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MASTERARBEIT

Titel der Masterarbeit

On the Gause predator–prey model with a refuge

Verfasser

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Contents

1 Introduction

In the 30s of the last century Russian biologist Georgii Frantsevich Gause ventured various experiments to test the biological models of Lotka and Volterra. He found that the actual interactions of predators and prey contradicted the results found by Lotka and Volterra. In his experiments there was a distinct chance for the prey and for the predators to die out. In another setup, with different kinds of predators and prey, there were strong signs that suggested that there was something like a convergence to a limit cycle. These are results that are not predicted by the models of Lotka and Volterra.

In the setup, that we are especially interested in, there was something like a refuge for the prey. If the amount of prey was below a certain threshold the predators started to die and became significantly fewer. The prey on the other hand was protected and didn't diminish. Above the threshold it was the other way round. Prey started to decline and predators to rise. Gause casted those observations into differential equations as an alternative approach to the Lotka-Volterra model of predator-prey interactions.

A few years ago Vlastimil Křivan reanalyzed these equations of Gause. Gause was ahead of its day with his equations because he used non-continuous equations for which no concept of solutions existed at that time. Křivan now used the approach of Filippov, who created a way to deal with these kinds of equations in the 60s of the last century. With this approach these equations could now be dealt with rigorously and Křivan showed what kind of behaviour could be expected from them. The problem with the behaviour now was that for some parameter-values infinite growth was possible. Needless to say that for any biological model infinite growth in a finite world is not a realistic option. In this master thesis the work of Křivan is redone but with an altered equation. We will change the equations of Gause/Křivan

$$\begin{aligned} \dot{x} &= rx - yf(x), \\ \dot{y} &= y(-d + ef(x)), \\ f(x) &= \begin{cases} 0 & \text{if } x < \hat{x} \\ \frac{sx}{1+hsx} & \text{if } x > \hat{x} \end{cases} \end{aligned}$$

to one of the most often used versions of the Gause model, which is - ironically enough - not what Gause himself used. The equation of Gause/Křivan in the absence of predators reads $\dot{x} = rx$, whose solutions are not bounded for a positive starting population of prey. We will change this term to logistic growth. The equation for the prey in the absence of predators will now read $\dot{x} = rx(1 - \frac{x}{K})$. The term K is the carrying capacity of the system, which is the maximal amount of prey that can be sustained in this biological setting. r is the growth factor of the prey. d determines how long the predators live.

$f(x)$ describes how the predators consume the prey. The success of the hunt depends on the amount of prey around. More predators only increase the amount of prey caught linearly, which can be interpreted that they don't change the nature of the hunt in any way, e.g. by collective hunt or by stealing each other's prey. What percentage of the caught biomass of the prey is actually converted into predators is described by e. In our special case of the Gause model as well as the version of Gause/Křivan $f(x)$ is the Holling type II functional response.

It seems this adaptation suggests itself. This adaptation - chapter 2.1 and most of 2.2 here - has already been done in [10] without the author's knowledge. But from chapter 2.3 on the research should be original research.

After we analyze this adaptation and redo the work of Křivan for this set of equation we will see what happens when we leave out the specialized version of the Gause model and turn to the general Gause model. We will see in which ways the situation of the attractors is actually influenced by the concrete form of the Gause model.

After this quick look towards the general Gause model we return to the special version of the Gause model and we will see what happens when we drop the assumption of a constant refuge and instead assume a non-constant one. A constant refuge makes a lot of sense if we, e.g., imagine a cave where the hunted rabbits hide from the wolves, but that might not always be the best model of reality. A burrow might be safe sometimes but if a lot of foxes are on the prowl not all burrows might be safe and some will be dug up. We will therefore look at the situation where the refuge is no longer constant but depends on the amount of predators around. A lot of predators will mean a smaller refuge and few predators will mean relative safety for the prey.

2 The Gause Model with Refuge

Without further ado we now come to the mathematical part. The equations for our version of the Gause-model are given by the two dimensional system

$$\begin{aligned} \dot{x} &= rx(1-\frac{x}{K}) - yf(x) \\ \dot{y} &= y(-d+ef(x)) \end{aligned} \tag{1}$$

and the function $f(x)$ is defined as

$$f(x) = \begin{cases} 0 & \text{if } x < \hat{x} \\ \frac{sx}{1+hsx} & \text{if } x > \hat{x} \end{cases}$$

for a certain value $\hat{x}$. Like $\hat{x}$ are r, K, d, e, s, h parameters. We will say we are in the System (S1)

$$\begin{aligned} \dot{x} &= rx(1-\frac{x}{K}) \\ \dot{y} &= -dy \end{aligned} \tag{2}$$

if we are on the "left" side of the $\hat{x}$-line (meaning $x < \hat{x}$) and in the System (S2)

$$\begin{aligned} \dot{x} &= rx(1-\frac{x}{K}) - y\frac{sx}{1+hsx} \\ \dot{y} &= y(-d+e\frac{sx}{1+hsx}) \end{aligned} \tag{3}$$

if we are on the "right" side of the $\hat{x}$-line (meaning $x > \hat{x}$).

Let us look at the dynamic on the axes as a first step. On the y-axis with $x = 0$ we have $\dot{x} = 0 - yf(0) = 0$ and $\dot{y} = y(-d + ef(0)) = -dy$. We see that the y-axis is invariant and every orbit on it converges to the origin, because we have exponential decay here. On the x-axis with $y = 0$ we have $\dot{x} = rx(1 - \frac{x}{K})$ and $\dot{y} = 0$. We derive from this that the x-axis is invariant and we have logistic growth, which implies that the orbits converge to the point $(K, 0)$.

Now we will derive the isoclines:

$$\dot{x} = 0 \Leftrightarrow rx(1-\frac{x}{K}) = yf(x) \Leftrightarrow rx - \frac{r}{K}x^2 = yf(x)$$

1.) $(x < \hat{x})$ $rx = \frac{r}{K}x^2 \Leftrightarrow x = K \vee x = 0$

2.) $(x > \hat{x})$ $rx - \frac{r}{K}x^2 = \frac{ysx}{1+hsx} \Leftrightarrow$

$$y = -\frac{rh}{K}x^2 + (rh - \frac{r}{Ks})x + \frac{r}{s} = -\frac{hr}{K}(x + \frac{1}{hs})(x - K)$$

$\dot{y} = 0 \Leftrightarrow dy = eyf(x) \Leftrightarrow y = 0 \vee d = ef(x)$

1.) $(x < \hat{x})$ $y = 0 \vee d/e = 0 \Leftrightarrow y = 0$

2.) $(x > \hat{x})$ $y = 0 \vee d(1 + hsx) = esx \Leftrightarrow y = 0 \vee x = \dfrac{d}{s(e - dh)}$

We define $x^* = \frac{d}{s(e-dh)}$. However x^* as an isocline does only exist if $x^* > \hat{x}$. This also implies that $e > dh$, otherwise x^* would be negative.

We see that the x-isocline is a second degree polynomial with a negative leading term and zeros at $-\frac{1}{hs}$ and K respectively, from this follows that we always have a point of intersection with the y-isocline, if $x^* > \hat{x}$ and $x^* < K$ holds. This point of intersection is obviously an equilibrium and we will define it as (x^*, y^*). We already know the value of x^*. y^* can easily be calculated if we insert x^* into the equation for the y-isocline. We get:

$$y^* = \frac{-hr}{K}(x^* + \frac{1}{hs})(x^* - K) = \frac{er(eKs - d(1 + hKs))}{(e - dh)^2 Ks^2}. \tag{4}$$

We can now start to draw phase portraits depending on the relations between $x^*, \hat{x}$ and K. See Figure 1 for phase portraits of the various cases.

As we can see from the phase portraits the cases 4, 5 and 6, where $\hat{x} > K$ holds, are rather uninteresting. If the carrying capacity for the prey in the logistic growth-dynamics is smaller than the refuge size $\hat{x}$, then all orbits in the interior converge to $(K, 0)$. This makes sense from a biological point. If the prey can't grow over a certain point due to biological restraints and they are still all inside the refuge, then it's impossible for the predators to hunt the prey and the predators will die out. Case 3 is somewhat similar with all orbits, beside the y-axis, converging to $(K, 0)$. In this case the biological explanation for the bad performance of the predators lies in their need for extremely high densities of prey for positive growth. These densities though are not possible for the prey to sustain under the dominant biological conditions embodied in the logistical growth capacity K.

