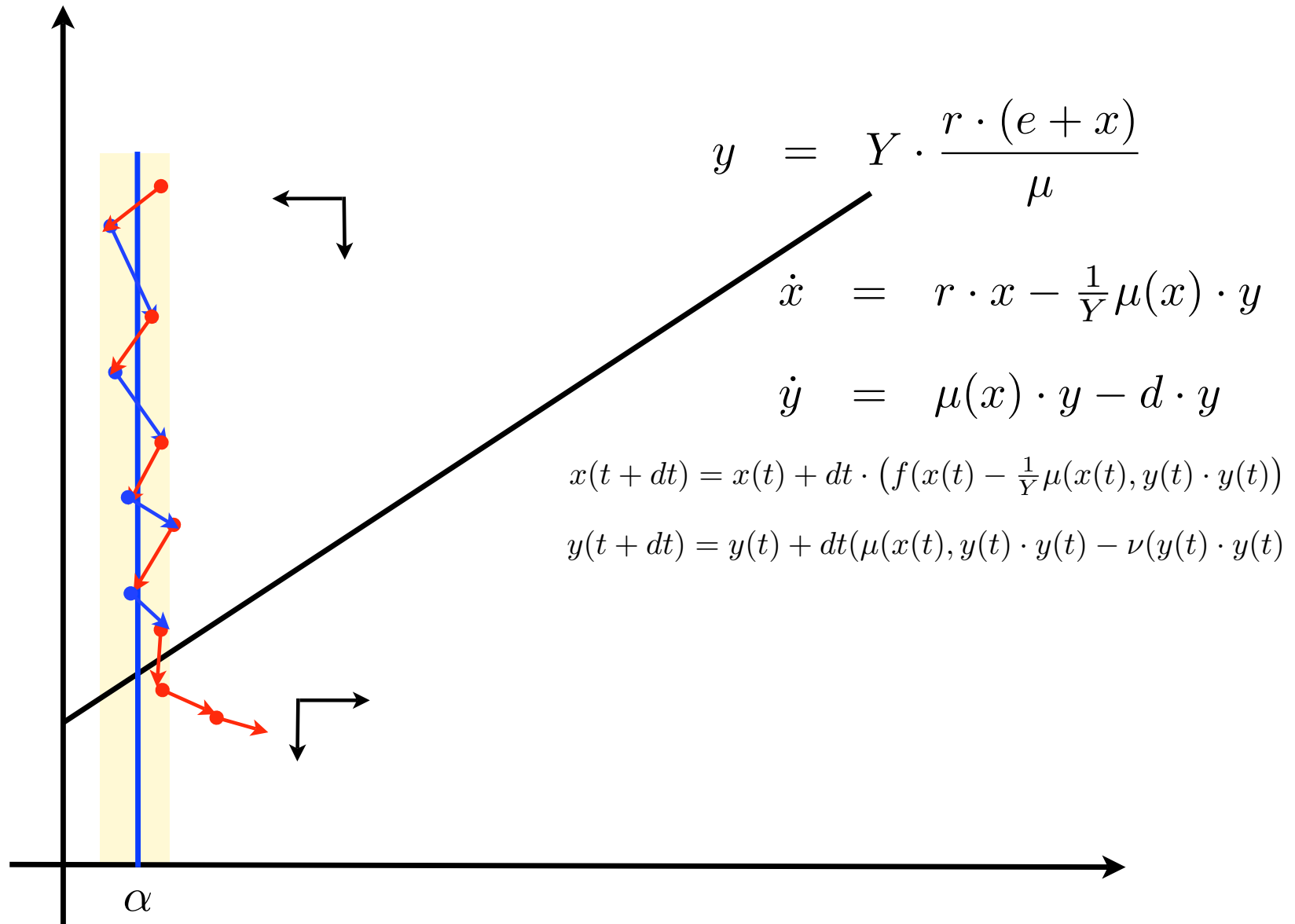
Mathématiques du modèle de Gause



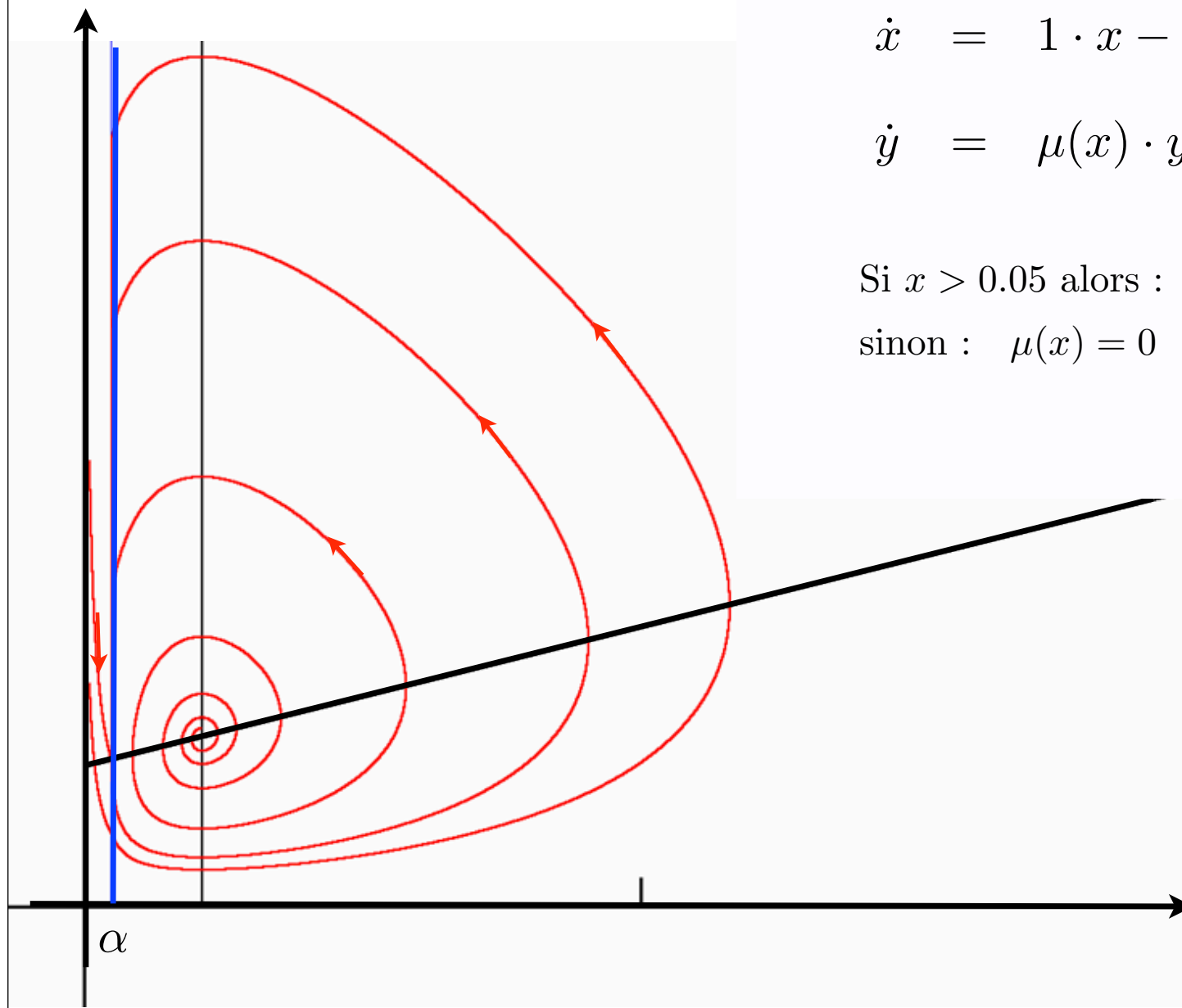
Mathématiques du modèle de Gause



Mathématiques du modèle de Gause



