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Analysis of the Predator-Prey Model with Climax Prey Population

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Abstract. The aim of the contribution is to study ODE predator-prey system with a prey population embodying the Allee effect. Particular stationary points are analyzed and the results are illustrated by graphs of numerical solutions for various values of model parameters.

1 Introduction

The relation between predator and its prey (or to say it less specifically, the producer-consumer relation) represents one of the most important interactions of two populations. It constitutes basis of any food chain and it represents one of the driving powers of evolution since the both populations are forced to never-ending increase or to extinction. The classical two-ODE Lotka-Volterra model of the interaction is simple, illustrative, but unrealistic. Incorporation of a carrying capacity for the prey population to it makes it slightly more realistic. But such model do not admit periodic solutions that might explain observed cyclical changes in abundances of the natural populations. Hence, Gause-type models based on clear ecological assumptions and, in particular cases, possessing limit cycle solutions are considered to be the appropriate models of the predator-prey interaction (cf. e.g. [2]). These models often yields a conclusion, that neither the predator population nor the prey one could extinct (from what we could say that we don't have to limit whaling because whales as the prey couldn't extinct). But this is not true in general.

The contribution analyse a generalized Gause-type predator-prey model with the prey population exhibiting both Allee effect and intraspecific competition. A population of a such type is called a climax one. It is limited above by carrying capacity of its environment and below by a certain threshold abundance necessary for its survival.

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2 Introduction to Model Analysis

When we want to analyse autonomous system of two differential equations we examine each nullcline, i.e. curves where at least one derivative is equal to zero, and stationary points (intersections of nullclines) as well.

We have autonomous system of this type:

$$\begin{aligned} x_1' &= f_1(x_1, x_2)\,, \\ x_2' &= f_2(x_1, x_2)\,, \end{aligned} \tag{1}$$

we use so-called *variation matrix*:

$$\boldsymbol{J}(\hat{x}_1, \hat{x}_2) = \begin{pmatrix} f_{11}' & f_{12}' \\ f_{21}' & f_{22}' \end{pmatrix},$$

where

$$\begin{aligned} f_{11}' &= \frac{\partial f_1(\hat{x}_1, \hat{x}_2)}{\partial x_1}\,, \quad f_{12}' = \frac{\partial f_1(\hat{x}_1, \hat{x}_2)}{\partial x_2}\,, \\ f_{21}' &= \frac{\partial f_2(\hat{x}_1, \hat{x}_2)}{\partial x_1}\,, \quad f_{22}' = \frac{\partial f_2(\hat{x}_1, \hat{x}_2)}{\partial x_2}\,, \end{aligned}$$

and $(\hat{x}_1, \hat{x}_2)$ is stationary point.

Since the system is two-dimensional, we are able to establish qualitative properties of each separate stationary point by analysis of characteristic polynomial of the variation matrix. We find eigenvalues λ_1, λ_2 of variation matrix $\boldsymbol{J}(\hat{x}_1, \hat{x}_2)$ and if:

- $\lambda_1, \lambda_2 \in \mathbb{R}$ and $\lambda_1\lambda_2 > 0$ then stationary point $(\hat{x}_1, \hat{x}_2)$ is a *node*,
- $\lambda_1, \lambda_2 \in \mathbb{R}$ and $\lambda_1\lambda_2 < 0$ then stationary point $(\hat{x}_1, \hat{x}_2)$ is a *saddle*,
- $\lambda_{1,2} = \pm\beta i$, i.e. λ_1, λ_2 are imaginary numbers then stationary point $(\hat{x}_1, \hat{x}_2)$ is *centre* or *rotation point*,
- $\lambda_{1,2} = \alpha \pm \beta i$, $\alpha \neq 0$, then stationary point $(\hat{x}_1, \hat{x}_2)$ is *focus*,
- real parts of λ_1 and λ_2 are negative, then stationary point $(\hat{x}_1, \hat{x}_2)$ is asymptotically stable,
- real part of λ_1 i λ_2 are positive, then stationary point $(\hat{x}_1, \hat{x}_2)$ is unstable.