The cases 1 and 2 are somewhat more complicated. We will begin with Case 2 and the stability of the equilibrium (x^*, y^*).

2.1 Case 2

In case 2 we have $x^* < K$ and $0 < \hat{x} < x^*$, which implies $e > dh$. We linearize the vector field at the equilibrium (x^*, y^*) and calculate the entries for the Jacobi-matrix. Since $x^* > \hat{x}$ holds this has been done before, e.g. in [4], [6].

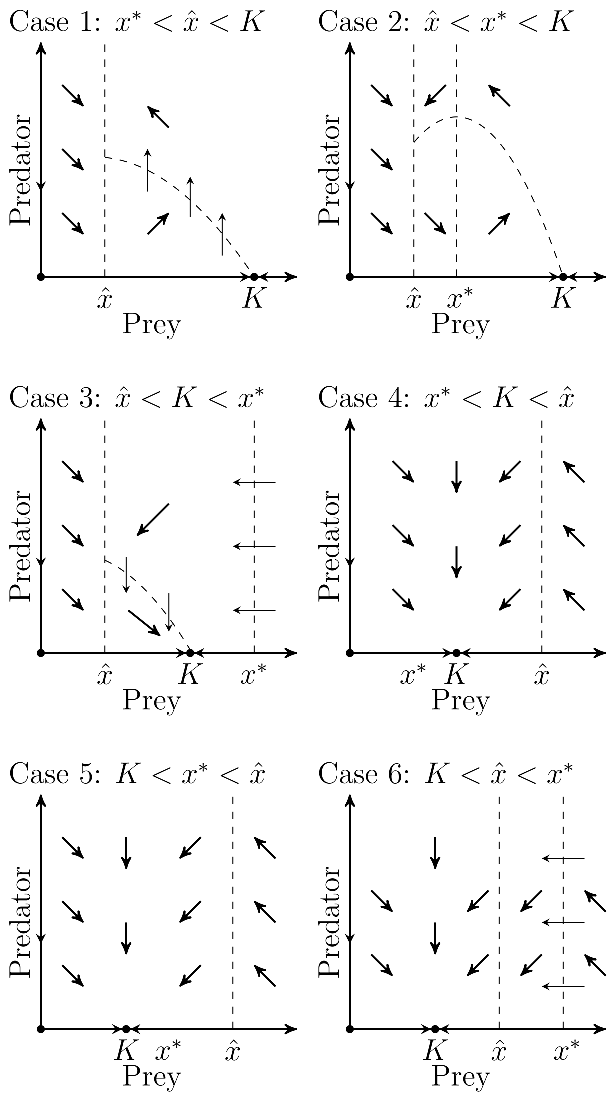

Figure 1: We have to differentiate various cases depending on the relation between $x^*, \hat{x}$ and K.

$$\begin{aligned}
\frac{\partial \dot{x}}{\partial x} &= r(1-\frac{x}{K}) - \frac{rx}{K} - \frac{y(s(1+hsx)-sxhs)}{(1+hsx)^2}\\
\frac{\partial \dot{x}}{\partial y} &= -\frac{sx}{1+hsx}\\
\frac{\partial \dot{y}}{\partial x} &= -d + \frac{esx}{1+hsx}\\
\frac{\partial \dot{y}}{\partial y} &= \frac{ey(s(1+hsx)-sxhs)}{(1+hsx)^2}
\end{aligned}$$

We evaluate the Jacobi-matrix for the equilibrium.

$$M = \begin{pmatrix} M_{11} & M_{12} \\ M_{21} & M_{22} \end{pmatrix} = \begin{pmatrix} \frac{\partial \dot{x}}{\partial x} & \frac{\partial \dot{x}}{\partial y} \\ \frac{\partial \dot{y}}{\partial x} & \frac{\partial \dot{y}}{\partial y} \end{pmatrix}\Bigg|_{(x^*,y^*)} = \begin{pmatrix} -\frac{dr(e+dh+hKs(dh-e))}{eKs(e-dh)} & -\frac{d}{e} \\ r(e-dh-\frac{d}{Ks}) & 0 \end{pmatrix}$$

We calculate the determinant of M:

$$\mathrm{Det}(M) = -M_{21}M_{21} = \frac{dr}{e}(e-dh-\frac{d}{Ks}) > 0 \Leftrightarrow Ks(e-dh) > d.$$

We are in Case 2 so $x^* < K$ holds:

$$x^* < K \Leftrightarrow \frac{d}{s(e-dh)} < K \Leftrightarrow d < Ks(e-dh).$$

The determinant is positive. We know that the determinant of a matrix is the product of its eigenvalues, $\mathrm{Det}(M) = \lambda_1\lambda_2$, and from this follows $\lambda_1\lambda_2 > 0$, so both eigenvalues have the same sign (if we had a complex eigenvalue the second eigenvalue would be its complex conjugated and it would have the same real part). We know the trace of M

$$\mathrm{Tr}(M) = -\frac{dr(e+dh+hKs(dh-e))}{eKs(e-dh)} > 0 \Leftrightarrow e+dh+hKs(dh-e) < 0.$$

The Routh-Hurwitz-Criterion tells us $Re(\lambda_1) < 0 \wedge Re(\lambda_2) < 0 \Leftrightarrow \mathrm{Tr}(M) < 0 \wedge \mathrm{Det}(M) > 0$. This means in this case: $Re(\lambda_{1,2}) < 0 \Leftrightarrow \mathrm{Tr}(M) < 0$ or that the equilibrium is asymptotically stable if and only if $\mathrm{Tr}(M) < 0$ (or $e + dh > (e-dh)hKs$).

For the further analysis of our system we need to know a few things about the Gause-model. Cheng showed in 1981 that the limit cycle is unique and exists if the equilibrium (x^*, y^*) is unstable [1]. The paper of Hsu, Hubbell and Waltman [6] shows that the equilibrium (x^*, y^*) is globally asymptotically stable if $\mathrm{Tr}(M) \leq 0$. See also [4], chapter 4.3, for further details.

Let us assume the equilibrium to be stable.

Case 2a: Case 2 with a stable equilibrium ($\mathbf{Tr}(M) \leq 0$)

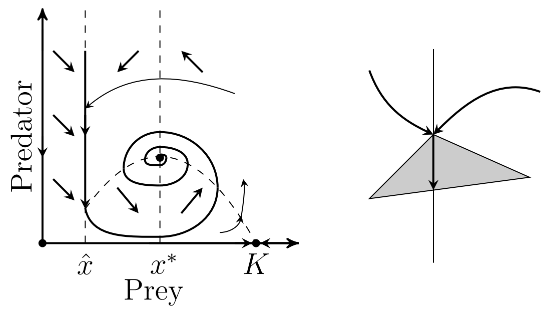

Figure 2: On the left side: Case 2 with a stable equilibrium. This will be case 2a. On the right side: A depiction of the Filippov-Cone on the $\hat{x}$-line.

Case 2a is rather simple. All orbits starting in (S1) will sooner or later hit the $\hat{x}$-line. The orbits starting in (S2) which don't hit the $\hat{x}$-line can only converge to (x^*, y^*) because it's the only attractor in (S2). Convergence to $(K, 0)$ is not possible because it is a saddle point with its stable manifold on the x-axis. Now the orbits in (S2) which do hit the $\hat{x}$-line will do so above the x-isocline because the dynamic below it is away from the $\hat{x}$-line. At the $\hat{x}$-line and above the x-isocline we have the dynamics in both (S1) and (S2) pointing towards the $\hat{x}$-line and so the dynamics will collide at the $\hat{x}$-line. Following the theory of Filippov for discontinuous ODEs we will look at the cone which is spanned by the vectors of the two colliding orbits. The cone will intersect with the $\hat{x}$-line and starting from the cone end the $\hat{x}$-line will continue through the body of the cone. See Figure 2.2 for clarification.

The orbits collide at the $\hat{x}$-line and "merge" there into one orbit. Corresponding to Filippov the cone represents the possible directions the orbit can take. Theoretically all directions contained in the cone are possible, but if we look at the dynamics in (S1) and (S2) we see that the orbits there point towards the $\hat{x}$-line. Therefore the orbit can't continue into (S1) or (S2). But the orbit can continue on the $\hat{x}$-line, which is also contained in the cone. The orbit will now follow the discontinuity between (S1) and (S2) until it either hits an equilibrium or the dynamics in (S1) or (S2) no longer point in the direction of the $\hat{x}$-line.

