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Predator-prey models with non-analytical functional response

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ABSTRACT

In this paper we study the generalized Gause model, with a logistic growth rate for the prey in absence of the predator, a constant death rate for the predator and for several different classes of functional response, all non-analytical. First we consider the piecewise-linear functional response of Holling type I, which essentially has a linear functional response on a bounded interval and a constant functional response for large enough prey density. Next we consider differentiable modifications of this type of functional response, one being a concave down function, the other one being a sigmoidal function.

Our main interest is the number of closed orbits of the systems under consideration and the global stability of the system. We compare the generalized Gause model with a functional response that is non-analytical with the generalized Gause model with a functional response that is analytical (e.g., Holling type II or III) and show that the behaviour in the first case is more complicated. As examples of this more complicated behaviour we mention: the co-existence of a stable equilibrium with a stable limit cycle and the existence of a family of closed orbits.

1. Introduction

The two main types of interaction between any pair of biological species, which are of interest to the ecologist, are either when they are competing together for some common source of food supply, or when one of the species preys upon the other. In this paper we will restrict our attention to the latter case.

The existence and the number of isolated periodic solutions (limit cycles) is one of the most delicate problems connected with two-dimensional predator-prey models.

One of the first examples of a biological system modelling the interaction between prey and predators was formulated by Lotka in 1925 [24] and Volterra in 1927 [30]:

$$\frac{dx}{dt} = \alpha x - \beta xy, \quad \frac{dy}{dt} = -\delta y + \gamma xy. \tag{1.1}$$

In system (1.1) $x(t)$ and $y(t)$ denote prey and predator densities respectively, as functions of time. Furthermore, all constants are assumed to be positive. Obviously, the attention is restricted to $x \geq 0$, $y \geq 0$.

It is a well-known fact that system (1.1) has a family of periodic orbits, but no limit cycles. Due to the fact that (1.1) has a center, system (1.1) lacks structural stability. That is, the topological character of the phase portrait of (1.1) can be changed if we take into account arbitrarily small additional effects. If for example (1.1) is modified to include the effect of competition among the prey (by adding $-\epsilon x^2$ to the first equation of (1.1)), then the resulting system no longer has a center and the population oscillations decay, see [8].

A generalization of system (1.1) was suggested by Gause in 1934 [10]

$$\frac{dx}{dt} = \alpha x - p(x)y, \quad \frac{dy}{dt} = -\delta y + \gamma p(x)y. \tag{1.2}$$

Here $\alpha > 0$ is the growth rate of the prey in absence of the predator; $\delta > 0$ is the death rate of the predator in absence of the prey; $\gamma > 0$ is the rate of conversion of consumed prey to predator. Finally, $p(x)$ is the capture rate of prey per predator or functional response of a predator.

For most examples that appear in the literature (see the bibliography in [8]) it is assumed that $p(0) = 0$ and $p'(x) > 0$ for all $x > 0$.

The generalized Gause model for the interaction of the two species is (see [8]):

$$\frac{dx}{dt} = xg(x) - p(x)y, \quad \frac{dy}{dt} = -\delta y + \gamma p(x)y. \tag{1.3}$$

System (1.3) incorporates density-dependent prey growth in absence of the predator. This is introduced in the model, because it

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is quite unrealistic to assume that the prey density will become infinitely large in absence of predators, as will happen for (1.1) and (1.2).

The growth rate $g(x)$ satisfies $g(0)>0$, $g'(x)<0$ for all $x>0$ and there exists a $k>0$ such that $g(k)=0$. The constant k is called the carrying capacity of the prey. A growth rate of this type is thought to model the situation where the food supply for the prey is limited. For high densities of prey they will compete for the resources.

A famous example that belongs to systems of type (1.3) is a system first mentioned by Rosenzweig & McArthur in 1963 [25]:

$$\frac{dx}{dt} = ax(1-bx) - p(x)y, \quad \frac{dy}{dt} = -\delta y + \gamma p(x)y. \tag{1.4}$$

where $p(x) = \frac{x}{c+x}$ and a, b, c, γ and δ are positive constants. System (1.4) is important because it is a structurally stable model which can exhibit persistent oscillations.

The uniqueness of the limit cycle of system (1.4) was first proved by Cheng [3]. However, his arguments are rather tedious; a simplified proof was given by Kuang & Freedman [16]. Both in [3,16] it is proved that system (1.4) has at most one closed orbit, a stable limit cycle. This means that, within systems of class (1.4) the limit cycle is structurally stable. Later it was proved in [18] that if system (1.4) has a limit cycle Γ, then it is hyperbolic. This means that for any arbitrarily small $\mathbb{C}^1$ perturbation of (1.4) there are no other limit cycles in a sufficiently small neighbourhood of the perturbed stable limit cycle Γ'.

The functional response $p(x)$ in system (1.4) was suggested by the biologist Holling in 1959 [11]. In fact, based on actual field data, he argued that the functional response should not only be a monotonically increasing, but also a bounded function. The function $p(x) = \frac{x}{c+x}$ is referred to as a functional response of Holling type II. For $p(x) = \frac{x^2}{c+x^2}$, we say the functional response is of Holling type III. This sigmoidal curve is modelling predators which exhibit some form of learning behaviour. Below a certain threshold density the predator is capturing only a small number of prey but above this threshold the predators increase their feeding rates, until some saturation level is reached. The existence and uniqueness of the limit cycle for system (1.4) with functional response of Holling type III was proved by Chen & Zhang [6]. A more general type of functional response was introduced by Kazarinov & van der Driessche [15]: $p(x) = \frac{x^n}{c+x^n}, c>0, n\geq 1$. They only studied the existence of limit cycles. The uniqueness and hyperbolicity of the limit cycle in this case is proved in [18].

Although we will restrict ourselves to monotonic functional responses, some authors also considered non-monotonic, unimodal functional responses, see [9,27,32]. This type of function is assumed to model group defense. Initially the function grows with x, but as the prey density gets larger, the prey can defend themselves successfully against the predators. It is known that system (1.3), with $p(x)$ non-monotonic, can have two limit cycles, see [26]. The non-monotonic functional response satisfying $p(x) = \frac{mx}{a+bx+x^2}$, originally dubbed Monod-Haldane functional response, see [2], is sometimes referred to as Holling Type IV, see [12].

Recent research related to the generalized Gause system (1.3) studies the impact of impulsive control [7,22], mutual interference [20,28], harvesting [13,23] and singular perturbation analysis [19].

As can be seen from the terminology, another type of functional response was proposed by Holling. The function which satisfies $p(x)=ax$ for $0<x\leq x_0$ and $p(x)=ax_0$ for $x>x_0$ is referred to as a functional response of Holling type I. Note that this function is continuous but not differentiable. System (1.4) with functional response of Holling type I was studied by Nangen [21]. He proved that for certain parameter values system (1.4) can have at least two limit cycles. This implies the remarkable result that for a suitable choice of the parameters, system (1.4) exhibits coexistence of a stable equilibrium and a stable limit cycle. As the paper of Liu is in Chinese we will summarize it here and we will also include the case $b=0$, which was not considered in [21]. Note that $b=0$ implies that the carrying capacity of the prey has become infinitely large.

The systems which we consider in this paper belong to a family of predator-prey systems of the form (1.4) extending the Holling I type functional response, essentially replacing the linear function $p(x)=x$ on the interval $0\leq x\leq 1$ by a cubic function. The system has the following form:

$$\frac{dx(t)}{dt} = xg(x) - p(x)y, \quad \frac{dy(t)}{dt} = -\delta y + p(x)y. \tag{1.5}$$

with $g(x) = \phi(1-\frac{x}{k})$, $p(x) = x(1+(x-1)(a_0+a_1x))$, for $0\leq x\leq 1$, $p(x)=1$, for $x>1$, and $\phi>0$, $k>0$, $\delta>0$.

Here we have chosen a rescaling of the two variables x, y and a scaling of the time parameter t in such a way to make the parameter γ equal to 1, to make the point where the functional response changes character at $x=1$ and to make $p(1)=1$.

We will consider several special cases of system (1.5) all satisfying the additional natural condition that $p'(x)\geq 0$ on the interval $0\leq x\leq 1$:

(1) $a_0=a_1=0$ which implies $p_1(x)=x$ for $0\leq x\leq 1$ and $p_1(x)=1$ for $x>1$. This is the Holling type I case which we will review. We will indicate some new results in this case as well.