The characteristic equation $\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) - \lambda\boldsymbol{I} = 0$ implies

$$\lambda_{1,2} = \frac{\operatorname{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) \pm \sqrt{\operatorname{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2))^2 - 4\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2))}}{2}$$

This relation allows us to reformulate the statement above. Let $\hat{\boldsymbol{x}} = (\hat{x}_1, \hat{x}_2)$ be a stationary point of (1). Then the following holds:

1. if $\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) < 0$ then $\lambda_1\lambda_2 < 0$ and $\hat{\boldsymbol{x}}$ is saddle;

2. let $\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) > 0$ and, consequently, we distinguish the following three cases

   (a) $4\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2) < \mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2))^2$, then
   $\mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) < 0$ then $\lambda_{1,2} < 0$ and $\hat{\boldsymbol{x}}$ is stable node;
   $\mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) > 0$ then $\lambda_{1,2} > 0$ and $\hat{\boldsymbol{x}}$ is unstable node;

   (b) $4\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2) > \mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2))^2$, then
   $\mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) < 0$ then $\lambda_{1,2} < 0$ and $\hat{\boldsymbol{x}}$ is stable focus;
   $\mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) > 0$ then $\lambda_{1,2} > 0$ and $\hat{\boldsymbol{x}}$ is unstable focus;

   (c) $\mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) = 0$ then $\hat{\boldsymbol{x}}$ is rotation point or focus.

3 Analysis of the Model

We consider the model:

$$x_1' = \left[\varepsilon_1 \left(\frac{x_1}{\theta} - 1\right)\left(1 - \frac{x_1}{K}\right) - \gamma_1 x_2\right] x_1$$
$$x_2' = (-\varepsilon_2 + \gamma_2 x_1) x_2,$$

where ε_1 denotes intrinsic grow rate of prey population, θ minimal abundance of prey population for provide its reproduction, K carrying capacity for prey population, γ_1 intensity of predation, ε_2 death rate of starving predator population and γ_2 rate of conversion consumed pray into predator growth rate.

The system possesses four nullclines: $x_1 = 0$, $x_2 = \frac{\varepsilon_1}{\gamma_1}\left(\frac{x_1}{\theta} - 1\right)\left(1 - \frac{x_1}{K}\right)$ are x_1-nullclines and $x_2 = 0$, $x_1 = \frac{\varepsilon_2}{\gamma_2}$ are x_2-nullclines. There are also four stationary points (see Fig. 1):

$$(0,0); \quad (\theta, 0); \quad (K, 0); \quad \left(\frac{\varepsilon_2}{\gamma_2}, \frac{\varepsilon_1}{\gamma_1 K \theta}\left(\frac{\varepsilon_2}{\gamma_2} - \theta\right)\left(K - \frac{\varepsilon_2}{\gamma_2}\right)\right)$$

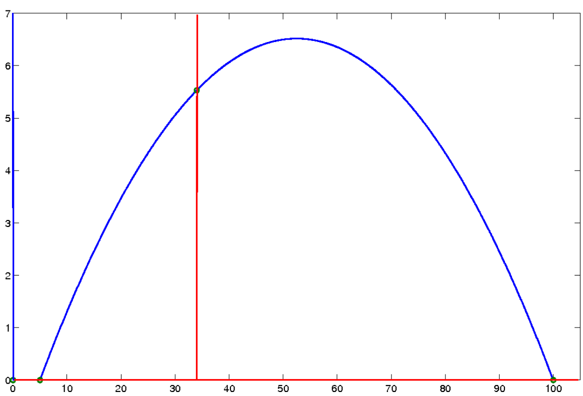

Figure 1 Nullclines and stationary points of the system

Variation matrix of this system is:

$$\boldsymbol{J}(\hat{x}_1, \hat{x}_2) = \begin{pmatrix} \varepsilon_1\left(-\frac{3\hat{x}_1^2}{\theta K} + 2\hat{x}_1\left(\frac{1}{\theta} + \frac{1}{K}\right) - 1\right) - \gamma_1 \hat{x}_2 & -\gamma_1 \hat{x}_1 \\ \gamma_2 \hat{x}_2 & -\varepsilon_2 + \gamma_2 \hat{x}_1 \end{pmatrix}$$

And now, we look closer on each stationary point:

1. **$(0,0)$**

   Variation matrix for this stationary point is:

$$\boldsymbol{J}(0,0) = \begin{pmatrix} -\varepsilon_1 & 0 \\ 0 & -\varepsilon_2 \end{pmatrix}.$$