In our subcase 2a we have no equilibrium on the $\hat{x}$-line because the dynamics above the x-isocline always point downwards in both (S1) and (S2) and so we will always have a cone showing downwards. Below we x-isocline we have the dynamics in (S2) pointing away from the $\hat{x}$-line. So, the merged orbit will leave the $\hat{x}$-line after it has crossed the x-isocline. Starting from this point - let us call it x_0 - it can't hit the $\hat{x}$-line again. Let us assume that it would hit the $\hat{x}$-line again. To show that this is impossible, we have to observe this orbit in (S2) alone, which means that in all of $\mathbb{R}^2_+$ (S2) holds. If this orbit now hits the $\hat{x}$-line again, it also has to hit the x-isocline again, but necessarily to the "left" side of x_0, otherwise it wouldn't follow the dynamics in (S2). This orbit would then have to continue to spiral away from the equilibrium, but this is in contradiction to the paper of Hsu, Hubbell and Waltman [6], which states that if the equilibrium in (S2) is stable, it is globally asymptotically stable. We see that the orbit doesn't hit the $\hat{x}$-line again and spirals inwards towards the equilibrium. Hence all orbits in our model will converge to (x^*, y^*).

Case 2b: An unstable equilibrium (Tr$(M) > 0$)

Now, if we assume the equilibrium to be unstable, we know that we would have a limit cycle in the (S2) system due to Poincaré-Bendixson. We can now distinguish 2 subcases depending on if the limit cycle is hit by the $\hat{x}$-line or not.

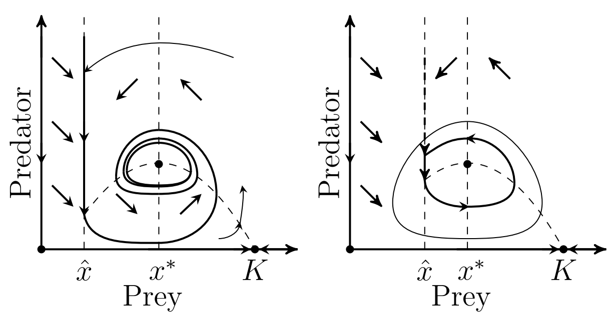

Figure 3: Case 2 with an unstable equilibrium this time. We have to distinguish between the case where the $\hat{x}$-line "cuts" the limit cycle (the right picture) and the case when it does not (the left one). The thin line in the left picture shows the limit cycle if it hadn't been cut by the $\hat{x}$-line.

The first of these two cases is similar to case 2a. We already know the dynamics on the $\hat{x}$-line because the situation is the same as in 2a. So we have all orbits reaching the (S2) system. In (S2) we have only the equilibrium (x^*, y^*) and the limit cycle as potential attractors. Due to (x^*, y^*) being unstable we know that all orbits can only converge to the limit cycle.

Now, if the limit cycle is hit by the $\hat{x}$-line we have a somewhat different dynamic in (S2). Like before we have the orbit starting just below the point where the $\hat{x}$-line intersects with the x-isocline - let us refer to this point as $(\hat{x}, y_{iso})$. Contrary to the subcase before this time the orbit is spiraling away from (x^*, y^*) and therefore it will hit the $\hat{x}$-line again. Considering the dynamics on the $\hat{x}$-line the orbit will take a path that will again lead it to $(\hat{x}, y_{iso})$ and repeat it's way from there on. We get a periodic orbit. It is easy to see that all the other orbits in (S2) will eventually lead into the $\hat{x}$-line and from there into this periodic orbit. It is so to speak by default stable and attracting and because the equilibrium is unstable, it's the only attractor in our subcase. All orbits will ultimately merge with this "limit cycle".

2.2 Case 1 ($x^* < \hat{x} < K$)

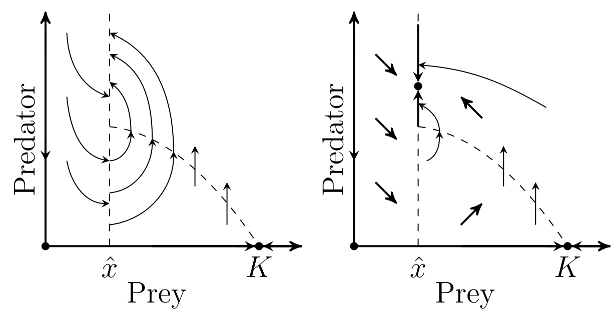

Figure 4: Case 1.

The difference to case 2 is that we have no equilibrium in the discontinuous vector field, so where do the orbits in the interior converge to? All orbits in (S1) and (S2) will hit the $\hat{x}$-line. Below $(\hat{x}, y_{iso})$ the $\hat{x}$-line is clearly semi permeable from left to right, but above it both the dynamics in (S1) and (S2) point towards it. Let us look at the point $(\hat{x} + \epsilon, y_{iso})$. For $\epsilon \to 0$ we get in (S2) an arbitrarily big positive slope, while the slope in (S1) has at a certain fixed value at $(\hat{x}, y_{iso})$. Following the Filippov approach for such discontinuous ODEs we get the dynamics on the $\hat{x}$-line pointing upwards at $(\hat{x}, y_{iso})$. Now if we look at the equations for (S1) and (S2) for $(\hat{x}, c)$ with $c \in \mathbb{R}$ and c arbitrarily large, we have a very steep slope in (S1) and a rather moderate positive slope in (S2). Following Filippov again we get the dynamic at $(\hat{x}, c)$ pointing downwards. To understand what is happening on the $\hat{x}$-line we need the following definition first.

Definition. Filippov equilibrium. We call a point F a Filippov equilibrium if 0 is in its Filippov cone and therefore $x(t) \equiv F$ is a Filippov solution.

Now let us see where the orbits collide in a way that we get something like an equilibrium on the $\hat{x}$-line. In (S1) we get a vector $f_1 = (r\hat{x}(1-\hat{x}/K), -dy)$ and in (S2) $f_2 = (r\hat{x}(1-\hat{x}/K) - ys\hat{x}/(1+hs\hat{x}), y(-d+es\hat{x}/(1+hs\hat{x})))$. These two vectors now span a cone $C = \{\alpha f_1 + (1-\alpha) f_2,\ \alpha \in [0,1]\}$. The tangential vector for the orbit will lie in this cone and will be realized for a certain α, i.e. $f^C = (\alpha r\hat{x}(1-\hat{x}/K) + (1-\alpha)(r\hat{x}(1-\hat{x}/K) - ys\hat{x}/(1+hs\hat{x})), \alpha(-dy) + (1-\alpha)(y(-d+es\hat{x}/(1+hs\hat{x}))))$ for a certain $\alpha \in [0,1]$. We have to consider that the orbits on this part of the $\hat{x}$-line have to stay on the $\hat{x}$-line. Hence the movement in the x-direction is 0, i.e. $\dot{x} = 0$, so the direction in C which will eventually be taken, i.e. f^C, has a first entry of 0. We see:

$$\begin{aligned}
&\alpha r\hat{x}(1-\hat{x}/K) + (1-\alpha)(r\hat{x}(1-\hat{x}/K) - \frac{ys\hat{x}}{1+hs\hat{x}}) = 0 \Leftrightarrow \\
&r\hat{x}(1-\hat{x}/K) = (1-\alpha)\frac{ys\hat{x}}{1+hs\hat{x}} \Leftrightarrow \\
&\alpha = 1 - \frac{r(1-\hat{x}/K)(1+hs\hat{x})}{sy}.
\end{aligned}$$

We now know the value of α and can insert it into f^C

$$f^C = (0, -dy + \frac{er(K-\hat{x})\hat{x}}{K}).$$

We have a Filippov equilibrium exactly if $f^C = (0,0)$, because then no motion is happening at that point.

$$f^C = (0,0) \Leftrightarrow y = \frac{er(K-\hat{x})\hat{x}}{dK} := \hat{y}$$

We do know from our graphical considerations that $\hat{y}$ has to lie somewhere above y_{iso}, but we can also show this analytically.

$$\begin{aligned}
&\hat{y} > y_{iso} \Leftrightarrow \frac{er(K-\hat{x})\hat{x}}{dK} > \frac{r}{Ks}(K-\hat{x})(1+hs\hat{x}) \Leftrightarrow \frac{e\hat{x}}{d} > \frac{1}{s}(1+hs\hat{x}) \Leftrightarrow \\
&es\hat{x} > d(1+hs\hat{x})
\end{aligned}$$

We know that for case 1 holds $x^* < \hat{x}$.

$$\frac{d}{s(e-dh)} < \hat{x} \Leftrightarrow d < es\hat{x} - dhs\hat{x} \Leftrightarrow d(1+hs\hat{x}) < es\hat{x}$$

We have shown that we always have exactly one Filippov equilibrium in case 1 which is attracting all orbits in the interior of $\mathbb{R}^2_+$. So $(\hat{x}, \hat{y})$ is actually an attracting Filippov equilibrium.