(2) $a_0=-1, a_1=0$ which implies $p_2(x)=x(2-x)$ for $0\leq x\leq 1$ and $p_2(x)=1$ for $x>1$. Note that $p_2(x)\in\mathbb{C}^1$ but $p_2(x)\notin\mathbb{C}^2$. We will prove that for $p(x)=p_2(x)$ system (1.5) has at most one limit cycle.

(3) $a_0=1, a_1=-2$ which implies $p_3(x)=x^2(3-2x)$ for $0\leq x>1$ and $p_3(x)=1$ for $x\geq 1$. This sigmoidal function also satisfies $p_3(x)\in\mathbb{C}^1$ but $p_3(x)\notin\mathbb{C}^2$.

We will show that for $p(x)=p_3(x)$ system (1.5) has at least one limit cycle if the positive equilibrium is unstable but if the positive equilibrium is stable, then for certain parameter values two limit cycles can coexist.

We now discuss the biological motivation for considering the proposed functional responses $p_2(x)$ and $p_3(x)$. For the functional response of Holling type I, clearly a threshold for the prey density is present, after which the function is assumed to be constant. Before this threshold is reached, the function increases linearly. In [14,28,29] the interpretation of introducing a cut-off in the response function is motivated. According to Seo and Kot [28] and Seo and DeAngelis [29] it is plausible that individual predators abruptly stop increasing their feeding rates when the prey density exceeds a threshold value: predators will have little difficulty (since the prey density has exceeded a threshold value) capturing and assimilating prey, but will switch their time to other activities once their ingestion rates are large enough to satisfy their energetic needs. In [14] the Holling type I cut-off response function is recognized to be the Blackman's equation often occurring in filter feeders which satisfy the handling and satiation conditions of the Holling type I functional response.

One can thus argue that a functional response with a cut-off, i.e. with a threshold for the prey density, is a realistic assumption for predator-prey systems.

The function $p_2(x)$ is the simplest possible function with a cut-off, with the same qualitative properties as Holling type II, i.e. a differentiable function with a non-positive second order derivative. Likewise, the function $p_3(x)$ is the simplest possible function with a cut-off, with the same qualitative properties as Holling type III, i.e. a sigmoidal, differentiable function. Obviously, many more functional responses with a cut-off could be considered, with the same qualitative properties as Holling type II and III. However, the aim of this paper is to show that even the simplest choices, i.e. $p_2(x)$ and $p_3(x)$, lead to richer dynamics, than predator-prey systems with Holling type II and III functional responses.

For future reference we observe that system (1.5) can be transformed into a so-called generalized Liénard equation, a fact which we will use frequently when studying the existence or uniqueness of limit cycles.

Applying the rescaling of time $t = \frac{\bar{t}}{p(x)}$ and the nonlinear transformation $y \equiv e^v$ to system (1.5) we get:

$$\frac{dx(t)}{dt} = F(x) - e^v, \quad \frac{dv(t)}{dt} = g(x), \tag{1.6}$$

where

$$\begin{aligned} F(x) &= \frac{\phi}{k}\frac{k-x}{(1+(x-1)(a_0+a_1x))}, \quad 0 < x \le 1 \\ &= \frac{\phi}{k}x(k-x), x > 1, \\ g(x) &= 1 - \frac{\delta}{x(1+(x-1)(a_0+a_1x))}, \quad 0 < x \le 1 \\ &= 1-\delta, x > 1, \end{aligned} \tag{1.7}$$

and

$$\phi > 0, \quad k > 0, \quad \delta > 0. \tag{1.8}$$

Note that we follow the tradition in the literature of denoting the function on the right hand side of $\frac{dy}{dt}$ as $g(x)$ in the Liénard system. This is not the same function as the function $g(x)$ in (1.5).

2. Holling type I, a non-differentiable functional response

In this section we study the family of systems (1.5) of the generalized Gause model type, where the functional response is of Holling type I, i.e. $p(x) = x$ for $0 \le x \le 1$ and $p(x) = 1$ for $x > 1$.

We first consider the case where the prey has an infinitely large carrying capacity i.e. $k = \infty$, hence the prey is allowed to grow to infinity exponentially in absence of predators:

$$\frac{dx}{dt} = \phi x - p_1(x)y, \quad \frac{dy}{dt} = -\delta y + p_1(x)y, \tag{2.1}$$

with $p_1(x) = x$ for $0 \le x \le 1$ and 1 for $x > 1$.

Here $\phi > 0$ is the intrinsic growth rate in absence of predation.

We will determine the phase portrait of (2.1) for $x \ge 0$, $y \ge 0$.

To obtain the phase portrait of (2.1) we have to combine the trajectories for $0 \le x \le 1$ with those for $x > 1$.

For $0 \le x \le 1$ system (2.1) becomes

$$\frac{dx}{dt} = \phi x - xy, \quad \frac{dy}{dt} = -\delta y + xy. \tag{2.2}$$

Of course system (2.2) belongs to the class of Lotka-Volterra systems. Its first integral reads:

$$H(x, y) = x - \delta ln(x) + y - \phi ln(y), \tag{2.3}$$

and all trajectories in the first quadrant are closed and surround the center (δ, ϕ).

The singularity (δ, ϕ) exists for system (2.1) if and only if $0 < \delta < 1$.

For $x > 1$ system (2.1) becomes a linear system:

$$\frac{dx}{dt} = \phi x - y, \quad \frac{dy}{dt} = (1-\delta)y. \tag{2.4}$$

For $0 < \delta < 1$ the origin of (2.4) is an unstable node and for $\delta > 1$ it is a saddle. System (2.4) has a straight line solution $y = (\phi - 1 + \delta)x$ which is situated in the first quadrant if $\phi - 1 + \delta > 0$.

The corresponding phase portraits for system (2.4) are given in Figs. 1–3.

Combining the knowledge of (2.2) and (2.4) we conclude that for $\delta > 1$ system (2.1) has no positive equilibrium. The corresponding phase portrait is given in Fig. 4, where, as usual the phase plane has been compactified, see for instance Andronov et al.[1].

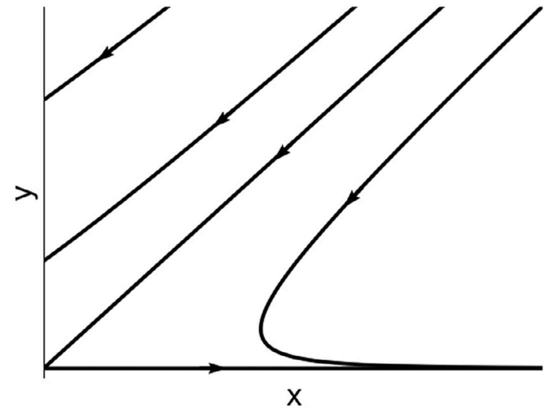

Fig. 1. Phase portrait for system (2.4) $\delta > 1$.

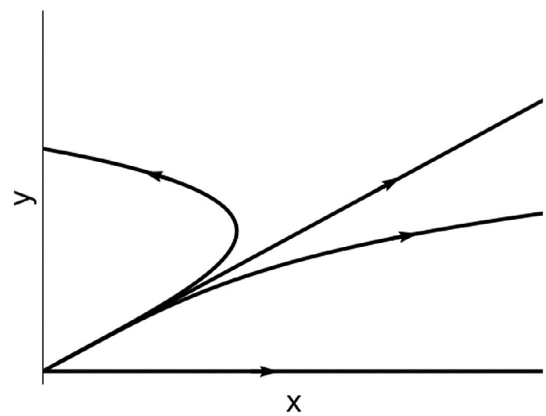

Fig. 2. Phase portrait for system (2.4) $0 < \delta < 1$; $\phi - 1 + \delta > 0$.

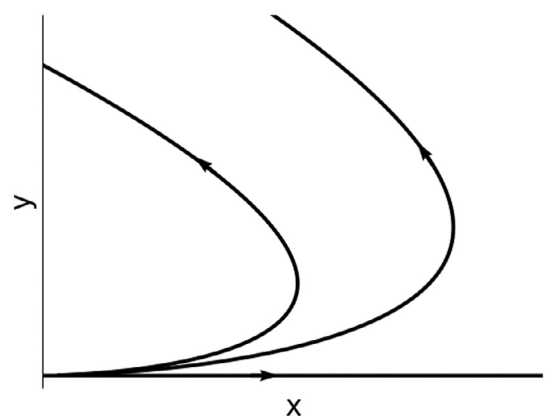

Fig. 3. Phase portrait for system (2.4) $0 < \delta < 1$; $\phi - 1 + \delta \le 0$.