Mathématiques du modèle de Gause

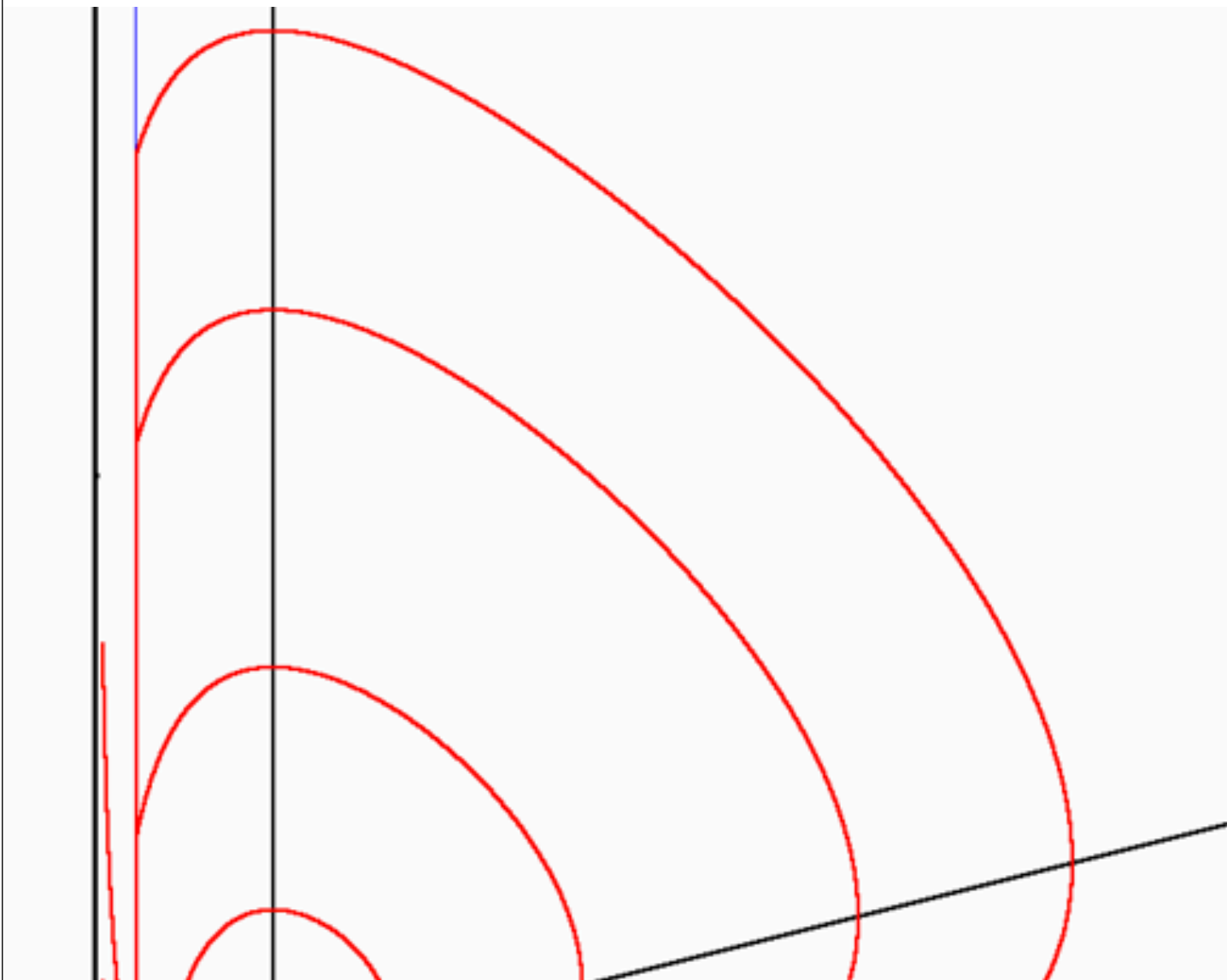


$$\dot{x} = 1 \cdot x - \frac{1}{1} \mu(x) \cdot y$$

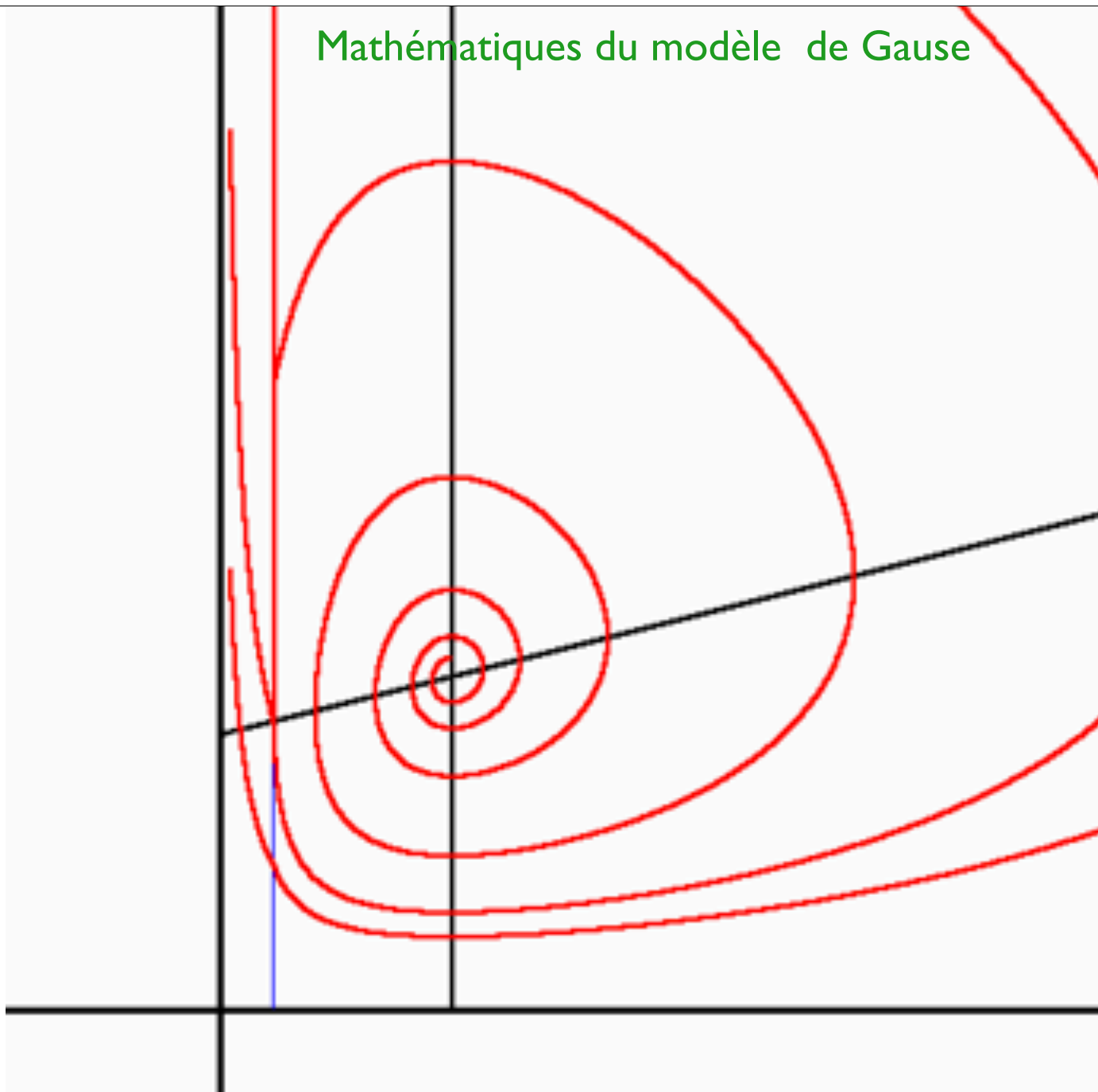
$$\dot{y} = \mu(x) \cdot y - 0.7 \cdot y$$