One might ask if $(\hat{x}, \hat{y})$ is reached in finite time. Every orbit will eventually hit the $\hat{x}$-line in finite time. If the orbit hits $(\hat{x}, \hat{y})$ directly, without taking a detour on the $\hat{x}$-line, the orbit will reach $(\hat{x}, \hat{y})$ in finite time. All other orbits in the interior of $\mathbb{R}^2_+$ will hit the $\hat{x}$-line in finite time, but they might not hit $(\hat{x}, \hat{y})$ in finite time. Let us look at the situation on the $\hat{x}$-line. Following the considerations before we know the movement in the x-direction is zero, i.e. $\dot{x} = 0$, and the movement is described by $f^C = (0, -dy + \frac{er(K-\hat{x})\hat{x}}{K}) = (0, -d(y + \hat{y}))$. Hence we have for the movement the equations

$$\begin{aligned} \dot{x} &= 0 \\ \dot{y} &= -d(y - \hat{y}) \end{aligned} \tag{5}$$

which are easily and explicitly solvable. We can ignore the x-direction for obvious reasons and look at the solution for the y-direction

$$y(t) = \hat{y} + e^{-dt}c \tag{6}$$

with a certain constant c depending on the initial conditions. Therefore almost all orbits will need infinitely long until they converge to $(\hat{x}, \hat{y})$.

Between case 1 and case 2

Another question that might be raised is what happens at the border case between case 1 and case 2 when $\hat{x}$ and x^* coincide. In Figure 5.1 we see the rough directions that every orbit will take and it is obvious that every one of them will eventually hit the $\hat{x}$-line above the x-isocline. The main difference between this border case and case 1 is the fact that the orbits above the x-isocline hit the $\hat{x}$-line at exactly 90°. This is because the y-isocline is overlapping with the $\hat{x}$-line.

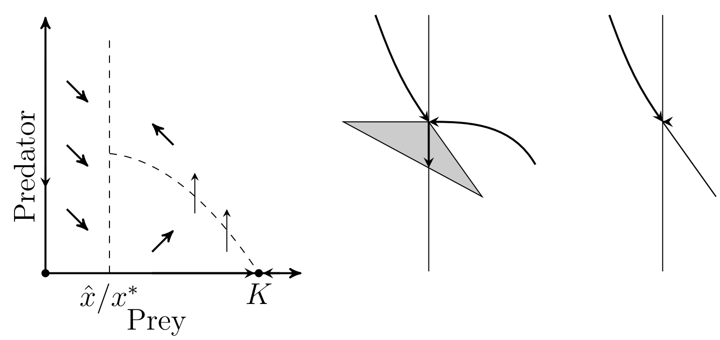

Figure 5: On the left: The rough directions of the orbits if $\hat{x}$ is equal to x^*. In the middle: The corresponding Filippov cone on the $\hat{x}$-line for $y > y_{iso}$ for this case. On the right: The Filippov Cone on the $\hat{x}$-line for $y = y_{iso}$.

Now if the orbits hit the $\hat{x}$-line at 90° the Filippov cone will be different from before. Let us take a random point on the $\hat{x}$-line above $(\hat{x}, y_{iso})$ and look at the Filippov cone there. f_2 is the vector for (S2) and it will point into (S1) exactly horizontally. f_1 will point slightly downwards, therefore the cone will point downwards as depicted in Figure 5.2. With the same argument we have used before we know that the dynamic has to stay on the $\hat{x}$-line and therefore the dynamics on the $\hat{x}$-line above $(\hat{x}, y_{iso})$ will point down towards $(\hat{x}, y_{iso})$. If we approach $(\hat{x}, y_{iso})$ on the $\hat{x}$-line, f_2 will become less and less pronounced, until its length becomes 0 when we reach $(\hat{x}, y_{iso})$. The Filippov cone will then have an area of 0 (Figure 5.3). In fact we can calculate the cone and get $C = \{\alpha f_1 : \alpha \in [0,1]\}$, because $f_2 = 0$ at $(\hat{x}, y_{iso})$. We see that $0 \in C$ and therefore $x(t) = (\hat{x}, y_{iso})$ is a solution. The orbit stays at $(\hat{x}, y_{iso})$. $(\hat{x}, y_{iso})$ is a Filippov equilibrium and because it is the only possible attractor left all interior orbits will eventually converge towards it. We see that if $\hat{x} = x^*$ holds $y_{iso} = y^* = \hat{y}$ also holds.

A Hopf bifurcation between case 2 and case 1

Let us assume that we are in case 2b with a fixed value for x^* and we let $\hat{x}$ grow from 0 to a value greater than x^*. At the beginning we have a limit cycle as our main attractor. At first the limit cycle won't be influenced by the growth of $\hat{x}$, but when the value of $\hat{x}$ grows big enough that the $\hat{x}$-line intersects with the limit cycle, it will start shrinking (Figure 3). When the value of $\hat{x}$ has reached the value of x^* we are in our border case and we know that the limit cycle has shrunk to a point. If we plot the value of $\hat{x}$ and the attractor we see that we have a supercritical Hopf bifurcation.

We don't get a Hopf bifurcation if we start in case 2a instead of 2b. The equilibrium will only move up the $\hat{x}$-line if $\hat{x}$ has grown greater than x^*.

We have now identified all possible cases for our model and analyzed every one of them so that we can understand their behaviour. But we can even do a bit more than that. We have always assumed the equations (2) and (3) to hold. But if we let that drop and just assume the general Gause-model we can do the following bit:

2.3 The General Case

We will have a short look and see what happens when we switch from the equations we have used until now, to the general case of the Gause model. First we need to know, what we are actually talking about. The general Gause model is defined by the following equations

$$\begin{aligned} \dot{x} &= x\ g(x) - y\ p(x) \\ \dot{y} &= y(-d + q(x)) \end{aligned} \tag{7}$$

with these restrictions:

- $g(x) > 0$ if $0 < x < K$; $g(K) = 0$; $g(x) < 0$ if $x > K$

- $p(0) = 0$; $p(x) > 0$ if $x > 0$
- $q(0) = 0$; $q(x) > 0$, $q'(x) > 0$ if $x > 0$.

The term $xg(x)$ describes how the prey would behave in the absence of predators. It is easy to see that it would converge towards $(K, 0)$. If there are predators around they will reduce the prey by $p(x)$ each. Therefore $yp(x)$ describes the total loss of prey due to predators. Predators are only killed by their natural demise which is described by $-yd$. A certain percentage dies in each fraction of time but they can increase by transforming the biomass of the prey caught into predators. This is described by $+yq(x)$.

The equations (7) hold to the "right" side of our discontinuity the $\hat{x}$-line and will be (S2) for the rest of 2.3. On the "left" side of the $\hat{x}$-line we have the refuge for the prey and therefore the equations for (S1) look like this:

$$\begin{aligned} \dot{x} &= x\ g(x) \\ \dot{y} &= -d\ y. \end{aligned} \tag{8}$$

There is no loss term for the prey anymore due to the absence of predators. The predators on the other hand can no longer repopulate because they find no prey. The only term left is the constant loss term d. Therefore the predators experience exponential decay and will decrease until the prey has repopulated enough, so that they have to leave the refuge and become potential food for the predators. We're back in (7).

The main difference to a specialized case of the Gause-model is that we can no longer assume that only one limit cycle is possible in (S2). We may have multiple limit cycles - [5] - or maybe none. We still have one equilibrium in $\mathbb{R}^2_+$ though, which lies in the interior of the limit cycles, if they exist.