   - $\det(\boldsymbol{J}(0,0)) = \varepsilon_1\varepsilon_2 > 0$ – so the stationary point is focus or node,
   - $\operatorname{tr}(\boldsymbol{J}(0,0)) = -(\varepsilon_1+\varepsilon_2) < 0$ – stationary point is stable.
   - $4\det(\boldsymbol{J}(0,0)) - \operatorname{tr}(\boldsymbol{J}(0,0))^2 = 4\varepsilon_1\varepsilon_2 - (\varepsilon_1+\varepsilon_2)^2 = -(\varepsilon_1-\varepsilon_2)^2 < 0$ – stationary point $(0,0)$ is *stable node.*

2. **$(\theta,0)$**

   Variation matrix for this stationary point is:

$$\boldsymbol{J}(\theta,0) = \begin{pmatrix} -\varepsilon_1\left(1-\frac{\theta}{K}\right) & -\gamma_1\theta \\ 0 & -\varepsilon_2+\gamma_2\theta \end{pmatrix}.$$

   - $\det(\boldsymbol{J}(\theta,0)) = \varepsilon_1\gamma_2\left(1-\frac{\theta}{K}\right)\left(\theta-\frac{\varepsilon_2}{\gamma_2}\right)$. The term $\left(1-\frac{\theta}{K}\right)$ is positive while the term $\left(\theta-\frac{\varepsilon_2}{\gamma_2}\right)$ could be positive or negative depending on $\frac{\varepsilon_2}{\gamma_2}$.

   (a) $\boxed{\theta > \frac{\varepsilon_2}{\gamma_2}}$

   In this case the term $\left(\theta-\frac{\varepsilon_2}{\gamma_2}\right)$ is positive and so $\det(\boldsymbol{J}(\theta,0))$ is also positive. The stationary point $(\theta,0)$ is node or focus.

   - $\operatorname{tr}(\boldsymbol{J}(\theta,0)) = \varepsilon_1\left(1-\frac{\theta}{K}\right)+\gamma_2\left(\theta-\frac{\varepsilon_2}{\gamma_2}\right)$ – sum of two positive numbers is also positive number, so $(\theta,0)$ is unstable.
   - $4\det(\boldsymbol{J}(\theta,0)) - \operatorname{tr}(\boldsymbol{J}(\theta,0))^2 = -\left[\varepsilon_1\left(1-\frac{\theta}{K}\right)-\gamma_2\left(\theta-\frac{\varepsilon_2}{\gamma_2}\right)\right]^2 < 0$ – the stationary point $(\theta,0)$ is *unstable focus.*

   (b) $\boxed{\theta < \frac{\varepsilon_2}{\gamma_2}}$

   In this case, the term $\left(\theta-\frac{\varepsilon_2}{\gamma_2}\right)$ is negative then also $\det(\boldsymbol{J}(\theta,0))$ is negative and the stationary point $(\theta,0)$ is *saddle.*

3. **$(K,0)$**

   Variation matrix for this stationary point is:

$$\boldsymbol{J}(K,0) = \begin{pmatrix} \varepsilon_1\left(1-\frac{K}{\theta}\right) & -\gamma_1 K \\ 0 & -\varepsilon_2+\gamma_2 K \end{pmatrix}.$$

   - $\det(\boldsymbol{J}(K,0)) = \varepsilon_1\gamma_2\left(1-\frac{K}{\theta}\right)\left(K-\frac{\varepsilon_2}{\gamma_2}\right)$. The term $\left(1-\frac{K}{\theta}\right)$ is negative and a sign of determinant also depend on parameter $\frac{\varepsilon_2}{\gamma_2}$.

(a) $\boxed{K > \frac{\varepsilon_2}{\gamma_2}}$

In this case, the term $\left(K - \frac{\varepsilon_2}{\gamma_2}\right)$ is positive and the determinant negative. The stationary point $(K, 0)$ is *saddle*.

(b) $\boxed{K < \frac{\varepsilon_2}{\gamma_2}}$

In this case, the term $\left(K - \frac{\varepsilon_2}{\gamma_2}\right)$ is negative, so $\det(\boldsymbol{J}(K,0))$ is positive. Stationary point $(K, 0)$ is node or focus.