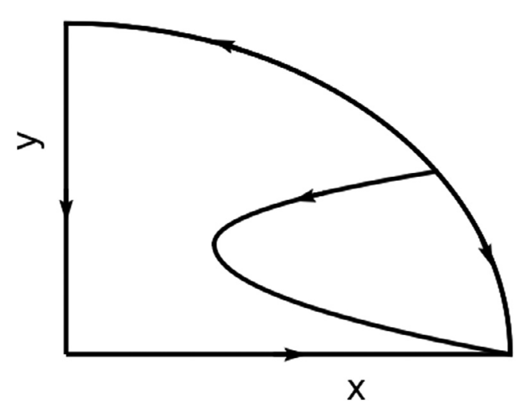

Fig. 4. Phase portrait for system (2.1) $\delta > 1$.

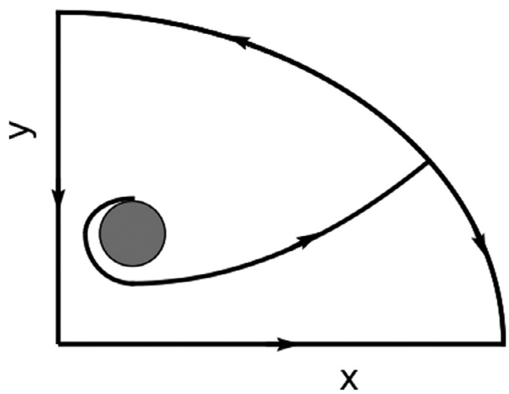

Fig. 5. Phase portrait for system (2.1) $0<\delta<1$; $\phi-1+\delta>0$.

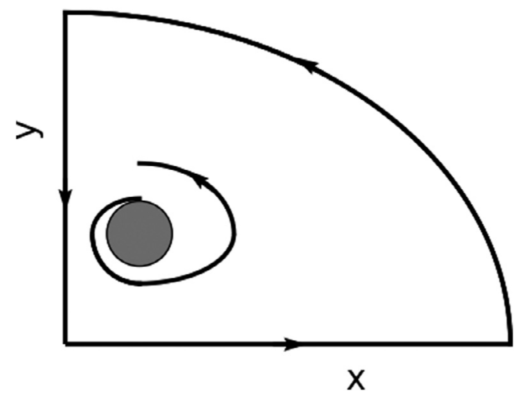

Fig. 6. Phase portrait for system (2.1) $0<\delta<1$; $\phi-1+\delta\le 0$.

For $0<\delta<1$ (2.1) has a positive equilibrium (δ, ϕ) which has a family of closed orbits in its neighbourhood. We can give the exact size of this neighbourhood.

Theorem 2.1. *Consider system (2.1) with $0<\delta<1$. Then all trajectories starting on or inside the oval $\Gamma=\{x>0, y>0 | x-\delta\ln(x)+y-\phi\ln(y)=1+\phi-\phi\ln(\phi)\}$ are closed. Trajectories starting outside this oval become unbounded.*

Proof. The first part is trivial because Γ is the integral curve of system (2.2) which is tangent to $x=1$. For the second part we compare the trajectories of system (2.4) with those of

$$\frac{dx}{dt}=\phi-y, \quad \frac{dy}{dt}=(1-\delta)y. \tag{2.5}$$

Take any point $A_0(1, y_0)$ with $0<y_0<\phi$, then the trajectory of (2.5) starting in A_0 will intersect the line $x=1$ in $A_1(1, y_1)$ with $y_1>\phi$. The first integral of (2.5) reads

$$K(x,y)=(1-\delta)x+y-\phi ln(y). \tag{2.6}$$

It follows that

$$1-\delta+y_1-\phi ln(y_1)=1-\delta+y_0-\phi ln(y_0). \tag{2.7}$$

Now we will follow the trajectory of (2.2) starting in $A_1(1, y_1)$. It will intersect $x=1$ in $A_2(1, y_2)$ with $y_2<\phi$. Using (2.3) we find

$$1-\delta+y_2-\phi ln(y_2)=1-\delta+y_1-\phi ln(y_1),$$

hence we conclude from (2.7) that $y_2=y_0$ and thus the trajectory starting in A_0 is closed.

It is also differentiable because $(\frac{dy}{dx})_{(2.2);x=1}=(\frac{dy}{dx})_{(2.5)}$.

For $x>1$ we get

$$(\frac{dK}{dt})_{(2.4)}=\phi(1-\delta)(x-1)\ge 0,$$

for $\delta<1$. It follows that trajectories of (2.4) intersect those of (2.5) from the left to the right for $x>1$. Because the trajectories of $(2.5)_{x>1}$ combined with those of $(2.2)_{x\le 1}$ are closed this completes the proof. □

All possible phase portraits of system (2.1) are depicted in Figs. 4–6.

The shaded regions in Figs. 5 and 6 denote the family of closed orbits.

Remark 2.2. For the case $\phi-1+\delta>0$, $0<\delta<1$ almost all trajectories starting outside the oval Γ will tend to infinity such that the predator becomes extinct while the prey density becomes unbounded. For trajectories starting on the semi-line $y=(\phi-1+\delta)x, x>1$, or for trajectories reaching this semi-line in finite time, both prey and predator densities become unbounded. However, a slight change in the initial conditions will again lead to extinction of the predator. For the case $\phi-1+\delta\le 0$, $0<\delta<1$ all trajectories are oscillatory.

Remark 2.3. The degenerate case $\delta=1$ is omitted.

Next we will consider the original Holling I system

$$\frac{dx}{dt}=\phi x(1-\frac{x}{k})-p_1(x)y, \quad \frac{dy}{dt}=-\delta y+p_1(x)y, \tag{2.8}$$

with $p_1(x)=x$ for $0\le x\le 1$, $p_1(x)=1$ for $x>1$ and $\phi>0$.

As mentioned before system (2.8) was investigated by Liu [21]. His main result is the following:

Theorem 2.4. *For certain parameter values system (2.8) has at least two limit cycles.*

As the paper by Liu is in Chinese and not easily accessible we will repeat here a sketch of the proof. First a lemma is stated that will appear to be useful in the rest of the paper.

Lemma 2.5. *Consider the generalized Gause model*

$$\frac{dx}{dt}=xg(x)-p(x)y, \quad \frac{dy}{dt}=-\delta y+\gamma p(x)y, \tag{2.9}$$

where $g(x)$ is a $\mathbb{C}^1$-function satisfying $g(0)>0, g'(x)<0, g(k)=0$ and $p(x)$ satisfies a Lipschitz condition while $p(0)=0, p'(x+0)\ge 0$ and $p'(x-0)\ge 0$, where $k, x>0$.

(a) Suppose (2.9) has a positive equilibrium $E(x^*, y^*)$. If $\frac{d}{dx}(\frac{xg(x)}{p(x)})_{x=x^*}>0(<0)$ then $E(x^*, y^*)$ is asymptotically unstable (stable).

(b) It is possible to indicate a closed curve J, containing and surrounding all singularities in the closed first quadrant, such that on this curve the vector field of (2.9) is either tangent or directed inwards. Furthermore, all trajectories starting outside J will reach J in finite time.

The proof of Lemma 2.5 can be found in [8]. Lemma 2.5 (a) is sometimes referred to as the Rosenzweig-McArthur criterion. The criterion can also be deduced from the observation that at $E(x^*, y^*)$, the divergence of the equivalent Liénard system (1.6) satisfies $\frac{dF(x))}{dx}|_{x=x^*}$. In Lemma 2.5 (b) the conclusion is that the system (2.9) is bounded, i.e. eventually all solutions will enter a bounded region in the phase plane and will stay there.

Remark 2.6. The closed curve mentioned in Lemma 2.5 (b) can be taken piecewise linear, see Fig. 7.

We will only give a sketch of the proof of theorem 2.4, see [21].