We can distinguish placement of x^*, $\hat{x}$ and K as before as case 1 to 6. The value of x^* now depends on $q(x)$, but for all practical purposes we can ignore this. x^* may now just refer to the x-value of the equilibrium. For case 3 to 6 almost nothing changes and all orbits converge to $(K, 0)$. In case 1 and 2 the equilibria in $(K, 0)$ and $(0, 0)$ are unstable and therefore not relevant as attractors. Due to the behaviour on the axes it is also impossible that there might be limit cycles around these equilibria. No further equilibrium, besides $(K, 0)$ and $(0, 0)$, away from the $\hat{x}$-line exists. If we look at case 1 we see that almost no changes appear. We can refer to Figure 4 and recognize that no relevant aspect changes. All orbits will converge to an equilibrium on the $\hat{x}$-line above the x-isocline. There is the theoretical possibility that there might be multiple equilibria on the $\hat{x}$-line though.

We have seen that we can switch to the general Gause model without major changes in the dynamics, in case 1 as well as case 3 to 6. Case 2 is slightly different.

If we assume that there are no limit cycles for system (S2) the case looks just as our non-general case 2 for a stable equilibrium before and all orbits have to converge to the equilibrium in the interior. The dynamics look just as in Figure 2. If we have exactly one limit cycle it looks like the non-general case 2 for an unstable equilibrium. We can then refer to Figure 3. If we assume multiple limit cycles we see in the following figure that there is an interesting effect.

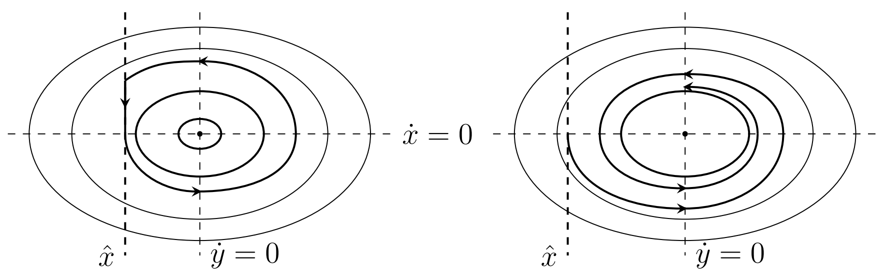

Figure 6: The general case 2. The left picture shows what happens when the biggest "intact" limit cycle is repelling. In the right picture it is attracting.

In case 2b we knew that there is exactly one limit cycle and that it had to be attracting, because there is no other limit cycle and all the equilibria are unstable. The general case 2 is more complicated because the number of limit cycles isn't restricted here. Let us assume that we have multiple, but only finitely many, limit cycles. Some of those may intersect with the discontinuity on the $\hat{x}$-line and some don't. If one limit cycle doesn't intersect with the $\hat{x}$-line it won't be disturbed by the discontinuity and adding the refuge will not have any influence on it. The same thing holds for its interior, because the interior of a limit cycle in two dimensions is invariant. Therefore the area inside the biggest "intact" limit cycle will not be changed. Limit cycles that intersect with the $\hat{x}$-line will obviously change. For these limit cycles we can refer to the argument used for case 2b. Like there, all these orbits will eventually hit the $\hat{x}$-line from where they will continue towards $(\hat{x}, y_{iso})$. The further fate of an orbit passing through $(\hat{x}, y_{iso})$ depends on the system (S2). We have one limit cycle which intersects with the $\hat{x}$-line and lies in the interior of all other limit cycles that intersect with the $\hat{x}$-line. Let this limit cycle be referred to as C_{in}. The biggest limit cycle in (S2) which doesn't intersect with the $\hat{x}$-line shall be referred to as C_{no}. The area between these two limit cycles would - if we had only the system (S2) - either converge towards C_{in} or C_{no} due to the absence of any other attractor. If it converges towards C_{in} we get an additional limit cycles just like in case 2b (3.2) and depicted in 6.1. If the area would converge to C_{no} we use the argument from case 2b again and we see that we get an additional limit cycle (6.2) and all of the intersected orbits will converge towards C_{no}.

3 A Non-Constant Refuge

In the paper by Gause we can read: "The threshold has in no way a firmly fixed value, but depends upon the concentration of [the prey]" [3, p.11]. And he goes on to tell us, that we don't actually have a constant refuge for the prey but it depends on the amount of prey and predators present and "consequently the [refuge-size], intrinsically accompany the interaction between [predator] and [prey]" [3, p.11]. Following this argument we will drop the assumption of a constant refuge, but for the sake of simplicity we will assume the discontinuity to be a line. In accordance with Gause we assume the slope of the line negative. This also agrees with the following consideration: If we have a certain amount of prey, they will be safer with few predators around. If the amount of predators would spontaneously increase, the prey would have a harder time to hide or run from them. So we can assume the refuge to be restricted by the line

$$L : y = \bar{k}(x - \hat{x}), \qquad \hat{x} > 0,\ \bar{k} < 0. \tag{9}$$

We will further assume that L intersects the x-axis to the "left" of $(K, 0)$. The form of L tells us that L intersects the x-axis at $(0, \hat{x})$. Hence $\hat{x} < K$ holds. We want L to intersect the x-axis to the "left" of $(K, 0)$ so that we get only one intersection of L and the x-isocline. Failing this the refuge for the prey would be bigger than the carrying capacity K.

The L-line will now divide between systems (S1) and (S2) as shown in Figure 7.1 and we will distinguish between case a - Figure 7.2 - and b - Figure 7.3, depending on whether the equilibrium of (S2) lies above or below L.

Our main interest lies in figuring out where the orbits converge to. We already know everything about the existence and stability of equilibria in (S1) and (S2), but nothing about the possible Filippov equilibria on L. We have to prove or disprove the existence of Filippov equilibria on L and analyze their stability, if they exist. Later on we will deal with the question about possible limit cycles.

3.1 Equilibria on L

Case a

Now in case a the dynamics in (S1) and (S2) never point directly on each other or exactly away from each other on L, so it's obviously not possible to actually get a Filippov equilibrium on L. One can easily see that by examining Figure 7.2. We know that there is no equilibrium in the interior of (S1) and exactly one in (S2). Therefore, we know that the only equilibrium in $\mathbb{R}^2_+$ lies in (S2) and it's location is already known due to considerations from the last chapter.

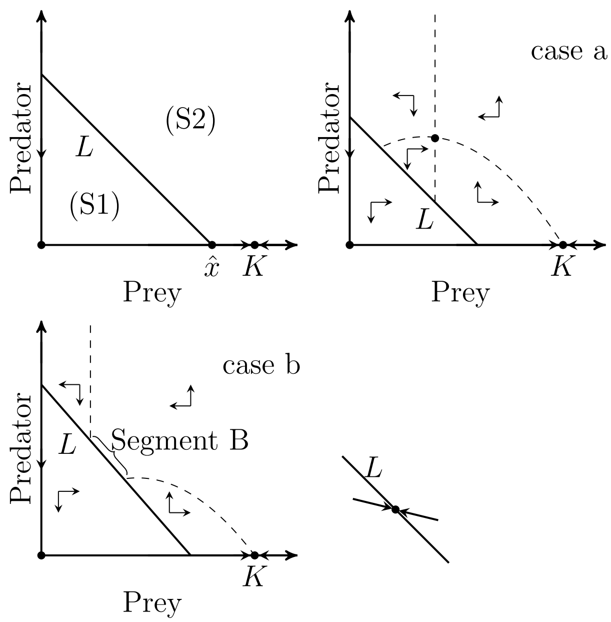

Figure 7: The top-left picture (Figure 7.1) shows us clearly where system (S1) and (S2) relative to L are. The top-right picture (Figure 7.2) gives us case a, where the equilibrium of (S2) is not cut out by L. The bottom-left (Figure 7.3) gives us case b where the equilibrium of (S2) is no longer existent but overlapped by (S1). The bottom-right picture (Figure 7.4) gives us the case where orbits on both sides of L are pointing towards it and that at the same angle, therefore at that point is a Filippov equilibrium.
The arrows in the figures show us the range of the directions of the vector field.

Case b

Case b is slightly more complicated. We see from Figure 7.3 that an equilibrium is only possible in segment B, because only there can the orbits point directly at each other or exactly away from each other. We will compare the slopes in (S1) and (S2) at L to see if we get a Filippov equilibrium. The slope in (S1) is given by the equation

$$k' = \frac{\dot{y}}{\dot{x}} = \frac{-yd}{rx(1 - x/K)} \tag{10}$$

and in (S2) by

$$k'' = \frac{\dot{y}}{\dot{x}} = \frac{y(-d + e\frac{sx}{1+hsx})}{rx(1 - x/K) - y\frac{sx}{1+hsx}}. \tag{11}$$

We need to find the points where the slopes in (S1) and (S2) point directly at each other or exactly away from each other on L. So, we need to find the points on L where $k' = k''$ holds. This might seem counterintuitive at first glance, but we can justify it.