- $\mathrm{tr}(\boldsymbol{J}(\theta,0)) = \varepsilon_1\left(1 - \frac{K}{\theta}\right) + \gamma_2\left(K - \frac{\varepsilon_2}{\gamma_2}\right)$ – sum of two negative numbers is also negative number, hence stationary point is stable.
- $4\det(\boldsymbol{J}(K,0)) - \mathrm{tr}(\boldsymbol{J}(K,0))^2 = -\left[\varepsilon_1\left(1 - \frac{K}{\theta}\right) - \gamma_2\left(K - \frac{\varepsilon_2}{\gamma_2}\right)\right]^2 < 0$ – stationary point $(\theta, 0)$ is *stable node*.

4. $\boldsymbol{\left(\frac{\varepsilon_2}{\gamma_2}, \frac{\varepsilon_1}{\gamma_1 K\theta}\left(\frac{\varepsilon_2}{\gamma_2} - \theta\right)\left(K - \frac{\varepsilon_2}{\gamma_2}\right)\right)}$

This stationary point belongs to positive quadrant only when $\frac{\varepsilon_2}{\gamma_2} \in (\theta, K)$. We denote it by $(\hat{x}_1, \hat{x}_2)$ for simplification.

Variation matrix of this stationary point is:

$$\boldsymbol{J}(\hat{x}_1, \hat{x}_2) = \begin{pmatrix} \frac{\varepsilon_1\varepsilon_2}{\theta K\gamma_2}\left(K + \theta - \frac{2\varepsilon_2}{\gamma_2}\right) & -\gamma_1\frac{\varepsilon_2}{\gamma_2} \\ \frac{\varepsilon_1\gamma_2}{K\theta\gamma_1}\left(\frac{\varepsilon_2}{\gamma_2} - \theta\right)\left(K - \frac{\varepsilon_2}{\gamma_2}\right) & 0 \end{pmatrix}.$$

- $\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) = \frac{\varepsilon_1\varepsilon_2}{\theta K}\left(\frac{\varepsilon_2}{\gamma_2} - \theta\right)\left(K - \frac{\varepsilon_2}{\gamma_2}\right) > 0$ – stationary point is node or focus.
- $\mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) = \frac{\varepsilon_1\varepsilon_2}{\theta K\gamma_2}\left(K + \theta - \frac{2\varepsilon_2}{\gamma_2}\right)$ – trace would be positive if $\frac{\varepsilon_2}{\gamma_2} < \frac{\theta+K}{2}$, stationary point $(\hat{x}_1, \hat{x}_2))$ would be unstable. Trace would be negative if $\frac{\varepsilon_2}{\gamma_2} > \frac{\theta+K}{2}$, and stationary point $(\hat{x}_1, \hat{x}_2))$ would be stable.
- $4\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)) - \mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2))^2 =$
$$= 4\frac{\varepsilon_1\varepsilon_2}{\theta K}\left(\frac{\varepsilon_2}{\gamma_2} - \theta\right)\left(K - \frac{\varepsilon_2}{\gamma_2}\right) - \left(\frac{\varepsilon_1\varepsilon_2}{\theta K\gamma_2}\right)^2\left(K + \theta - \frac{2\varepsilon_2}{\gamma_2}\right)^2$$
We also can express the term $4\det(\boldsymbol{J}(\hat{x}_1, \hat{x}_2))) - \mathrm{tr}(\boldsymbol{J}(\hat{x}_1, \hat{x}_2)))^2$ as a function of variable ε_2, so
$$f(\varepsilon_2) = 4\frac{\varepsilon_1\varepsilon_2}{\theta K}\left(\frac{\varepsilon_2}{\gamma_2} - \theta\right)\left(K - \frac{\varepsilon_2}{\gamma_2}\right) - \left(\frac{\varepsilon_1\varepsilon_2}{\theta K\gamma_2}\right)^2\left(K + \theta - \frac{2\varepsilon_2}{\gamma_2}\right)^2$$
For the sake of simplicity, we introduce new variable $\bar{\varepsilon}_2$ and new parameters $\bar{\varepsilon}_1$, α by
$$\bar{\varepsilon}_2 = \frac{\varepsilon_2}{\gamma_2}, \quad \bar{\varepsilon}_1 = \frac{\varepsilon_1}{\theta K}, \quad \alpha = \theta + K.$$
Then, we will examine the function
$$g(\bar{\varepsilon}_2) = f(\varepsilon_2) = 4\bar{\varepsilon}_1\bar{\varepsilon}_2\gamma_2(\bar{\varepsilon}_2 - \theta)(K - \bar{\varepsilon}_2) - (\bar{\varepsilon}_1\bar{\varepsilon}_2)^2(\alpha - 2\bar{\varepsilon}_2)^2. \quad (2)$$
Function $g(\bar{\varepsilon}_2)$ is a polynomial of the fourth degree so it has at most four roots. One could see that one of them is $\bar{\varepsilon}_2 = 0$.