Proof. Consider system (2.8) with $k>2$ and $\delta=1-\epsilon$. Then for $\epsilon=0$ system (2.8) is degenerate; all points satisfying $y=\phi x(1-\frac{x}{k})$, with $x>1$, are singular points, see Fig. 8.

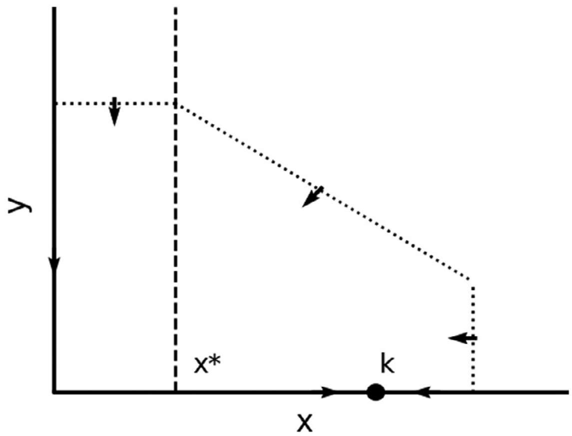

Fig. 7. The closed curve J.

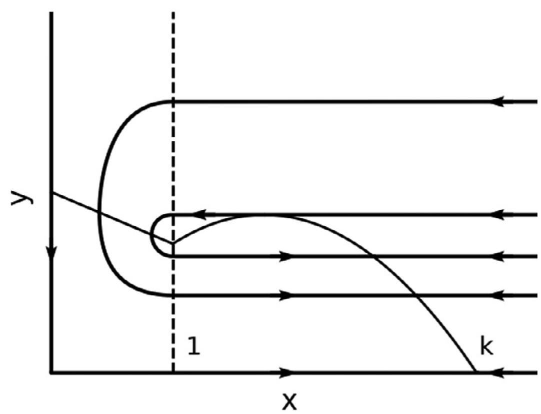

Fig. 8. System (2.9), $\epsilon = 0$.

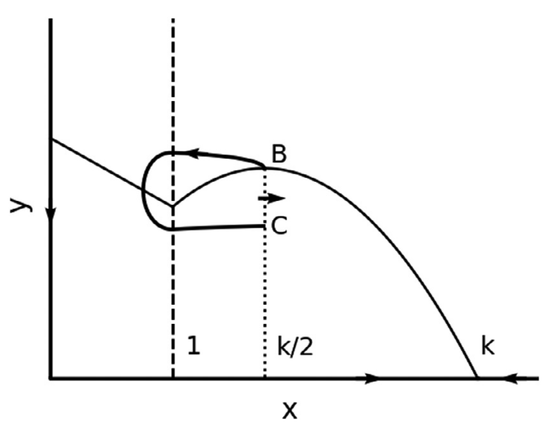

Fig. 9. The curve Γ in the proof of Theorem 2.4.

It is easy to see that for $0 < \epsilon \ll 1$ system (2.8) has a unique positive equilibrium (x^*, y^*) with $x^* < 1$. Next, consider the trajectory γ starting in $B(\frac{k}{2}, \frac{\phi k}{4})$ and ending in $C(\frac{k}{2}, \bar{y})$, its first intersection with the line $x = \frac{k}{2}$. Note that this situation is guaranteed if the singularity (x^*, y^*), for small ϵ, is a focus, not if it is a node. The node case was not considered in [21] and we will report on the investigation of this bifurcation mechanism in more detail in a future publication. For small enough ϕ the singularity is a focus and the argument holds true. In that case the vector field (2.8) is tangent or directed outward of the closed curve Γ, consisting of γ and the line segment CB, see Fig. 9. There is at least one stable limit cycle outside Γ by Lemma 2.5(b) and the Poincaré-Bendixson theorem. By Lemma 2.5(a) (x^*, y^*) is stable so again by the Poincaré-Bendixson theorem there is at least one unstable limit cycle inside Γ. $\square$

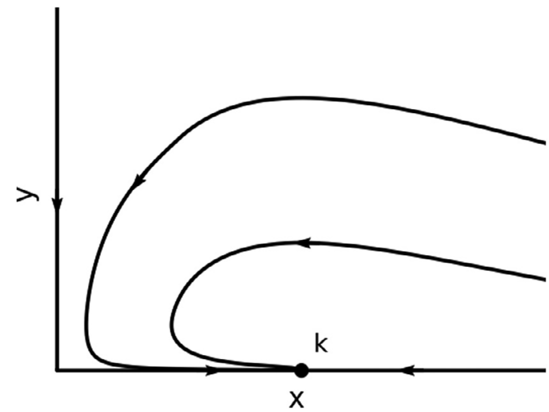

Fig. 10. System (3.1); $\delta > 1$.

3. A differentiable functional response

In this section we study the family of systems (1.5) of the generalized Gause model, where the functional response is differentiable: $p(x) \equiv p_2(x) = x(2 - x)$ for $0 \le x \le 1$ and $p(x) \equiv p_2(x) = 1$ for $x > 1$, i.e. $a_0 = -1$, $a_1 = 0$ in system (1.5).

The system takes the explicit form:

$$\frac{dx}{dt} = \phi x(1 - \frac{x}{k}) - p_2(x)y, \quad \frac{dy}{dt} = -\delta y + p_2(x)y. \tag{3.1}$$

A first observation is that (3.1) has two singularities on the x-axis: a saddle at $O(0, 0)$ and a singularity at $K(k, 0)$. The x-coordinate of a possible third singularity $E(x^*, y^*)$ has to satisfy:

$$-\delta + p_2(x) = 0. \tag{3.2}$$

Case 1: $\delta > 1$

Because $p_2(x) \le 1$, (3.2) has no solution hence (3.1) has only two singularities, the saddle O and a singularity at $K(k, 0)$. By studying the variational matrix at K it is easy to show that for this case K is a stable node. The corresponding phase portrait is given in Fig. 10.

Note that this case will lead to extinction of the predator.

Case 2: $\delta < 1$

Now there exists a unique x^* with $0 < x^* < 1$ such that (3.2) holds. The y-coordinate of $E(x^*, y^*)$ satisfies $y^* = \frac{\phi x^*(1-\frac{x^*}{k})}{\delta}$.

Subcase $k \le 1$

(i) If $k \le x^*$ then $y^* \le 0$ and the phase portrait is again as in Fig. 10.

(ii) For $k > x^*$, $E(x^*, y^*)$ is a positive equilibrium. Studying the variational matrices about K and E it is easy to show that K is a saddle whereas E is an antisaddle (i.e. an elementary singular point with index +1) that is asymptotically stable.

To obtain the phase portrait of system (3.1) we have to combine the trajectories for $0 \le x \le 1$ with those for $x > 1$.

For $0 \le x \le 1$ system (3.1) becomes

$$\frac{dx}{dt} = \phi x(1 - \frac{x}{k}) - x(2 - x)y, \quad \frac{dy}{dt} = -\delta y + x(2 - x)y. \tag{3.3}$$

System (3.3) has no limit cycles in the strip $0 \le x \le 1$ as can be seen by applying the Bendixson-Dulac criterion, see [1], with Dulac function $B(x, y) = \frac{1}{x(2-x)y}$.

For $x > 1$ system (3.1) becomes

$$\frac{dx}{dt} = \phi x(1 - \frac{x}{k}) - y, \quad \frac{dy}{dt} = -\delta y + y. \tag{3.4}$$

Obviously system (3.4) has no closed orbits in the first quadrant because for $y \ge 0$ $\frac{dy}{dt} \ge 0$ as $0 < \delta < 1$. Because $k \le 1$ trajectories of system (3.1) can only intersect $x = 1$ from the right to the

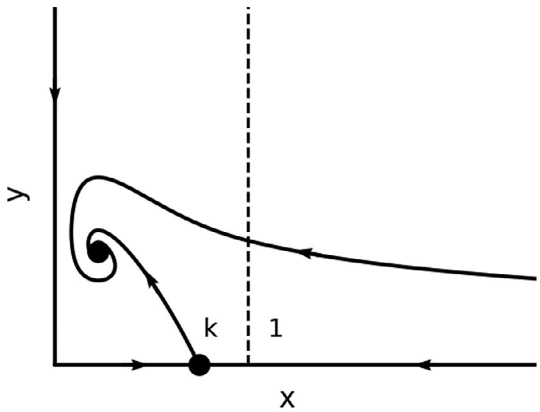

Fig. 11. System (3.1); $x^* < k \le 1$.