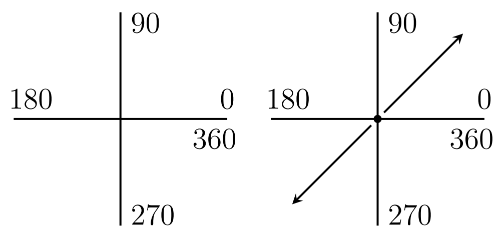

Figure 8: The left picture shows us how angles are seen in this work. The right one shows a point on L with the orbits in (S1) and (S2) respectively pointing away from each other and therefore creating a Filippov equilibrium. The difference in angles is exactly 180°.

Let us assume a point lies on L and is a Filippov Equilibrium. This point has vectors v_1 and v_2 pointing into (S1) and (S2), which can be described by angles, but also by slopes. Without loss of generality we can assume that these vectors have a length of 1. Let us say one of these vectors has an angle of l degrees. To get a Filippov equilibrium the vector in the other system would have to be off from l by exactly 180°. If we look at Figure 8.2 we see that both these vectors have exactly the same slope. Hence the equation $k' = k''$.

Let us assume this point isn't a Filippov Equilibrium. Let the vectors v_1 and v_2 be identical angles, therefore they would also have the same slope and the equation $k' = k''$ holds. The troublesome aspect lies in the fact that when we calculate the slope of a point we can't be sure if the corresponding vector has an angle of $x°$ or $(x+180)°$.

We know that if a point on L is a Filippov equilibrium the equation $k' = k''$ has to hold, but it is only a necessary, not a sufficient condition.

We insert the equations (10) and (11) into $k' = k''$ and get

$$\frac{-dy}{rx(1-\frac{x}{K})} = \frac{-dy + ef(x)y}{rx(1-\frac{x}{K}) - yf(x)}$$

$f(x)$ is short for $\frac{sx}{1+hsx}$ for the sake of lucidity. If we rearrange this equation we get:

$$\begin{aligned} -dy(rx(1-\frac{x}{K})) + df(x)y^2 =& - dy(rx(1-\frac{x}{K})) + ef(x)(rx(1-\frac{x}{K}))y \Leftrightarrow \\ df(x)y =& ef(x)(rx(1-\frac{x}{K})) \Leftrightarrow \\ y =& \frac{erx}{d}(1-\frac{x}{K}). \end{aligned} \tag{12}$$

If we plot (12) we get a parabola (Figure 9) intersecting the x-axis at $(0,0)$ and $(K,0)$. We know that L intersects the x-axis at $(\hat{x},0)$ and because $\hat{x} < K$ holds there is exactly one intersection of L and (12) in $\mathbb{R}^2_+$. Let this intersection be called F.

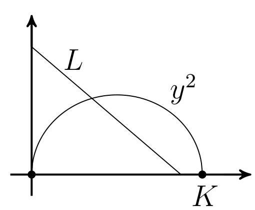

Figure 9: The Plot of (12) with L added to it.

(12) describes the points where $k' = k''$ holds. Therefore there is exactly one point on L where $k' = k''$ holds and it is the only possible Filippov equilibrium. We can't be completely sure that F is a Filippov equilibrium though. It might be that the vectors at F into (S1) and (S2) are identical and not apart by 180°. Like we stated before we can't rule out this possibility only because $k' = k''$ holds.

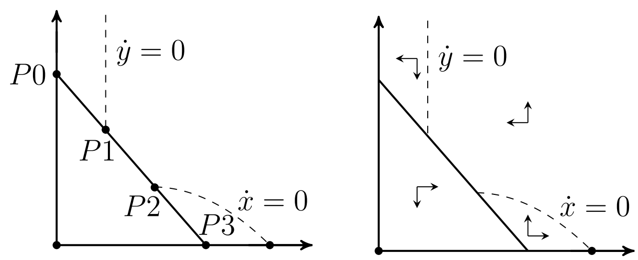

Figure 10: The left picture splits L into various parts depending on the direction of the orbits there. The arrows in the left picture show the direction of the orbits determined by their position relative to the isoclines.

But we can rule this possibility out if we consider the rough directions the orbits take in (S1) and (S2) along L. If we look at Figure 10.2 we see that all orbits in (S1) have a direction somewhere in the interval $[270°, 360°]$, which entails a negative slope. In (S2) the situation is slightly more complicated. Between $P0$ and $P1$ the orbits take a direction somewhere between $[180°, 270°]$, between $P1$ and $P2$ the interval is $[90°, 180°]$ and between $P2$ and $P3$ it's $[0°, 90°]$. The first thing we see is that between $P0$ and $P1$ as well as $P2$ and $P3$ the slope is positive. Because the equation $k' = k''$ can't hold if one value is positive and the other negative, F has to lie between $P1$ and $P2$. The angle for the vector v_1 for (S1) at F lies in the interval $[270°, 360°]$, the angle for v_2 lies in $[90°, 180°]$. Therefore the angles can't be identical and because the equation $k' = k''$ holds at F the slope for v_1 and v_2 is the same. We see that v_1 and v_2 are apart by $180°$ and hence F is a Filippov equilibrium.

We have shown the following theorem:

Theorem 1. *Let L be a line with a negative slope, where the dynamics on the "lefthand" side are defined by* (2) *and on the "righthand" side by* (3)*, then there exists an equilibrium in the interior of $\mathbb{R}^2_+$ and it is unique.*

We don't know if F is an attracting Filippov Equilibrium or not though. We will return to that question later on. First we want to create a tool that will help us in the handling of the classification of all the cases and their attractors, as well as the question of the stability of F.

3.2 Attracting and repelling segments on L

Attracting and repelling segments on L for (S1)

If we take a arbitrary orbit in (S1) it will sooner or later collide with L due to the invariance of the axes. We want to know what segments on L this orbit could hit and if there are multiple of them.

In (S1) the slope of the vector field at $L \cap y$-axis is -∞ or 270°. At $L \cap x-$axis it's 0 or 0°. The slope changes continuously in (S1) along L. We even know the exact formula for it, by filling L into (10).

$$k' = \frac{-yd}{rx(1-x/K)} = \frac{-\bar{k}d(x-\hat{x})}{rx(1-x/K)}$$

Now if we differentiate this equation with respect to x we get

$$\frac{\partial}{\partial x}\frac{-\bar{k}d(x-\hat{x})}{rx(1-x/K)} = -\frac{dK\bar{k}(x^2+\hat{x}K-2\hat{x}x)}{r(K-x)^2x^2} := h(x) \tag{13}$$

The sign of $h(x)$ is controlled by $sgn(x^2+\hat{x}K-2\hat{x}x)$, because the denominator is strictly positive in $(0,K)$. We know that $-dK\bar{k}$ is positive, therefore if $sgn(x^2+\hat{x}K-2\hat{x}x)$ is positive in $(0,K)$, $h(x)$ is positive in $(0,K)$. The graph of the function $h(x)$ has to look like a scaled version of $x^2+\hat{x}K-2\hat{x}x$. We remember that $\hat{x} < K$ holds.

$$x^2+\hat{x}K-2\hat{x}x > x^2+\hat{x}^2-2\hat{x}x = (\hat{x}-x)^2 \geq 0$$

We have shown that (13) is strictly positive and therefore the slope of the vector field along L grows strictly monotonically. If we start at $L \cap y-axis$ and end at $L \cap x-axis$ we get a development from $-\infty$ to 0. Considering that $\bar{k}$ is negative we have one point where the value of the slope is exactly $\bar{k}$. We can distinguish between a segment where the slope is smaller than $\bar{k}$ before this point is hit, which we will call $S1an$, and a segment where the slope is bigger than $\bar{k}$, which we will refer to as $S1ab$. Figure 11 will make this clearer.

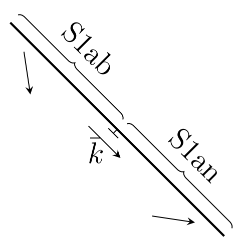

Figure 11: The picture shows the rough progress of the slope in (S1). Special emphasis is put unto the point with slope $\bar{k}$, which is symbolized by a nail-like symbol.

Every orbit in (S1) will eventually hit $S1an$. Every (S1)-orbit starting on $S1ab$ will head into (S1) but will sooner or later hit $S1an$.