Si $x > 0.05$ alors : $\mu(x) = \frac{4 \cdot x}{1 + x}$
sinon : $\mu(x) = 0$

Mathématiques du modèle de Gause



Mathématiques du modèle de Gause

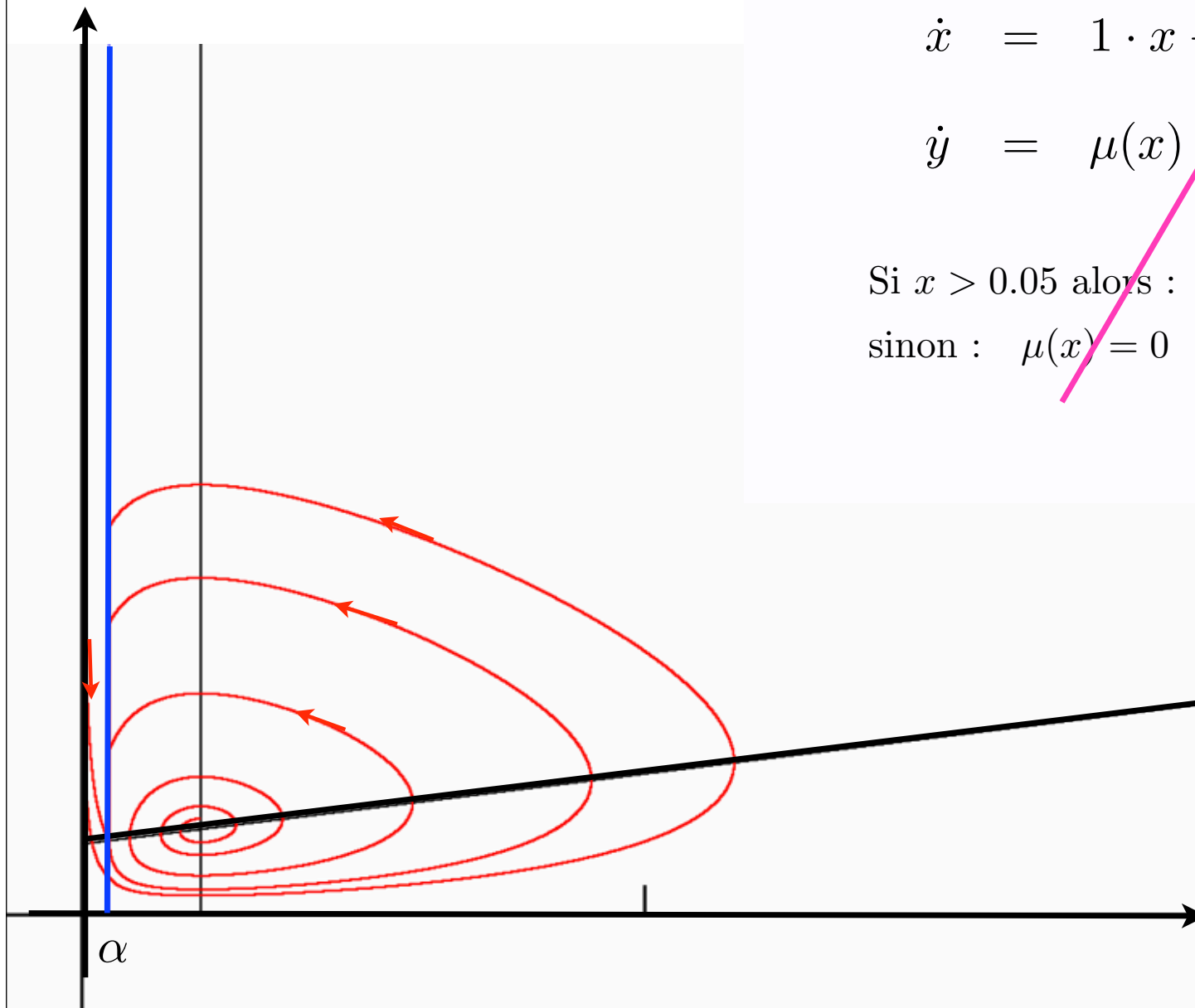


Mathématiques du modèle de Gause

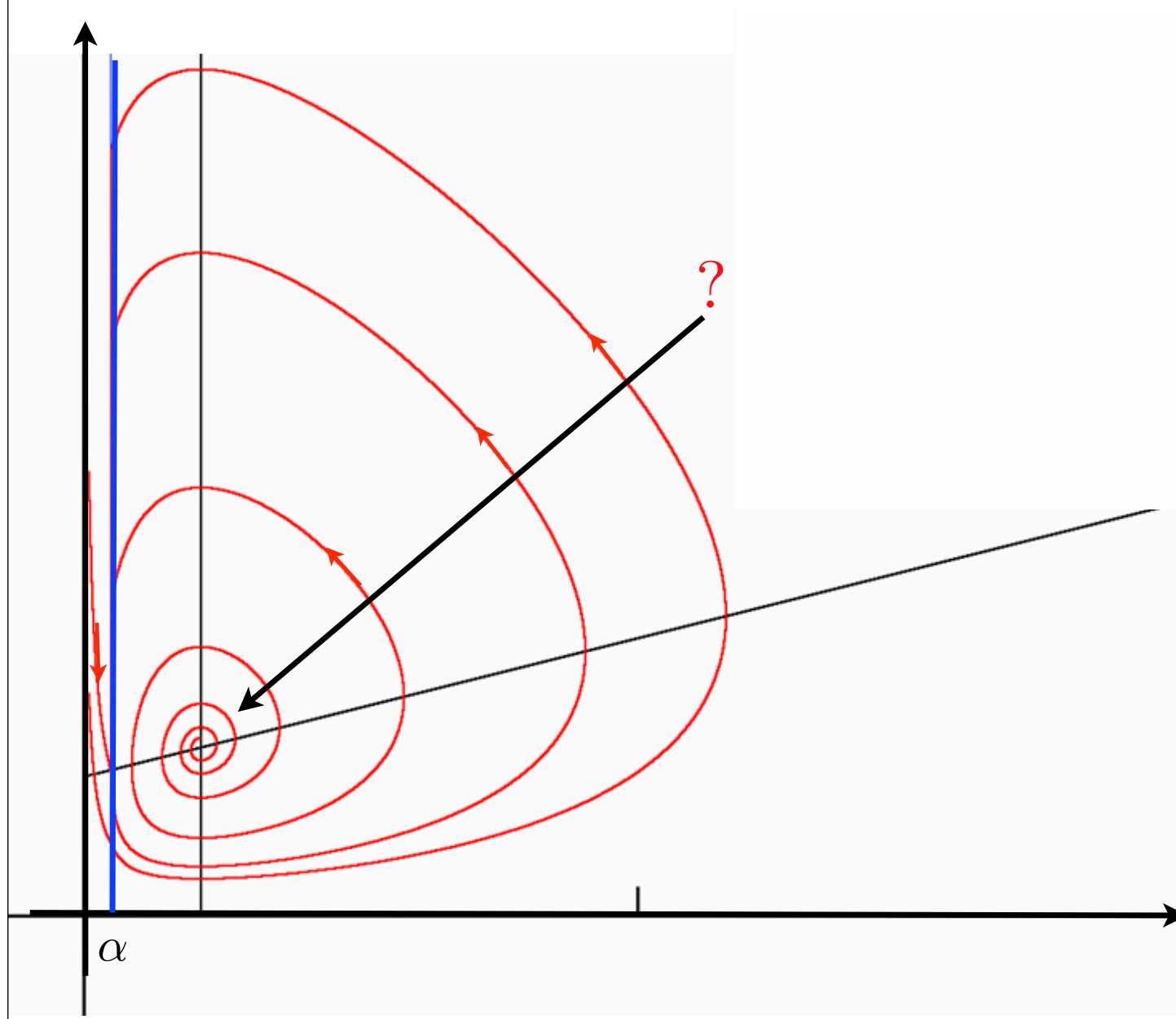
$$\dot{x} = 1 \cdot x - \frac{1}{0.5} \mu(x) \cdot y$$

$$\dot{y} = \mu(x) \cdot y - 0.7 \cdot y$$

Si $x > 0.05$ alors : $\mu(x) = \frac{4 \cdot x}{1 + x}$
sinon : $\mu(x) = 0$



Mathématiques du modèle de Gause



Petit cours de maths

1, 2 au lieu de x, y 1,2,...n

$$\frac{dx_1(t)}{dt} = f_1(x_1(t), x_2(t))$$

$$\frac{dx_2(t)}{dt} = f_2(x_1(t), x_2(t))$$

$$f_1(x_{1e}, x_{2e}) = 0$$

$$f_2(x_{1e}, x_{2e}) = 0$$

$$x_1(t) = x_{1e} + \varepsilon \delta_1(t)$$

$$x_2(t) = x_{2e} + \varepsilon \delta_2(t)$$

$$f_1(x_{1e} + \varepsilon \delta_1(t), x_{2e} + \varepsilon \delta_2(t)) = \dots$$

$$\dots = \frac{\partial f_1}{\partial x_1}(x_{1e}, x_{2e}) \varepsilon \delta_1(t) + \frac{\partial f_1}{\partial x_2}(x_{1e}, x_{2e}) \varepsilon \delta_2(t) + o(\varepsilon \delta_1, \varepsilon \delta_2)$$

$$\frac{d\delta_1}{dt} = \frac{\partial f_1}{\partial x_1}(x_{1e}, x_{2e}) \delta_1(t) + \frac{\partial f_1}{\partial x_2}(x_{1e}, x_{2e}) \delta_2(t)$$

$$\frac{d\delta_2}{dt} = \frac{\partial f_2}{\partial x_1}(x_{1e}, x_{2e}) \delta_1(t) + \frac{\partial f_2}{\partial x_2}(x_{1e}, x_{2e}) \delta_2(t)$$

$$\left(\begin{array}{c|c} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} \\ \hline \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} \end{array} \right)$$