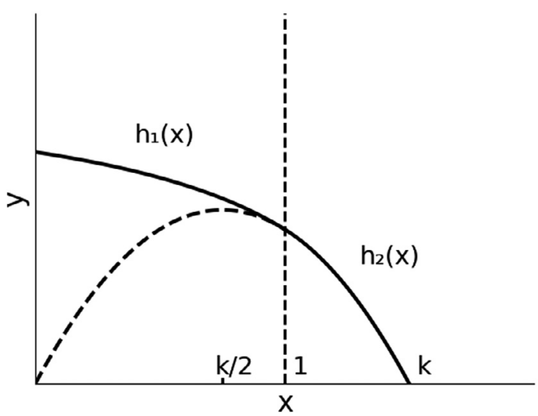

Fig. 12. The function $h(x)$ in the proof of Theorem 3.2.

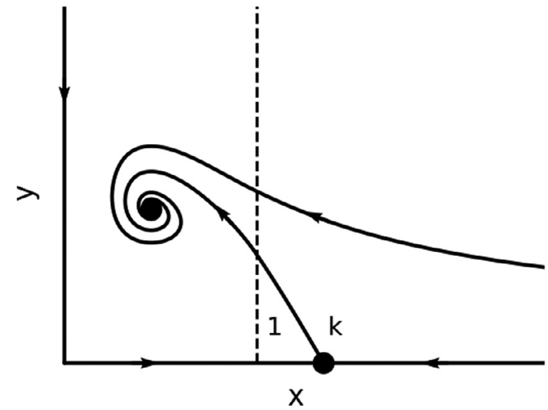

Fig. 13. System (3.1); $1 < k \le 2$.

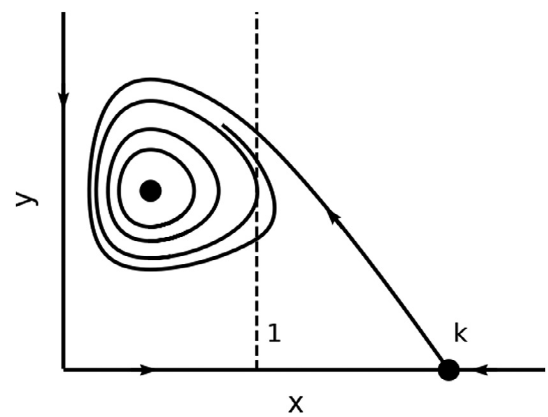

Fig. 14. System (3.1); $k = 2$.

left, so there can be no closed orbits intersecting $x = 1$. Applying Lemma 2.5 (b) we conclude that for this case $E(x^*, y^*)$ is globally stable. The corresponding phase portrait is given in Fig. 11.

Subcase $k > 1$

(i) $1 < k < 2$

First we study the shape of the ∞-isocline $y(x) = \phi \frac{x(1-\frac{x}{k})}{p_2(x)} \equiv h(x)$. Then for $0 \le x \le 1$, $h(x) \equiv h_1(x) = \phi \frac{(1-\frac{x}{k})}{(2-x)}$ and for $x > 1$, $h(x) \equiv h_2(x) = \phi x(1 - \frac{x}{k})$. Because $k < 2$ both $h_1(x)$ and $h_2(x)$ are decreasing, see Fig. 12.

By Lemma 2.5 (a) the positive equilibrium is asymptotically stable.

To prove the nonexistence of closed orbits we can again apply the Bendixson-Dulac criterion, with Dulac function $B(x, y) = \frac{1}{p_2(x)y}$. Then it follows by Lemma 2.5 (b) that $E(x^*, y^*)$ is globally stable. The corresponding phase portrait is sketched in Fig. 13.

(ii) $k = 2$

Now the ∞-isocline $y = h_1(x),\ 0 \le x \le 1$ satisfies $h_1(x) = \frac{\phi}{2}$ and the stability of $E(x^*, y^*)$ does not follow from Lemma 2.5 (a). In fact, for this case $E(x^*, y^*)$ is a center because system (3.3) with $k = 2$ has an integrating factor $\mu(x, y) = \frac{1}{x(1-\frac{x}{2})y}$ from which the first integral can be found:

$$Z(x, y) = \phi ln(y) - 2y + \delta ln(x) - \delta ln(2 - x) - 2x. \tag{3.5}$$

The oval $\Gamma = \{x > 0, y > 0 | Z(x, y) = \phi \ln(\frac{\phi}{2}) - \phi - 2\}$, i.e. the solution of (3.3) with $k = 2$ tangent to $x = 1$, plays an important role. As in Theorem 2.4, all trajectories starting on or inside Γ are closed. Next we will show that all trajectories starting outside Γ have Γ as their ω-limit set.

We will prove this by comparing the trajectories of system $(3.3)_{k=2}$ with those of the linear system:

$$\frac{dx}{dt} = \frac{\phi}{2} - y, \quad \frac{dy}{dt} = (1 - \delta)y, \tag{3.6}$$

for $x \ge 1$.

Because the first integral of (3.6) reads

$$M(x, y) = (1 - \delta)x + y - \frac{\phi}{2} ln(y), \tag{3.7}$$

it follows

$$\left.\frac{dM}{dt}\right|_{(3.4)} = -\frac{1}{2}(1 - \delta)\phi(x - 1)^2 \le 0 \tag{3.8}$$

Because all trajectories for the system obtained by combining $(3.6)_{k=2}$ for $0 \le x \le 1$ with (3.6) for $x > 1$ are closed, it follows from (3.8) and Lemma 2.5 (b) that all trajectories of $(3.1)_{k=2}$ which start outside Γ have Γ as their ω-limit set. The corresponding phase portrait is given in Fig. 14.

(iii) $k > 2$

A study of the ∞-isocline reveals that $h_1(x)$ is monotonically increasing whereas $h_2(x)$ has a unique maximum at $x = \frac{k}{2}$, see Fig. 15.

It follows from Lemma 2.5 (a) that $E(x^*, y^*)$ is unstable. By Lemma 2.5 (b) the Poincaré-Bendixson theorem can be applied to deduce that system (3.1) has at least one stable limit cycle. We will prove that this limit cycle is unique.

The standard procedure is to transform the system under consideration to a (generalized) Liénard system and then apply a theorem by Zhang [33,34] which guarantees uniqueness of the limit cycle. However, we will use a modification by Coppel [4,5] and Wang [31].

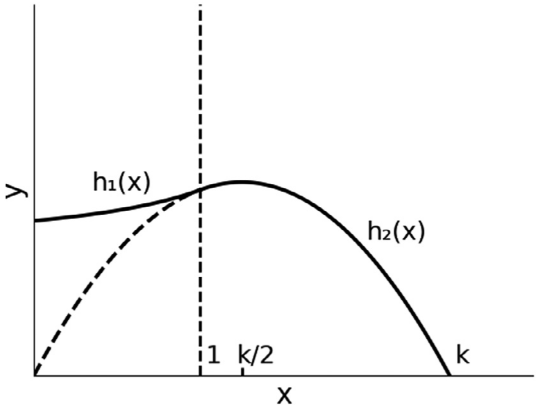

Fig. 15. The function $h(x)$.

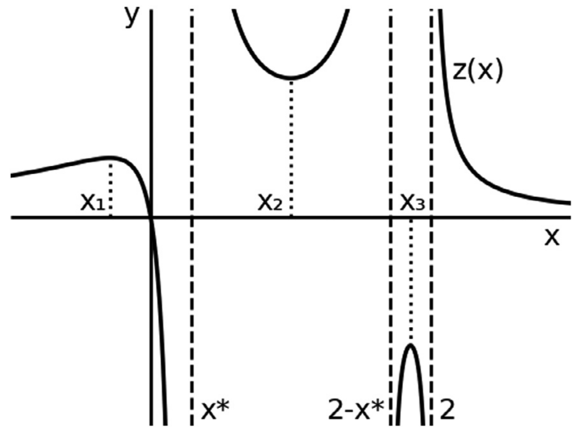

Fig. 16. The function $z(x)$ in the proof of Theorem 3.2.