We have shown:

Theorem 2. *The "attracting" segment $S1an$ and the "repelling" segment $S1ab$ on L exist and are unique.*

Attracting and repelling segments on L for (S2)

We have seen in Figure 11 that there exists one segment where the dynamics in (S1) is towards L called $S1an$ and one segment where the dynamics is away from L called $S1ab$. We will now show that there are similar segments on L for (S2), which we will call $S2an$ and $S2ab$. And we will then discuss how these segments determine the stability of the Filippov equilibrium.

We know that the slope in (S2) changes continuously, so if at one point on L the dynamics in (S2) is towards L then the dynamics in (S2) is towards L in a neighborhood of this point. From this we know that such an "attracting" segment $S2an$ has positive length. When $S2an$ ends, another segment has to start and due to there only being two possible kinds, the next segment has to be of type $S2ab$. With the same argument we know that $S2ab$ has positive size.

At the point $P0$ (Figure 10) the vector field is towards L so we have an $S2an$ segment there. At $P3$ the dynamic is away from L, so there is an $S2ab$ segment. We want to show that there is only one segment $S2an$ and $S2ab$ on all of L.

Similar to before we will calculate the slope in (S2) but this time we want to know which points in (S2) have a slope of exactly $\bar{k}$.

$$\begin{aligned}
&\bar{k} = \frac{\dot{y}}{\dot{x}} \Leftrightarrow \bar{k}\dot{x} = \dot{y} \Leftrightarrow \\
&\bar{k}rx(1 - \frac{x}{K}) - \bar{k}y\frac{sx}{1 + hsx} = -dy + ye\frac{sx}{1 + hsx} \Leftrightarrow \\
&\bar{k}hsrx(K - x)(\frac{1}{hs} + x) = y(\bar{k}sx - d(1 + hsx) + esx) \Leftrightarrow \\
&y = \frac{\bar{k}rx(x - K)(1 + hsx)}{Kd + Ksx(dh - e - \bar{k})} := R(x) \qquad (14)
\end{aligned}$$

If the segment-type changes from $S2an$ to $S2ab$ or the other way around then there will be a point in between those segments where the slope is exactly $\bar{k}$. We want to show that there is only one point on L where this is valid and therefore there is only one change from $S2an$ to $S2ab$. This would show that the segments $S2an$ and $S2ab$ are unique. For this we need to show that R intersects with L exactly once in $\mathbb{R}^2_+$. Let us call this our hypothesis for this chapter.

We can show this but we need to work quite a bit for it. First we need to fragment R into its denominator and numerator. We define them as

$$\bar{k}hsrx(x - K)(x + \frac{1}{hs}) := f_1 \qquad (15)$$

$$Kd + Ksx(dh - e - \bar{k}) := f_2. \qquad (16)$$

We are interested in the intersections of R and L. To compute them we need to solve $R = L$. We reshape this to

$$R = L \Leftrightarrow \frac{f_1}{f_2} = L \Leftrightarrow f_1 = Lf_2 \Leftrightarrow f_1 - Lf_2 = 0$$

f_1 is a third degree polynomial, $f_2 L$ is second degree and their difference third degree. Hence we need to find the zeros of a third degree polynomial. We can do this but the terms are rather unwieldy and don't tell us what we need to know. But we know that there are at most three of them and therefore that there are at most three intersections between L and R. This will help us prove our hypothesis.

We don't know for sure how R looks like exactly. But we know that it looks like f_1, whenever f_2 is strictly positive. We know that f_2 is strictly positive at 0 because Kd is positive, but we don't know if its zero $\frac{d}{(e-dh+\bar{k})s}$ - let us call it z_2 - is positive or negative. R will vary greatly depending on that (Figure 12.2 and 12.3).

If we plot f_1 it looks like Figure 12.1, because we know that it has zeros in $-\frac{1}{hs}, 0$ and K and it is positive for a small $\epsilon > 0$. We want to construct the rough plot of R through our knowledge of f_1 and distinction of cases of f_2.

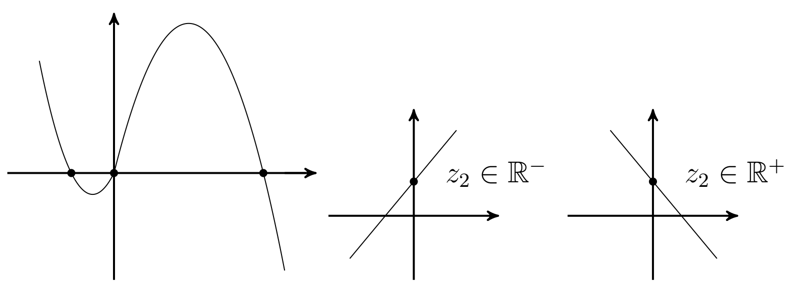

Figure 12: The very left picture shows the graph of f_1. The middle and the right picture show how f_2 looks like depending on the sign of z_2.

If we - for example - assume that $z_2 \in (\infty, -\frac{1}{hs})$, then R would have the opposite sign as f_1 in $(-\infty, z_2)$ and a pole in z_2. In (z_2, ∞) the plot of R would look like a scaled version of f_1. If we sketch that we get Figure 13.1. We see that there has to be at least one intersection of L and R in $\mathbb{R}^2_+$. We want to argue that the other two intersections are not on L. If we were to continue L on the rest of the plane it would intersect R somewhere in $[z_2, 0]$ - because R has a pole there and grows out of all bounds - and somewhere in $[K, \infty)$. One could argue that both L and R will go to $-\infty$ for $x \to \infty$ and therefore don't necessarily intersect, but R behaves roughly like a second degree polynomial while L is only linear and therefore they have to intersect. With this argument we have shown that two intersections lie away from $[0, K]$ and hence L and R can intersect only once in $[0, K]$. We see that there is one point on L where R holds and therefore only one transition from $S2an$ to $S2ab$.

The same has to be shown for the cases $z_2 \in (-\frac{1}{hs}, 0)$, $z_2 \in (0, K)$ and $z_2 \in (K, \infty)$ to complete the proof, but the argument is almost completely analogue and will therefore be omitted. One should only keep in mind that if $z_2 > 0$ holds the sign of R is opposite to f_1 for (z_2, ∞). Figure 13.2 - 13.4 should wipe away any lingering doubt.

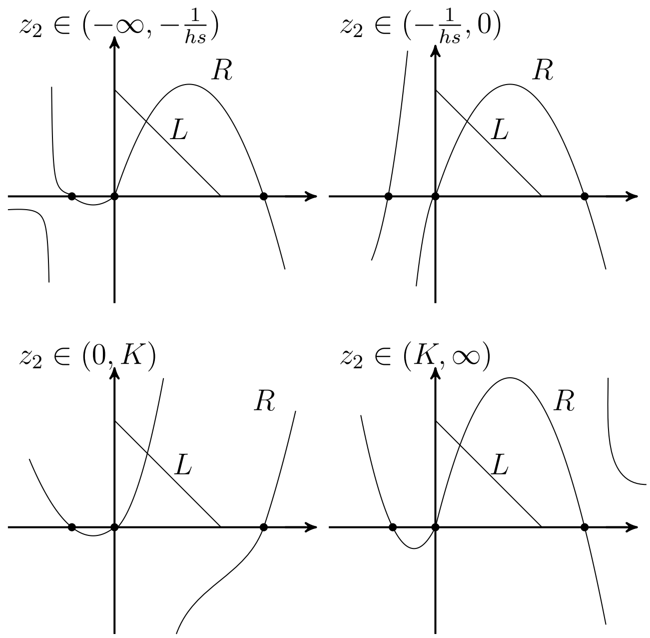

Figure 13: Rough sketches of R depending on the value of z_2. We see that L and R intersect.

There is also the possibility that $z_2 \in \{-\frac{1}{hs}, 0, K\}$ holds. But in this case R would be a second degree polynomial and could intersect with L at most twice. We know that at $L \cap y$-axis is an $S2an$-segment and at $L \cap x-$axis is an $S2ab$-segment, therefore the number of segment-changes - i.e. points of intersection - is odd. Neither zero nor two is odd and hence R intersects with L exactly once.

We have shown the following theorem:

Theorem 3. *The "attracting" segment $S2an$ and the "repelling" segment $S2ab$ on L exist and are unique.*

Now we will finally deal with the stability of F.