Petit cours de maths

$$\frac{d\delta_1}{dt} = \frac{\partial f_1}{\partial x_1}(x_{1e}, x_{2e})\delta_1(t) + \frac{\partial f_1}{\partial x_2}(x_{1e}, x_{2e})\delta_2(t)$$

$$\frac{d\delta_2}{dt} = \frac{\partial f_2}{\partial x_1}(x_{1e}, x_{2e})\delta_1(t) + \frac{\partial f_2}{\partial x_2}(x_{1e}, x_{2e})\delta_2(t)$$

$$(x_1, x_2) = x$$

$$(\delta_1, \delta_2) = \delta$$

$$a_{i,j} = \frac{\partial f_i}{\partial x_j}(x_e)$$

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

$$A\delta = \begin{bmatrix} a_{11}\delta_1 + a_{12}\delta_2 \\ a_{21}\delta_1 + a_{22}\delta_2 \end{bmatrix}$$

$$\frac{d\delta(t)}{dt} = A\delta(t)$$

$$\delta(t) = \delta e^{\lambda t}$$

$$\lambda \delta e^{\lambda t} = A \delta e^{\lambda t}$$

$$A\delta = \lambda \delta$$

(Valeur propre , Vecteur propre)

$$\left(\begin{array}{c|c} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} \\ \hline \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} \end{array} \right)$$

Petit cours de maths

$$\begin{aligned}\frac{d\delta_1}{dt} &= \frac{\partial f_1}{\partial x_1}(x_{1e}, x_{2e})\delta_1(t) + \frac{\partial f_1}{\partial x_2}(x_{1e}, x_{2e})\delta_2(t) \\ \frac{d\delta_2}{dt} &= \frac{\partial f_2}{\partial x_1}(x_{1e}, x_{2e})\delta_1(t) + \frac{\partial f_2}{\partial x_2}(x_{1e}, x_{2e})\delta_2(t)\end{aligned}$$

$$(x_1, x_2) = x$$

$$(\delta_1, \delta_2) = \delta$$

$$a_{i,j} = \frac{\partial f_i}{\partial x_j}(x_e)$$

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

$$A\delta = \begin{bmatrix} a_{11}\delta_1 + a_{12}\delta_2 \\ a_{21}\delta_1 + a_{22}\delta_2 \end{bmatrix}$$

$$\frac{d\delta(t)}{dt} = A\delta(t)$$

$$\delta(t) = \delta e^{\lambda t}$$

$$\lambda \delta e^{\lambda t} = A \delta e^{\lambda t}$$

$$A\delta = \lambda \delta$$

(Valeur propre , Vecteur propre)

$$\left(\begin{array}{c|c} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} \\ \hline \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} \end{array} \right)$$

Petit cours de maths

$$\left(\begin{array}{c|c} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} \\ \hline \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} \end{array} \right)$$

$$\lambda^2 - \left(\frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} \right) \lambda + \left(\frac{\partial f_1}{\partial x_1} \cdot \frac{\partial f_2}{\partial x_2} - \frac{\partial f_2}{\partial x_1} \cdot \frac{\partial f_1}{\partial x_2} \right) = 0$$

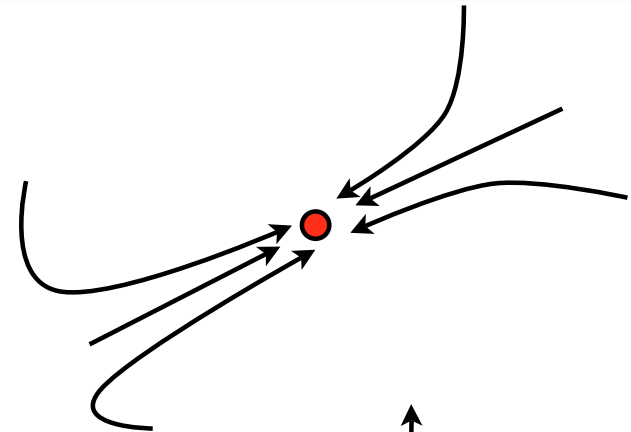
Equation du second degré.....
2 racines réelle ou complexes

Petit cours de maths

$$\lambda_1 < 0$$

$$\lambda_2 < 0$$

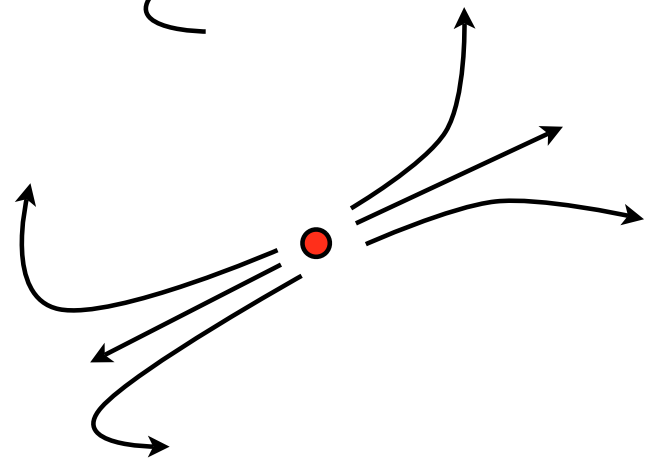
Nœud stable



$$\lambda_1 > 0$$

$$\lambda_2 > 0$$

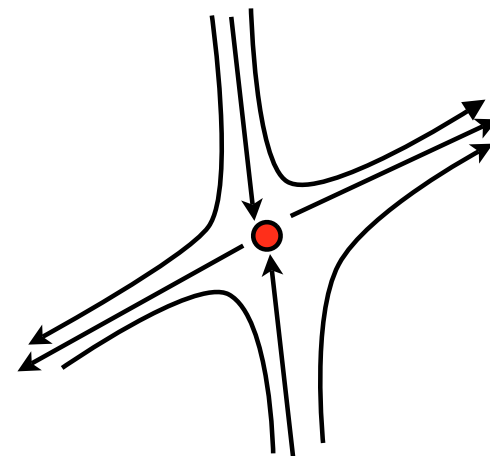
Nœud instable



$$\lambda_1 > 0$$

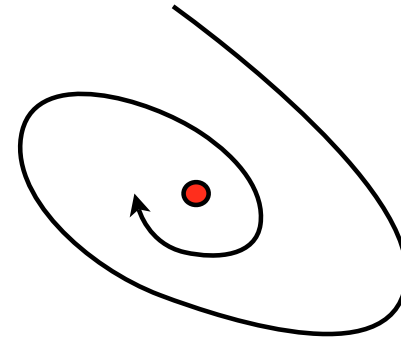
$$\lambda_2 < 0$$

Col



Petit cours de maths

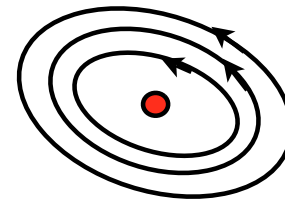
$a < 0$ Foyer stable



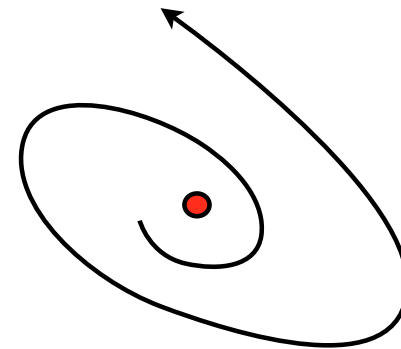
$$\lambda_1 = a + ib$$

$$\lambda_2 = a - ib$$

$a = 0$ Centre



$a > 0$ Foyer instable



Petit cours de maths

En dimension quelconque n

$$\lambda_1 = r_1; \quad \lambda_2 = r_2; \quad \dots, \lambda_p = r_p$$

$$\begin{cases} \lambda_{p+1} = \alpha_1 + i\beta_1 \\ \lambda_{p+2} = \alpha_1 - i\beta_1 \end{cases}$$

$$\begin{cases} \lambda_{p+3} = \alpha_2 + i\beta_2 \\ \lambda_{p+4} = \alpha_2 - i\beta_2 \end{cases}$$

.....