When we look closer at particular values of the function $g(\bar{\varepsilon}_2)$, i.e. $\bar{\varepsilon}_2 = \theta$, $\bar{\varepsilon}_2 = K$ and $\bar{\varepsilon}_2 = \frac{\alpha}{2}$. We could see that:

$$g(\theta) = -\left(\bar{\varepsilon}_1 \theta\right)^2 (K-\theta)^2 < 0$$
$$g(K) = -\left(\bar{\varepsilon}_1 K\right)^2 (\theta-K)^2 < 0$$
$$g\left(\frac{\alpha}{2}\right) = \frac{\bar{\varepsilon}_1 \gamma_2 \alpha}{2}(K-\theta)^2 > 0$$

These expressions shows at least two roots for positive $\bar{\varepsilon}_2$. The fourth root could be located between 0 and θ or on the negative part of the $\bar{\varepsilon}_2$ axis. The first derivative of the function $g(\bar{\varepsilon}_2)$ holds:

$$g'(\bar{\varepsilon}_2) = -16\bar{\varepsilon}_1\bar{\varepsilon}_2^3 + 12\bar{\varepsilon}_1(\alpha-\gamma_2)\bar{\varepsilon}_2^2 + 2\bar{\varepsilon}_1\alpha(4\gamma_2 - \alpha\bar{\varepsilon}_1)\bar{\varepsilon}_2 - 4\bar{\varepsilon}_1\theta K\gamma_2$$

so for the first root $\bar{\varepsilon}_2 = 0$ applies:

$$g'(0) = -4\bar{\varepsilon}_1\theta K\gamma_2 < 0\,,$$

consequently, function $g(\bar{\varepsilon}_2)$ is decreasing in 0. And according to (2):

$$\lim_{\bar{\varepsilon}_2 \to -\infty} g(\bar{\varepsilon}_2) = -\infty < 0$$

one could see, that the fourth root is negative. That is, because of two roots between θ and K points, the stationary point $(\hat{x}_1, \hat{x}_2)$ is node for $\varepsilon_2 = \theta$. As the parameter ε_2 increases, it became focus and further it turns into node again.

The behaviour of the system for different values $\bar{\varepsilon}_2$ is displayed on the Fig. 2–6. On the Fig. 2, solutions are figured individually for different initial conditions of population sizes of predator and prey. It could be seen that predator extirpate the prey at first and then extinct itself.

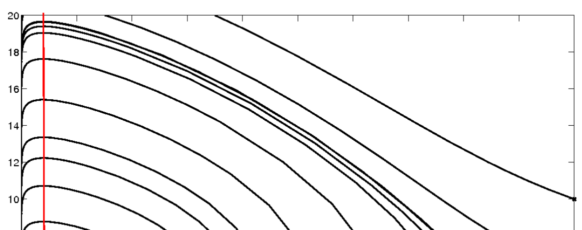

Figure 2 $\bar{\varepsilon}_2 < \theta$ – stationary point $(0,0)$ is stable node, and stationary point $(\theta, 0)$ is unstable node

We have the stationary point $(\hat{x}_1, \hat{x}_2)$ on the Fig. 3 as the unstable focus. Solutions are figured for almost the same initial conditions of populations nearby this unstable focus. We could also see, that both populations extinct (stationary point $(0,0)$ is stable node). But if we "come closer" with x_2-nullcline $\bar{\varepsilon}_2$ to the point $\frac{K+\theta}{2}$, we get unstable focus with stable *limit cycle* (see Fig. 4). In the case of stable limit cycle in the system, sizes of both populations fluctuate periodically in accordance with observation of natural predator-prey communities. For distant values of initial sizes of populations, trajectories don't "roll" soon enough through x_1-nullcline and they end in the point $(0,0)$ again.