Lemma 3.1. *Let $F(x)$, $g(x)$ be continuously differentiable functions on the open interval (r_1, r_2), and let $\Psi(y)$ be a continuousty differentiable function on $\mathbb{R}$ in:*

$$\frac{dx}{dt} = F(x) - \Psi(y), \; \frac{dy}{dt} = g(x), \tag{3.9}$$

such that

(i) $d\Psi/dy > 0, \forall y \in \mathbb{R}$,

(ii) there exists $x_0 \in (r_1, r_2)$ such that $(x - x_0)g(x) > 0$ for $x \neq x_0$, and $g(x_0) = 0$,

(iii) the function $f(x) \equiv \frac{dF(x)}{dx}$ has a unique zero $x_f \in (r_1, r_2)$, with $x_f > x_0$,

(iv) $f(x_0)\frac{d}{dx}(\frac{f(x)}{g(x)}) < 0$, for $x \in (r_1, x_0) \cup (x_f, r_2)$.

Then in the strip $r_1 < x < r_2$ system (3.9) has at most one limit cycle, which is hyperbolic if it exists.

As indicated in (1.6) the systems we study can be transformed into this generalized Liénard form with $F(x) = \phi\frac{x(1-\frac{1}{k}x)}{p_2(x)} - \phi\frac{(1-\frac{1}{k}x^*)}{(2-x^*)}$,

$\Psi(y) = e^y - \frac{\phi(1-\frac{1}{k}x^*)}{(2-x^*)}$

$g(x) = \frac{p_2(x)-\delta}{p_2(x)}$.

For $0 \le x \le 1$ we define $F(x) \equiv F_1(x) = \phi\frac{(1-\frac{1}{k}x)}{(2-x)} - \phi\frac{(1-\frac{1}{k}x^*)}{(2-x^*)}$, $g(x) \equiv g_1(x) = \frac{x(2-x)-\delta}{x(2-x)}$; for $x > 1$, $F(x) \equiv F_2(x) = \phi x(1 - \frac{1}{k}x) - \phi\frac{(1-\frac{1}{k}x^*)}{(2-x^*)}$ and $g(x) \equiv g_2(x) = 1 - \delta$.

We will prove that all conditions of Lemma 3.1 hold for system (3.9) using the functions defined in system (1.6).

Because for all $x > k$, $\frac{dx}{dt} \le 0$ in system (3.1), it follows that any possible limit cycle of system (3.9) should be located in the strip $0 < x < k$. Therefore we can take $r_1 = 0, r_2 = k$.

It is easy to check that conditions (i), (ii) are satisfied with $x_0 = x^*$. Next we will verify condition (iii). Let $f_i(x) \equiv \frac{d}{dx}F_i(x)$, $i = 1, 2$. Then $f_1(x) = \phi\frac{1-\frac{2}{k}}{(2-x)^2}$ and $f_2(x) = \phi(1 - \frac{2x}{k})$.

The function $f(x) = \frac{d}{dx}F(x)$ has a unique zero $x = \frac{k}{2}$. Obviously $x_f > 1 > x_0$ hence condition (iii) is satisfied. Since $f(x_0) = f(x^*) > 0$ condition (iv) is satisfied if $\frac{d}{dx}(\frac{f_1(x)}{g_1(x)}) < 0$ on $0 < x < x^*$ and $\frac{d}{dx}(\frac{f_2(x)}{g_2(x)}) < 0$ on $\frac{k}{2} < x < k$.

The latter part is trivial since $\frac{f_2(x)}{g_2(x)} = \phi\frac{1-\frac{2}{k}x}{1-\delta}$.

Now let us study the graph of $z(x) = \frac{f_1(x)}{g_1(x)} = \phi\frac{(1-\frac{2}{k})x}{(2-x)(x(2-x)-\delta)}$. The vertical asymptotes of $z(x)$ are $x = x^*$, $2 - x^*$ and $x = 2$. Furthermore, $z(x)$ has the x-axis as a horizontal asymptote. Obviously $x = 0$ is the only zero of $z(x)$.

Because the numerator of $\frac{d}{dx}(\frac{f_1(x)}{g_1(x)})$ is a third order polynomial it follows that $\frac{dz(x)}{dx}$ has at most three zeros. In fact, it can be shown that there are exactly three zeros $x_1 < x_2 < x_3$ satisfying $x_1 < 0$, $x^* < x_2 < 2 - x^* < x_3 < 2$, see Fig. 16. Therefore the function $z(x)$ is monotonically decreasing for $0 < x < x^*$.

Hence all conditions of Lemma 3.1 are satisfied and therefore system (3.1) has exactly one limit cycle, which is stable and hyperbolic.

We will omit the degenerate case $\delta = 1$, for which case system (3.1) has no closed orbits. The results obtained in this section are summarized in the following theorem.

Theorem 3.2. *(a) If system (3.1) has an asymptotically stable positive equilibrium then it is globally stable.*

(b) If the positive equilibrium is unstable then it is surrounded by a unique limit cycle that is stable and hyperbolic.

(c) If for $k = 2$ system (3.1) has a positive equilibrium, then it is a center. There exists an oval Γ such that all trajectories starting on or inside Γ are closed whereas trajectories starting outside this oval have Γ as their ω-limit set.

4. A sigmoidal differentiable functional response

In this section we study the family of systems (1.5) of the generalized Gause type, where the functional response has a sigmoidal shape, $p(x) \equiv p_3(x) = x^2(3 - 2x)$ for $0 \le x \le 1$ and $p(x) \equiv p_3(x) = 1$ for $x \ge 1$, i.e. $a_0 = 1$, $a_1 = -2$ in system (1.5).

The system takes the explicit form:

$$\frac{dx}{dt} = \phi x(1 - \frac{x}{k}) - p_3(x)y, \quad \frac{dy}{dt} = -\delta y + p_3(x)y. \tag{4.1}$$

Note that $p_3(x) \in \mathbb{C}^1$ but $p_3(x) \notin \mathbb{C}^2$.

In analysing the phase portrait of system (4.1) we will encounter cases that also appeared in Section 3. For these cases the proofs are omitted.

Case 1: $\delta > 1$

The only singularities of system (4.1) are the saddle $O(0, 0)$ and the stable node at $(k, 0)$. The corresponding phase portrait is as given in Fig. 10.

Case 2: $\delta < 1$

There exists a unique $0 < x^* < 1$ such that $p_3(x^*) - \delta = 0$. The y-coordinate of $E(x^*, y^*)$, the possible positive equilibrium of system (4.1), satisfies $y^* = \frac{\phi x^*(1-\frac{x^*}{k})}{\delta}$.

Subcase $k \le 1$

(i) If $k \le x^*$ then $y^* \le 0$ and the phase portrait is as in Fig. 10.

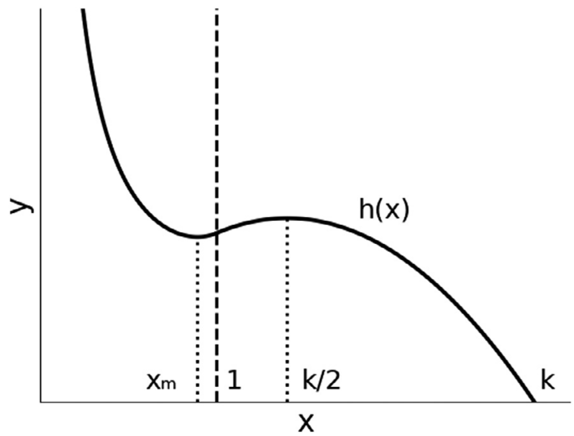

Fig. 17. The function $h(x)$.

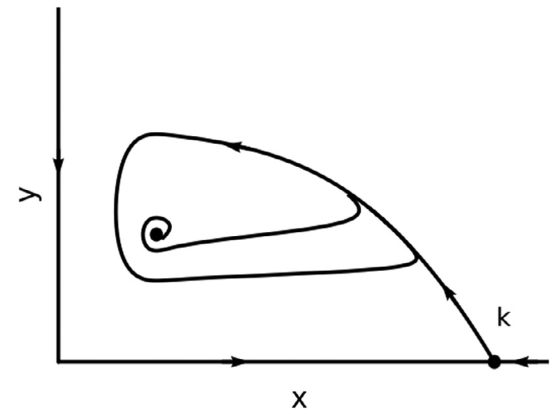

Fig. 18. System (4.1); $\phi=1,\ k=4,\ \delta=.972$.