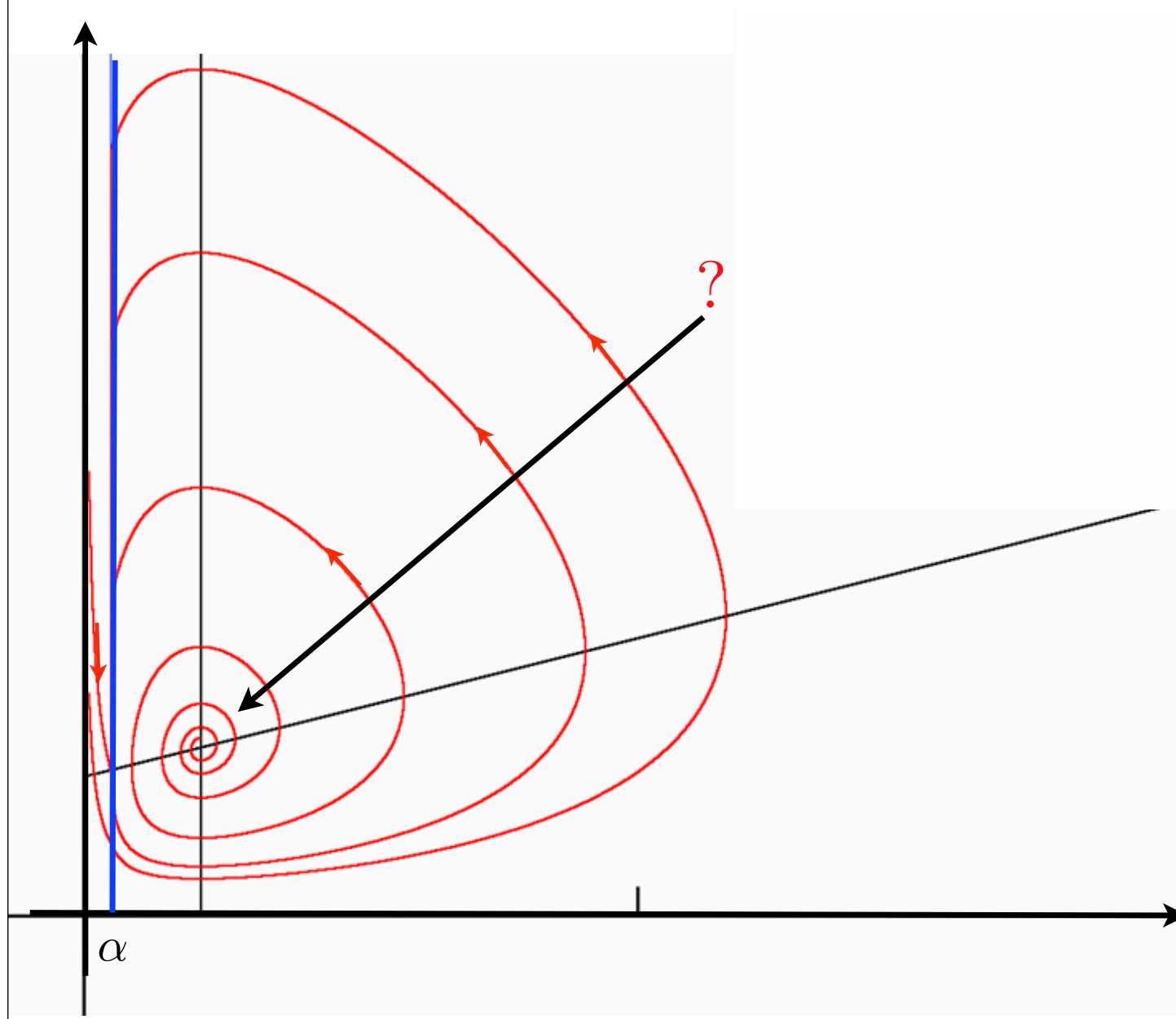
$$\begin{cases} \lambda_{p+2q-1} = \alpha_q + i\beta_q \\ \lambda_{p+2q} = \alpha_q - i\beta_q \end{cases}$$

$$p + 2q = n$$

Stable

$$r_1 < 0; r_2 < 0; \dots; r_p < 0; \alpha_1 < 0; \dots; \alpha_q < 0$$

Mathématiques du modèle de Gause



Mathématiques du modèle de Gause

$$\dot{x} = r \cdot x - \frac{1}{Y} \mu(x) \cdot y$$

$$\mu(x) = \frac{\mu \cdot x}{e + x}$$

$$\dot{y} = \mu(x) \cdot y - d \cdot y$$

On se débarrasse de Y

$$\tilde{y} = \frac{1}{Y} y$$

$$\dot{x} = r \cdot x - \mu(x) \cdot \tilde{y}$$

$$\dot{\tilde{y}} = \frac{1}{Y} [\mu(x) Y \cdot \tilde{y} - d \cdot Y \tilde{y}]$$

Mathématiques du modèle de Gause

$$\dot{x} = r \cdot x - \mu(x) \cdot y$$

$$\dot{y} = \mu(x) \cdot y - d \cdot y$$

$$\mu(x) = \frac{\mu \cdot x}{e + x}$$

$$\left(\begin{array}{c|c} f'_x & f'_y \\ \hline g'_x & g'_y \end{array} \right) = \left(\begin{array}{c|c} r - \mu'(x_e) \cdot y_e & \mu(x_e) \\ \hline \mu'(x_e) \cdot y_e & \mu(x_e) - d \end{array} \right)$$

$$\lambda^2 - \left(\frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} \right) \lambda + \left(\frac{\partial f_1}{\partial x_1} \cdot \frac{\partial f_2}{\partial x_2} - \frac{\partial f_2}{\partial x_2} \cdot \frac{\partial f_1}{\partial x_1} \right) = 0 \quad ?$$

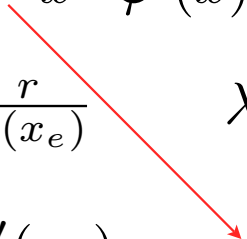
Mathématiques du modèle de Gause

- $\mu(x_e) = d$
 - $y_e = (r/d) \cdot x_e$
 - $\mu(x) = x \cdot \varphi(x)$; $\varphi(x) = \frac{\mu}{e+x}$
 - $\mu'(x) = x \cdot \varphi'(x) + \varphi(x)$
 - $y_e = \frac{r}{\varphi(x_e)}$
- $$\left(\begin{array}{c|c} r - \mu'(x_e) \cdot y_e & \mu(x_e) \\ \hline \mu'(x_e) \cdot y_e & \mu(x_e) - d \end{array} \right)$$

$$\lambda^2 - \left(\frac{\partial f_1}{\partial x_1} + \frac{\partial f_2}{\partial x_2} \right) \lambda + \left(\frac{\partial f_1}{\partial x_1} \cdot \frac{\partial f_2}{\partial x_2} - \frac{\partial f_2}{\partial x_2} \cdot \frac{\partial f_1}{\partial x_1} \right) = 0$$

$$\lambda^2 - (r - \mu'(x_e) \cdot y_e) \lambda + (d \cdot \mu'(x_e) \cdot y_e) = 0$$

Mathématiques du modèle de Gause

- $\mu(x_e) = d$
 - $y_e = (r/d) \cdot x_e$
 - $\mu(x) = x \cdot \varphi(x)$; $\varphi(x) = \frac{\mu}{e+x}$
 - $\mu'(x) = x \cdot \varphi'(x) + \varphi(x)$
 - $y_e = \frac{r}{\varphi(x_e)}$ $\lambda^2 - (r - \mu'(x_e) \cdot y_e) \lambda + (d \cdot \mu'(x_e) \cdot y_e) = 0$
- $$\mu'(x_e) \cdot y_e = x_e \cdot \varphi'(x_e) \cdot y_e + \varphi(x_e) \cdot y_e$$
- 