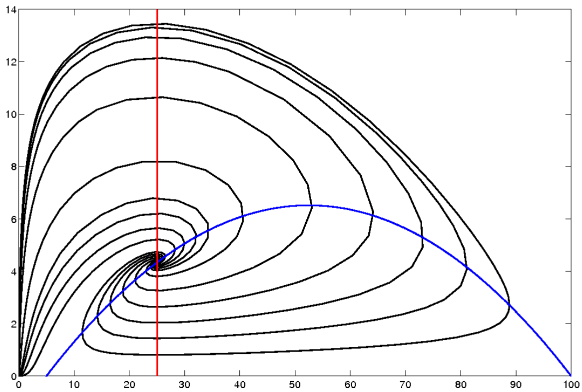

Figure 3 $\bar{\varepsilon}_2 \in (\theta, \frac{\theta+K}{2})$ – stationary point $(\hat{x}_1, \hat{x}_2)$ is unstable focus

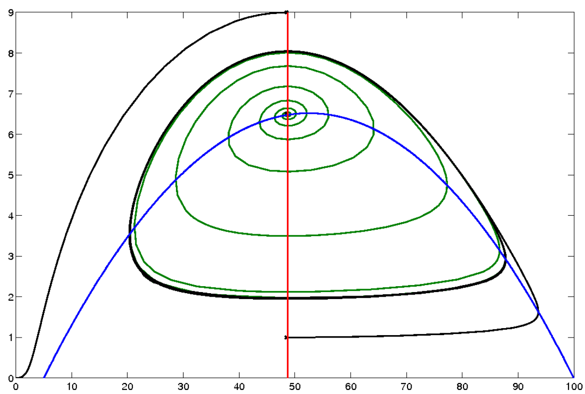

Figure 4 $\bar{\varepsilon}_2 \to \frac{\theta+K}{2}$ – unstable focus with limit cycle

If $\bar{\varepsilon}_2 > \frac{K+\theta}{2}$, the stationary point $(\hat{x}_1, \hat{x}_2)$ is stable focus and both, predator and its prey, coexist with stable size of their populations (see Fig. 5). But if the size of the predator population is big according to the size of the prey population, predator could get the size of prey populations under its threshold. Then, prey can't keep up the population of the predator, the predator extinct followed by the prey.

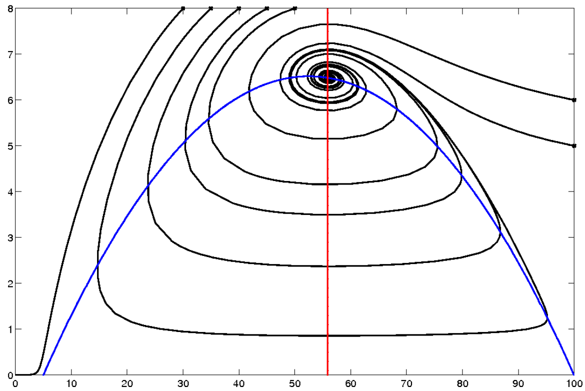

Figure 5 $\bar{\varepsilon}_2 <\in (\frac{\theta+K}{2}, K)$ – stationary point $(\hat{x}_1, \hat{x}_2)$ is stable focus

At last, when $\bar{\varepsilon}_2 > K$, there are two possible situations (Fig. 6). The size of prey population is big enough to survive predators atacks, but predator can't live from it and extinct. Because of lack of predator population, prey population settle down on its carrying capacity K. The second possibility is that prey populations isn't big enough and predator population extirpate it under its threshold. After this, both populations extinct.

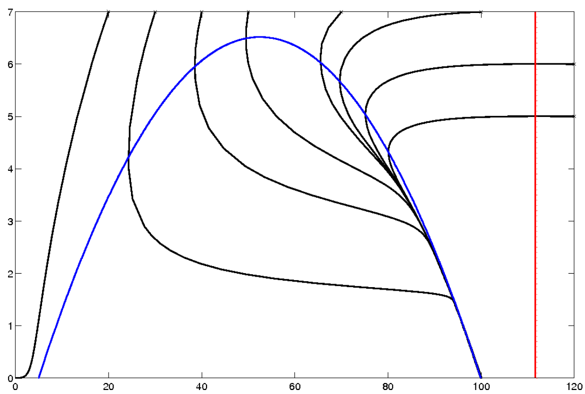

Figure 6 $\bar{\varepsilon}_2 > K$ – stationary point $(K, 0)$ is stable node

4 Conclusion

We analysed behaviour of the predator-prey system with climax prey population. This analysis shows that both population could extinct in this case. This conclusion should brought as a warning before too simplifying conclusions (and we should keep population of whales after all).

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