(ii) If $k>x^*$ then $E(x^*,\ y^*)$ is a positive equilibrium. It can be shown, in the same way as for the corresponding case in Section 3, that E is globally stable. The phase portrait is the same as in Fig. 11.

Subcase $k>1$

(i) $k<2$

We study the shape of the ∞-isocline $y(x)=\frac{\phi x(1-\frac{x}{k})}{p_3(x)}\equiv h(x)$. Let, for $0\le x\le 1$, $h(x)\equiv h_1(x)=\frac{\phi(1-\frac{x}{k})}{x(3-2x)}$ and for $x\ge 1$, $h(x)\equiv h_2(x)=\phi x(1-\frac{x}{k})$. For this case $h(x)$ always has a negative slope, hence by Lemma 2.5 (a) $E(x^*,\ y^*)$ is asymptotically stable. By using the Dulac function $B(x,y)=\frac{1}{p_3(x)y}$ it can be shown that E is globally stable. The corresponding phase portrait is like the one given in Fig. 13.

(ii) $k=2$

Now the ∞-isocline is also monotonically decreasing but for $x=\frac{k}{2}$, we have $\frac{dh}{dx}=0$, hence if $x^*=\frac{k}{2}$, then Lemma 2.5 (a) cannot be applied to determine the stability of $E(x^*,\ y^*)$. However, we can still use the Dulac function $B(x,y)=\frac{1}{p_3(x)y}$ to show that E is globally stable. In fact, for this case if $x^*=\frac{k}{2}$, then the eigenvalues of the variational matrix at E become purely imaginary.

(iii) $k>2$

In this case the ∞-isocline has both a relative maximum and a relative minimum, see Fig. 17. Note that $h(x)$ has a relative maximum at $x=\frac{k}{2}$.

Let $h(x)$ obtain its relative minimum at $x=x_m$. If $x_m<x^*<1$ then according to Lemma 2.5 (a) $E(x^*,\ y^*)$ is unstable and hence by Lemma 2.5 (b) system (4.1) has at least one limit cycle.

We have tried to prove the uniqueness of this limit cycle by applying a lemma similar to Lemma 3.1 but without the desired result. We hope to be able to solve the following open problem in the future by applying some improvement of Lemma 3.1.

Open Problem 4.1 *If system (4.1) has an unstable positive equilibrium, then it is surrounded by exactly one closed orbit, a stable, hyperbolic limit cycle.*

A natural way to try to tackle Open Problem 4.1 is to transform system (4.1) to a generalized Liénard system

$$\frac{dx}{dt}=F(x)-\Psi(y),\quad \frac{dy}{dt}=g(x), \tag{4.2}$$

and then apply a lemma similar to Lemma 3.1. The main condition to be satisfied would be the monotonicity of $\frac{f(x)}{g(x)}$ on $(0,x^*)\cup(x^*,k)$, see [34]. However, for the parameter values $\phi=1, k=4, \delta=0.972$, we can show that $x_m<x^*<1<x_m$, while $\frac{f(x)}{g(x)}$ has both a relative minimum and a relative maximum on $(0,\ x_m)$.

The phase portrait of system (4.1) for this choice of parameters is shown in Fig. 18.

If $x^*=x_m$, then $(\frac{dh}{dx})_{x=x^*}=0$ and so we cannot apply Lemma 2.5 (a). For this case the variational matrix at $E(x^*,\ y^*)$ has purely imaginary eigenvalues, therefore this equilibrium is either a center or a weak focus.

Recall that a weak focus is a singularity which is a center for the linearized system but not a center for the nonlinear system. If the origin is a weak focus then the canonical form of the system reads:

$$\frac{dx}{dt}=-y+F_2(x,y),\quad \frac{dy}{dt}=x+G_2(x,y), \tag{4.3}$$

where $F_2(x,\ y)$ and $G_2(x,\ y)$ denote terms of at least second degree. There exists a function $V(x,\ y)$ defined in the neighbourhood of the origin such that its rate of change along orbits of system (4.3) is of the form:

$$\frac{dV}{dt}=V_1(x^2+y^2)^2+V_2(x^2+y^2)^3+\dots$$

The V_i's are called focal values and the stability of the origin is determined by the first non-vanishing focal value. The order of the weak focus is K if $V_1=V_2=\ldots=V_{K-1}=0$ but $V_K\neq 0$. Under perturbation of the coefficients of (4.3) at most K limit cycles bifurcate out of a weak focus of order K. Such limit cycles are said to be of small amplitude. For an ample discussion on the computation of focal values we refer to Andronov [1]. Here we will use the algorithm described in [17] to compute V_1.

We will determine the first non-vanishing focal value for the system (4.1) in case it has a weak focus at $x=x^*<1$.

An elementary calculation reveals that at $E(x^*,\ y^*)$ the trace of the variational matrix satisfies

$$P(x)=\frac{\frac{2}{k}x^2-4x+3}{2x-3}. \tag{4.4}$$

Therefore $P(x^*)=0$ and $0<x^*<1$ imply that

$$x^*=k-\frac{1}{2}\sqrt{2k(2k-3)}. \tag{4.5}$$

Because $E(x^*,\ y^*)$ is a singularity of system (4.1) we also have

$$\delta=x^{*^2}(3-2x^*),\quad y^*=\frac{\phi(1-\frac{x^*}{k})}{x^*(3-2x^*)}, \tag{4.6}$$

where x^* satisfies (4.5). Note that if (4.5) and (4.6) hold then $E(x^*,\ y^*)$ is a center for the linearized system.

After the translation $x=u+x^*, y=v+y^*$, the algorithm described in [17], implemented in Maple, can be used to determine the first focal value.

The expression thus obtained is a very complicated function of ϕ and k and it is difficult to determine its sign.

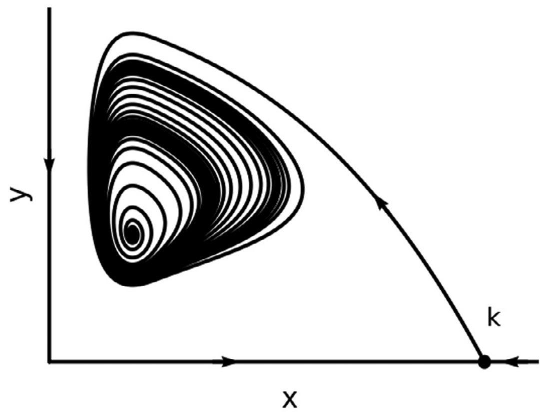

Fig. 19. System (4.1); $\phi = 1,\ k = 4,\ \delta = .86$.

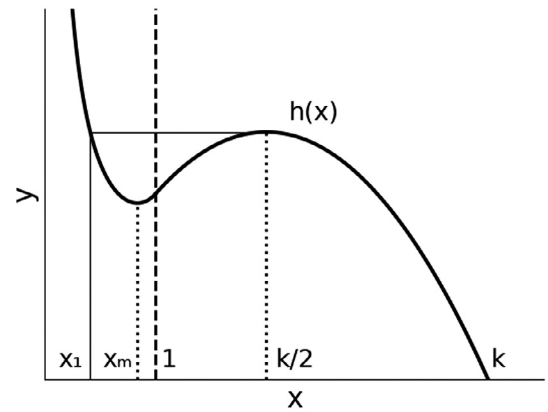

Fig. 20. The function $h(x)$.

An alternative approach is to treat x^* as a parameter and solve $P(x^*) = 0$ with respect to k. Then from (4.4) we obtain

$$k = \frac{2{x^*}^2}{4x^* - 3}. \tag{4.7}$$

This value of k should also be substituted in the second equation of (4.6).

Again using the program described in [17] it follows that the sign of the first focal value V_1 corresponds to the sign of

$$\frac{(5 - 4x^*)}{4x^*(3 - 2x^*)(1 - x^*)}. \tag{4.8}$$

Because $0 < x^* < 1$ it is easy to see that $V_1 > 0$.

This means that the weak focus is of first order and unstable. By Lemma 2.5 (b) if $x^* = x_m$, then there is at least one stable limit cycle Γ_1 surrounding $E(x^*, y^*)$.