Mathématiques du modèle de Gause

- $\mu(x_e) = d$
- $y_e = (r/d) \cdot x_e$
- $\mu(x) = x \cdot \varphi(x)$; $\varphi(x) = \frac{\mu}{e+x}$
- $\mu'(x) = x \cdot \varphi'(x) + \varphi(x)$
- $y_e = \frac{r}{\varphi(x_e)} \quad \lambda^2 - (r - \mu'(x_e) \cdot y_e) \lambda + (d \cdot \mu'(x_e) \cdot y_e) = 0$

$$\mu'(x_e) \cdot y_e = x_e \cdot \varphi'(x_e) \cdot y_e + \varphi(x_e) \cdot y_e$$

$$\mu'(x_e) \cdot y_e = x_e \cdot \varphi'(x_e) \cdot y_e + r$$

Mathématiques du modèle de Gause

- $\mu(x_e) = d$
- $y_e = (r/d) \cdot x_e$
- $\mu(x) = x \cdot \varphi(x)$; $\varphi(x) = \frac{\mu}{e+x}$
- $\mu'(x) = x \cdot \varphi'(x) + \varphi(x)$
- $y_e = \frac{r}{\varphi(x_e)}$

$$\mu'(x_e) \cdot y_e = x_e \cdot \varphi'(x_e) \cdot y_e + r$$



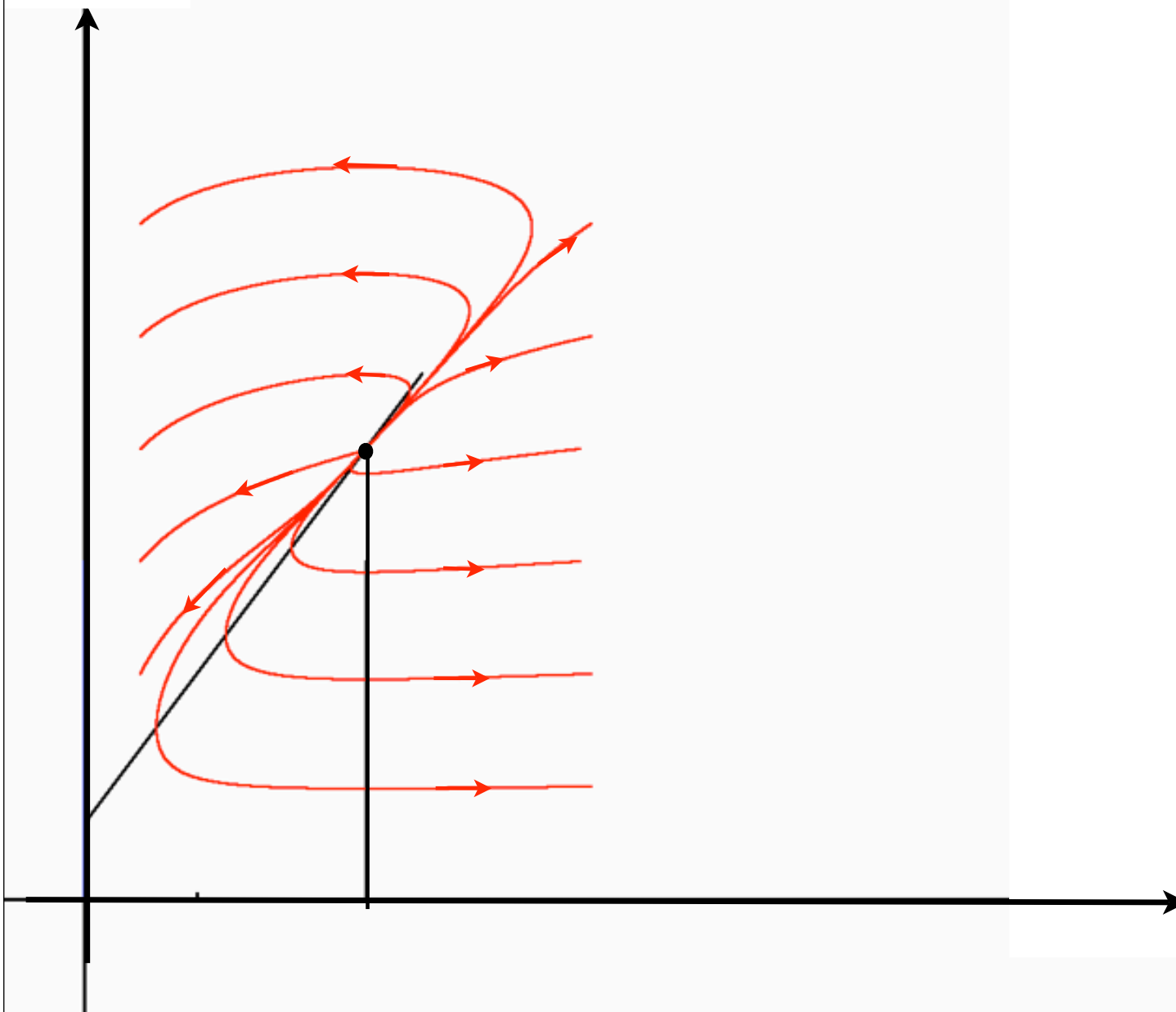
$$\lambda^2 - (r - \mu'(x_e) \cdot y_e) \lambda + (d \cdot \mu'(x_e) \cdot y_e) = 0$$

$$\lambda^2 - (-x_e \cdot \varphi'(x_e) \cdot y_e) \lambda + (d \cdot \mu'(x_e) \cdot y_e)$$

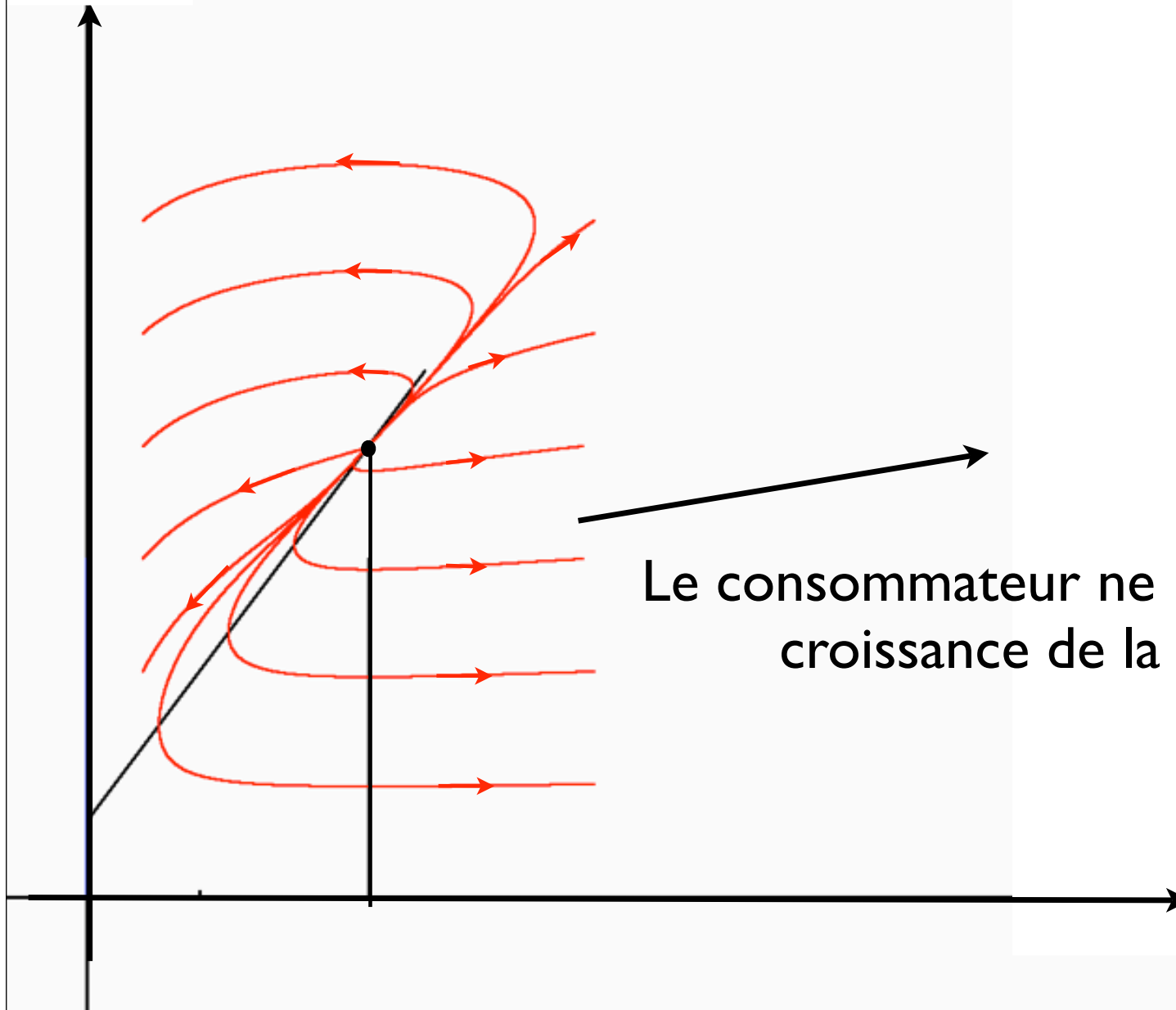
$$(-x_e \cdot \varphi'(x_e) \cdot y_e) > 0$$

Toujours instable

Mathématiques du modèle de Gause



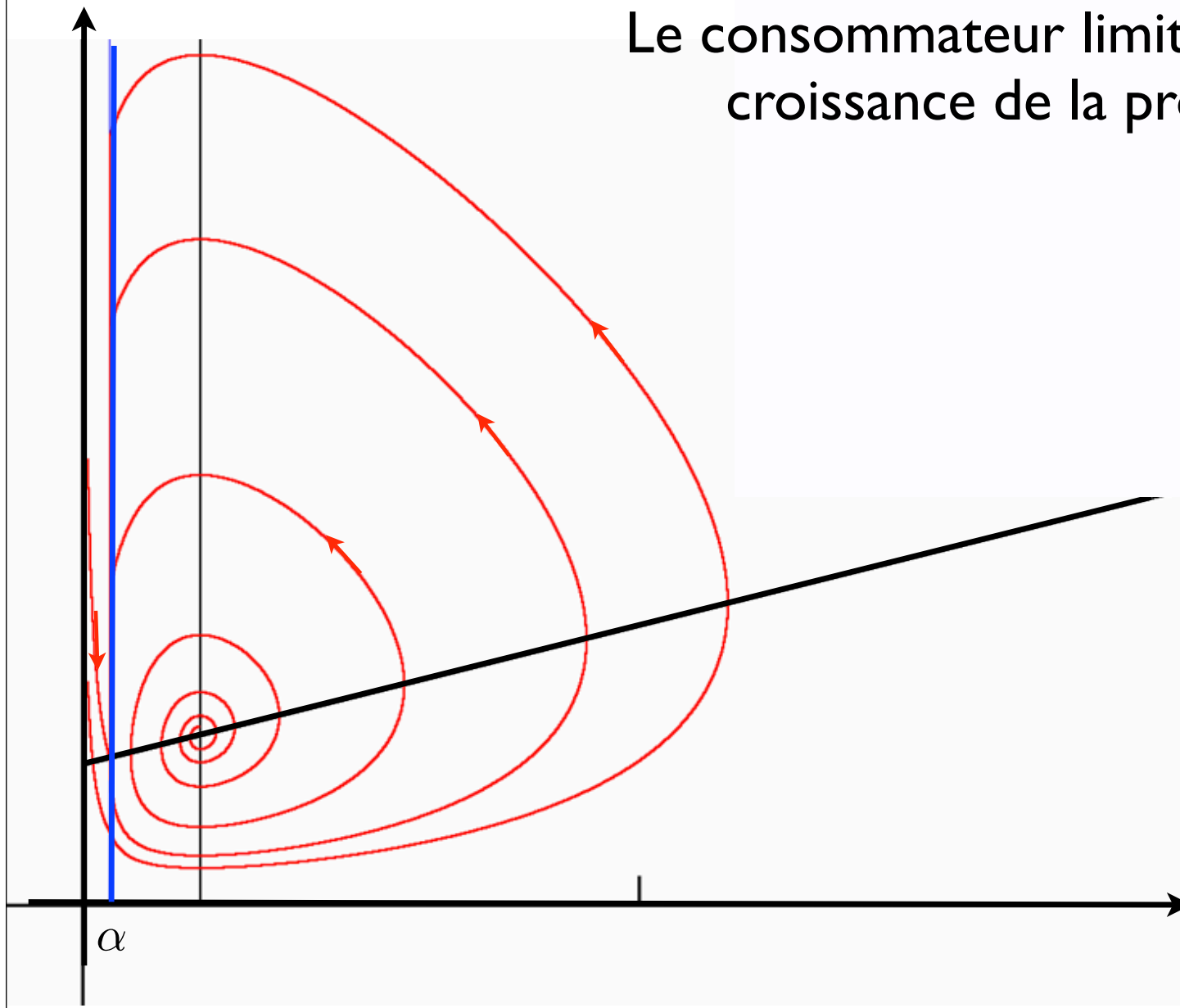
Mathématiques du modèle de Gause



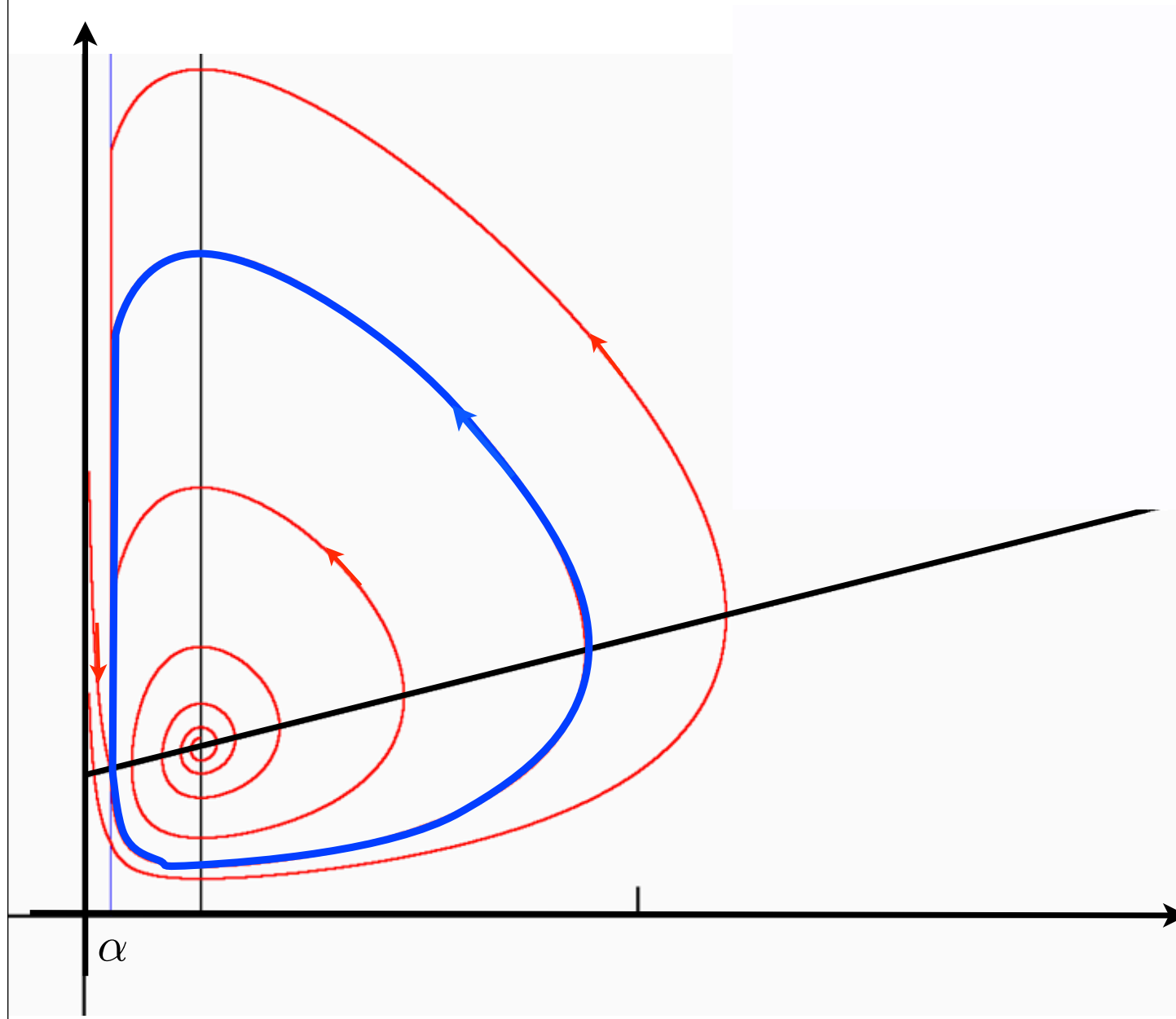
Le consommateur ne limite pas la croissance de la proie.