For $0 < x_m - x^* \ll 1$ the stability of $E(x^*, y^*)$ is changed and hence an additional unstable limit cycle Γ_2 is generated through the Andronov-Hopf bifurcation. Notice that for this case system (4.1) exhibits bistable behaviour because both the positive equilibrium $E(x^*, y^*)$ and the outer most limit cycle are stable. We have no theorems available to ascertain that system $E(x^*, y^*)$, or the equivalent Liénard system (4.2), has at most two limit cycles, although numerical experiments point in this direction, see Fig. 19.

This leads to another open problem for system (4.1).

Open Problem 4.2 *If system (4.1) has an asymptotically stable positive equilibrium $E(x^*, y^*)$, and $0 < \delta < 1$, $x^* < x_m < 1 < \frac{k}{2}$, then $E(x^*, y^*)$ is surrounded by at most two limit cycles.*

We have seen that for the case $x^* < x_m$ it is possible that (4.1) has two limit cycles. Hence the asymptotic stability of $E(x^*, y^*)$ does not imply its global stability. However, we will show that for x^* sufficiently small $E(x^*, y^*)$ is globally stable.

Again consider the function $h(x)$, the ∞-isocline of system (4.1). Let $h(x)$ obtain its relative maximum at x_m, see Fig. 20.

Because $\lim_{x \downarrow 0} h(x) = \infty$ and $\frac{dh}{dx} < 0$ for $x \in (0, x_m)$, it follows that there exists a unique $x_1 \in (0, x_m)$ such that $h(x_1) = h(\frac{k}{2})$.

Theorem 4.1. *If $0 < \delta < 1$, $k > 2$ and $0 < x^* < x_1$ then system (4.1) has no closed orbits. As a consequence $E(x^*, y^*)$ is globally stable.*

Proof. First we transform system (4.1) to a generalized Liénard system using (1.6). We get:

$$\frac{dx}{dt} = F(x) - \Psi(y), \quad \frac{dy}{dt} = g(x), \tag{4.9}$$

with $F(x) = \phi \frac{x(1-\frac{1}{k}x)}{p_3(x)} - \phi \frac{(1-\frac{1}{k}x^*)}{x^*(3-2x^*)}$,

$\Psi(y) = e^y - \phi \frac{(1-\frac{1}{k}x^*)}{x^*(3-2x^*)}$

$g(x) = \frac{p_3(x) - \delta}{p_3(x)}$.

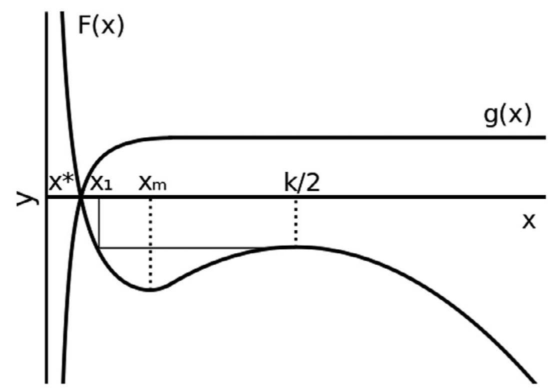

Fig. 21. $F(x)$ and $g(x)$ in system (4.9).

For $0 \le x \le 1$ we define $F(x) \equiv F_1(x) = \phi \frac{(1-\frac{1}{k}x)}{x(3-2x)} - \phi \frac{(1-\frac{1}{k}x^*)}{x^*(3-2x^*)}$, $g(x) \equiv g_1(x) = \frac{x^2(3-2x)-\delta}{x^2(3-2x)}$; for $x \ge 1$, $F(x) \equiv F_2(x) = \phi x(1 - \frac{1}{k}x) - \phi \frac{(1-\frac{1}{k}x^*)}{x^*(3-2x^*)}$ and $g(x) \equiv g_2(x) = 1 - \delta$.

First notice that $F(x) = h(x) - h(x^*)$ hence $F(x^*) = 0$. It is easy to see that if $x^* \le x_1$ then $F(x) \le 0$ for $x > x^*$, see Fig. 21.

Furthermore $F(x) > 0$ for $x < x^*$ and $g(x) > 0$ ($g(x) < 0$) for $x > x^*$ ($x < x^*$), see Fig. 21.

Next consider the family of closed orbits given by the level curves of

$$\lambda(x, y) = \int_{y^*}^{y} \Psi(\xi) d\xi + \int_{x^*}^{x} g(\tau) d\tau. \tag{4.10}$$

Note that all level curves of λ contain $E(x^*, y^*)$ in their interior.

The rate of change of λ along the trajectories of (4.9) satisfies

$$\frac{d\lambda}{dt} = \Psi(y)(\frac{dy}{dt})_{(4.9)} + g(x)(\frac{dx}{dt})_{(4.9)} = F(x)g(x),$$

and therefore $\frac{d\lambda}{dt} \le 0$. It follows that the trajectories of (4.9) intersect the level curves of $\lambda(x, y)$ in the exterior-to-interior direction. Therefore there cannot be any closed orbits. □

Remark 4.2. If x^* is decreased from x_m then at least two limit cycles exist initially but by the time that x^* reaches x_1 they must have disappeared. This can only happen through a saddle-node bifurcation for limit cycles, implying the existence of a semi-stable limit cycle for a certain value $x_{ss} \in (x_1, x_m)$. In our situation the semi-stable limit cycle is stable on the outside and unstable on the inside.

5. Conclusions

In this paper we studied the generalized Gause model, with a logistic growth rate for the prey in absence of the predator, a constant death rate for the predator and for three different classes of functional response, all non-analytical:

$$\frac{dx}{dt} = \phi x(1 - \frac{x}{k}) - p(x)y, \quad \frac{dy}{dt} = -\delta y + p(x)y. \tag{5.1}$$

In this section we will briefly discuss the differences between the results obtained in the previous sections and the results known from the literature, where $p(x)$ is either of Holling type II or III.

Case 1.

If $p(x)$ is of Holling type I, i.e. $p(x) = p_1(x) = 1$ for $x > 1$ and $p_1(x) = x$ for $0 \leq x \leq 1$ then for certain parameter values system (5.1) has (at least) two limit cycles. If these occur, then the positive equilibrium is asymptotically stable. Hence for this case asymptotic stability of the positive equilibrium does not imply global stability. If $k = \infty$, i.e. the carrying capacity of the prey is infinitely large, then (5.1) can have a family of closed orbits. These phenomena cannot occur when the functional response is of Holling type II, i.e. $p(x) = \frac{x}{c+x}$ because then (5.1) has at most one closed orbit, a stable limit cycle, see [3,16].

Case 2.

If $p(x)$ satisfies $p(x) = p_2(x) = 1$ for $x > 1$ and $p_2(x) = x(2 - x)$ for $0 \leq x \leq 1$ then system (5.1) has at most one limit cycle. However, if a certain relation between the parameters in (5.1) holds (denoting in parameter space the change of stability of the positive equilibrium) then system (5.1) has a family of closed orbits. This is the difference with the case where the functional response is of Holling type II because then the change of stability of the positive equilibrium happens through the Andronov-Hopf bifurcation, see [16].

Case 3.

In this case $p(x)$ satisfies $p(x) = p_3(x) = 1$ for $x > 1$ and $p_3(x) = x^2(3 - 2x)$ for $0 \leq x \leq 1$.

For this sigmoidal functional response, for a certain choice of parameters system (5.1) has (at least) two limit cycles. If the functional response is of Holling type III, i.e. $p(x)$ is the sigmoidal function $p(x) = \frac{x^2}{c+x^2}$ then (5.1) has at most one limit cycle, see [6].

It is clear that if we compare the generalized Gause model with a functional response that is non-analytical (e.g. Holling type I) with a functional response that is analytical then the behaviour in the first case is more complicated. As examples of this more complicated behaviour we have seen, the co-existence of a stable equilibrium with a stable limit cycle and the existence of a family of closed orbits.

For future research we aim at studying the general case of system (1.5). This system exhibits an even richer variety of behaviour than the special cases studied in this paper. Especially the dependence on the carrying capacity is more complicated. For example, there are cases (keeping the functional response monotonic) where (1.5) has at least two limit cycles for the carrying capacity satisfying $0 < k < 2$, in contrast to the cases of this paper where $k > 2$ was a necesssary condition for the existence of at least two limit cycles.

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