Mathématiques du modèle de Gause

Le consommateur limite pas la croissance de la proie.



Mathématiques du modèle de Gause



Mathématiques du modèle de Gause

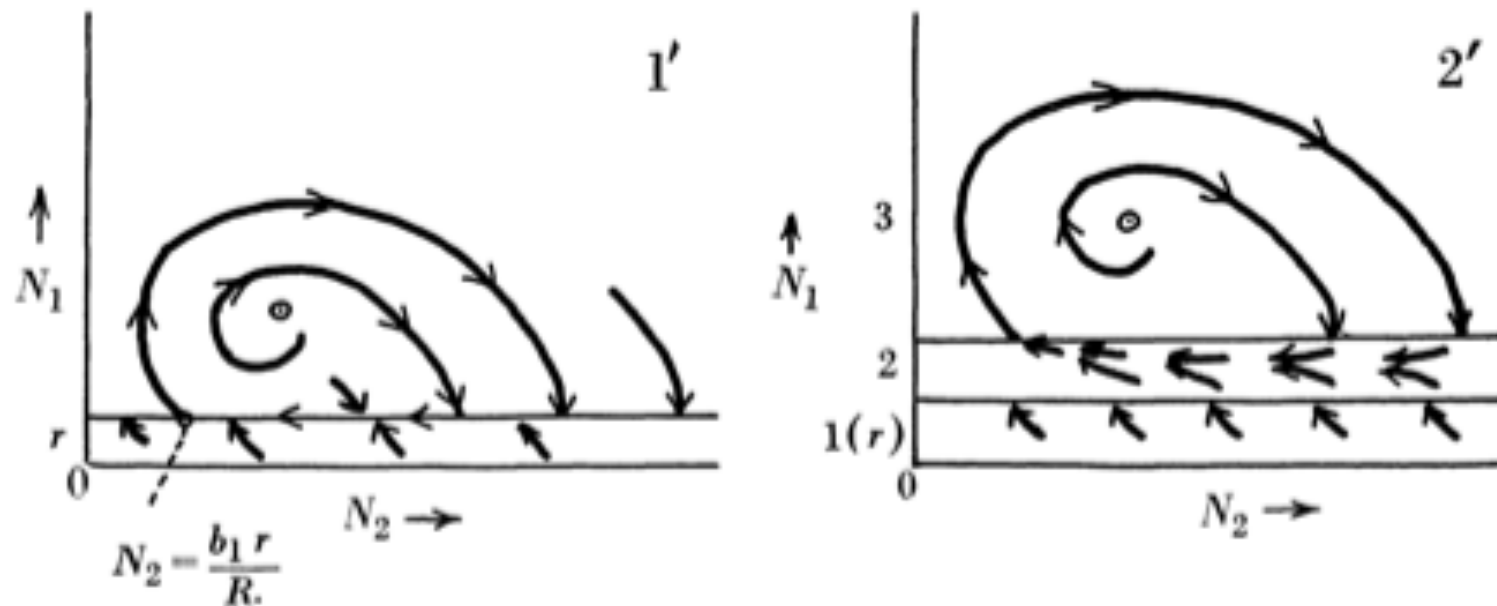
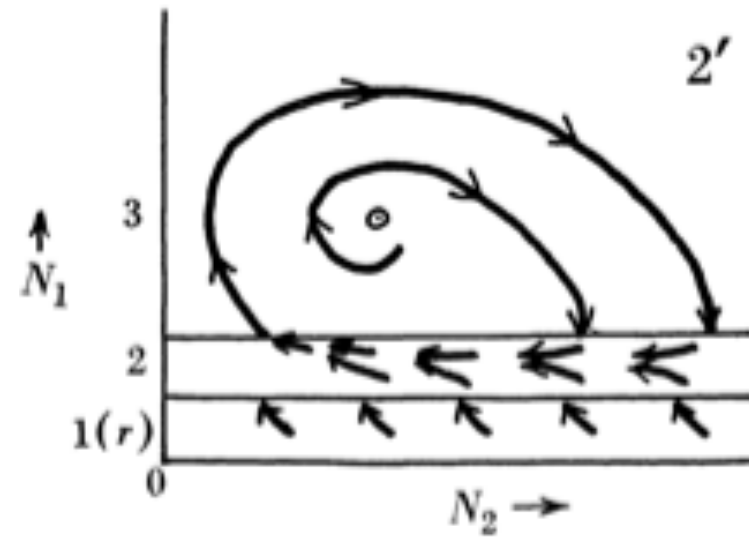
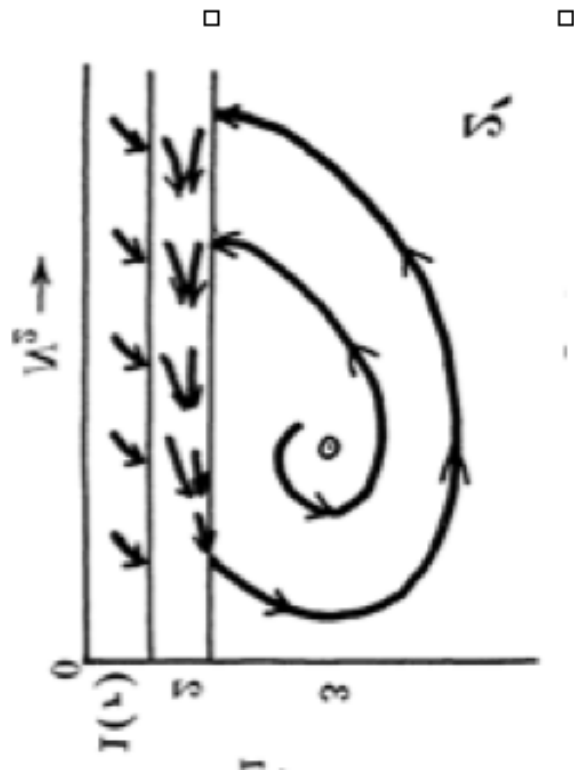


Fig. 5. Theoretical curves of interaction between *Parametecium bursaria* and *Saccharomyces exiguus*.

Mathématiques du modèle de Gause



Tramecium bursaria and *Saccharomyces exiguus*.

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Managing Editor: S. Levin

22

Francesco M. Scudo
James R. Ziegler

The Golden Age of Theoretical Ecology: 1923–1940

A Collection of Works by V. Volterra, V. A. Kostitzin,
A. J. Lotka and A. N. Kolmogoroff



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TRAVAUX EN COURS

Tewfik Sari

*Contrôle non linéaire
et applications*COURS DONNÉS À L'ÉCOLE D'ÉTÉ DU CIMPA,
DE L'UNIVERSITÉ DE TLEMCEHERMANN  ÉDITEURS DES SCIENCES ET DES ARTSEquations différentielles
à second membre discontinu

Claude Lobry

Tewfik Sari

1 Introduction

Après une introduction justifiant l'intérêt de l'étude des équations différentielles à second membre discontinu nous proposons trois approches différentes de la question. La première, celle de Filippov est ancienne et bien connue. Les deux autres, qui, on le verra, sont élémentaires, se retrouvent de façon plus ou moins cachée dans la littérature, mais ne semblent pas avoir fait l'objet d'un exposé didactique. Nous éviterons que des difficultés techniques ne cachent des idées très simples nous limiterons à des fonctions *discontinues régulières* de \mathbb{R}^2 ou de \mathbb{R}^3 . Nous généraliserons par là la généralisation naturelle de fonctions continues par morceaux. Ces fonctions définies par la donnée d'un nombre fini de sous variétés régulières plongées se coupant transversalement telles que le complémentaire de leur union soit constitué localement d'un nombre fini d'ouverts ; sur chacun de ces ouverts la fonction est la restriction d'une fonction différentiable définie sur l'espace. Pour simplifier encore nous supposons que les fonctions sont globalement bornées. La généralisation des résultats exposés à des fonctions régulières définies sur des espaces de dimension supérieure et à des fonctions non bornées, voire des fonctions admettant des points d'accumulation de discontinuités, est immédiate. Enfin la généralisation à des fonctions mesurables quelconques nous semble posée.