3.3 A Criterion for the Stability of F in Case b

We have shown that there is exactly one segment $S2ab$ and $S2an$ each. The same holds true for $S1ab$ and $S1an$. If we plot those segments along L we see, that either $S2an$ is contained in $S1ab$ or the other way around (excluding the situation where they are identical), because at $P0$ the dynamics in (S2) are towards L and in (S1) away from L.

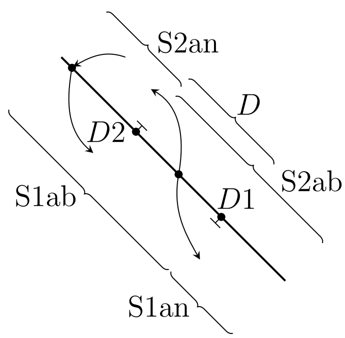

Figure 14: We have here an example where $S2an \subset S1ab$ holds. The segments $S1an$, $S1ab$, $S2an$, $S2ab$ and D are clearly shown. If we look at a point "left" of $D2$, and therefore outside of D, and the direction the orbits there take, we see that it can't be an equilibrium. We can now assume the equilibrium inside D. Due to the placement of $D1$ and $D2$ the orbits there lead away from it and hence the equilibrium is unstable.

We have a segment in between the points where the slope in (S1) and (S2) is exactly $\bar{k}$. Let us call this segment D. It's easy to see that the equilibrium on L can only be in this segment D, because only there can the dynamics in (S1) and (S2) point directly at each other, which is necessary for the equilibrium. If $S2an$ is contained in $S1ab$ the segment D is repelling and obviously so is the equilibrium. If it is the other way around, with $S1ab$ being contained in $S2an$, then the segment D is attracting and therefore also the equilibrium.

Theorem 4. *If $S2an \subset S1ab$ holds, F is unstable. If $S1ab \subset S2an$ holds, F is asymptotically stable.*

What we could use right now is a criterion for distinguishing between these cases and therefore determining the stability of the equilibrium. Luckily that is not such a complicated undertaking and we will go about it in the following way: We will find a formula for a function for all points in (S2) with a slope of $\bar{k}$ and one for (S1). These functions intersect with L exactly once each. Depending which intersection is further to the "right" or "left" the situation is that either $S2an$ is contained in $S1ab$ or $S1ab$ is being contained in $S2an$, which in turn determines the stability of the equilibrium.

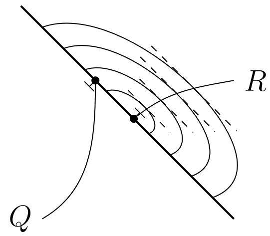

Figure 15: The graph R depicts all those points with a slope of $\bar{k}$. We can see that it crosses the orbits at all those points where the tangent with a slope of $\bar{k}$ intersects. The same holds true for Q, but this is left out for the sake of clarity. Here $D1$ is “left” of $D2$.

As before we calculate the points where $\frac{\dot{y}}{\dot{x}} = \bar{k}$ holds. Now if we fill in the equations for (S1) we get:

$$\frac{\dot{y}}{\dot{x}} = \bar{k} \Leftrightarrow -dy = \bar{k}\ rx(1 - x/K) \Leftrightarrow$$
$$y = -\frac{\bar{k}rx(1 - x/K)}{d} \qquad := Q(x)$$

We have already done so for (S2), but nevertheless

$$\frac{\dot{y}}{\dot{x}} = \bar{k} \Leftrightarrow -y(d - ef(x)) = \bar{k}\ (rx(1 - x/K) - yf(x)) \Leftrightarrow$$
$$y = \frac{-\bar{k}rx(1 - x/K)}{d + (-e - \bar{k})f(x)} = R(x).$$

Calculating the intersections for (S1)/Q respectively (S2)/R leads to rather unwieldy terms that will be omitted here, but it can easily be done. Following this approach we have a criterion for the stability of the equilibrium on L.

We have now finished with the preparations and can now start with the characterization and classification of the possible dynamics.

3.4 A Classification of the Dynamics

As the very first step we will talk about the dynamics close to the axes and very far away from them.

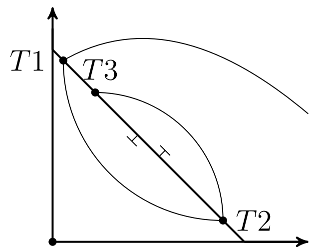

Figure 16: We have an Orbit starting far away from the axes and the equilibrium and see that it will converge somewhere closer to them. The nail-like symbols mark the transition between $S1ab$ and $S1an$ respectively $S2ab$ and $S2an$.

We know enough about our system (S2) to realize that the orbit of a point starting at the very "right" part of the $\mathbb{R}^2_+$-plane will eventually hit L. This intersection $T1$ will be in $S1ab$ and then $T2$ will be, if we started sufficiently far away, in $S2ab$. From there on the point $T3$ has to be in $S2an$ and further to the "right" on L than $T1$. This is because all orbits starting on L are to the "left" of $(K, 0)$. $(K, 0)$ has a unstable manifold starting there, which underlies the dynamics in (S2) and will eventually hit $S2an$. An orbit starting at $T2$ is fenced in by the unstable manifold and therefore $T3$ is further to the "right" than $T1$. From this all we see that the dynamics at the very edge will always point inwards. There has to exist an attractor because the orbits have to go somewhere and it has to lie somewhere "central". It is also possible that multiple attractors exist.

3.4.1 Case b

Let us begin with the classification of case b considering that it was the more recent case. We do know that we don't have an equilibrium in the interior of (S2), but one on L. We can now distinguish between two cases depending on the stability of the equilibrium.

Case b.1: $S2an \subset S1ab$

We will refer to this subcase as b.1. We already know from earlier considerations that the equilibrium lies somewhere between $D1$ and $D2$, as we have called those points where the slope in (S1) respectively (S2) is exactly $\bar{k}$. We also do know that the equilibrium is repelling due to $S2an \subset S1ab$.

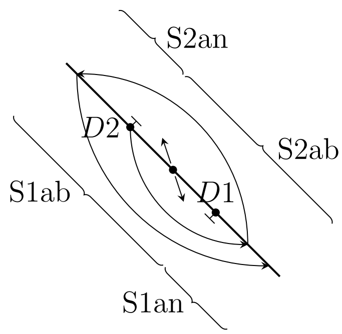

Figure 17: We know that $D2$ is "left" of $D1$ due to $S2an \subset S1ab$. The segments are clearly labeled and we can classify the dynamics from these assumptions.

We know that $S1ab$ will be mapped onto $S1an$, therefore an orbit starting at $D2$ will be mapped onto the interior of $S1an$. An orbit starting in $S2ab$ will be mapped onto $S2an$. Hence our orbit will continue from $S2ab$ and will be mapped onto $S2an$. $S2an$ lies to the "left" of $D2$, due to $S2an \subset S1ab$, so our orbit is further away from the equilibrium. Consequently our orbit will continue its journey and spiral away from the equilibrium as will all other orbits. Because there has to exist an attractor we know that a limit cycle exists, due to the absence of an attracting equilibrium. We also know from these considerations that the orbit of the limit cycle lies in (S1) as well as (S2) and might therefore be referred to as a "Filippov Cycle". We know that at least one limit cycle exists, but at this point we can't rule out the possible existence of multiple such limit cycles.

Definition. Filippov Cycle. We call a periodic orbit a Filippov cycle if one of two conditions holds:

1. the orbit is in (S1) as well as (S2),
2. the orbit is on the discontinuity for a positive length of time.

Most of our Filippov Cycles will be of the first kind, but we get the second kind for case a, for subcase a.6 and a.8 to be precise.

Case b.2: $S1ab \subset S2an$

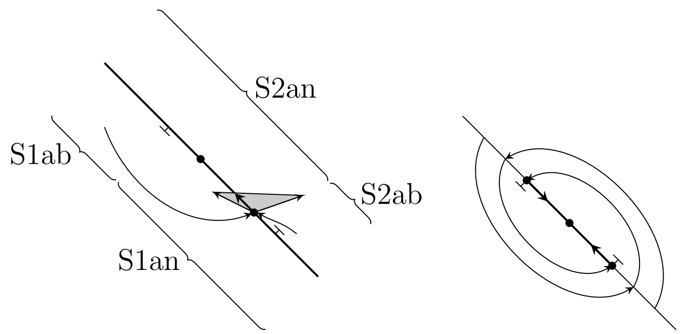

Figure 18: We have drawn a Filippov-Cone for a point close to $D2$ to show the dynamics between $D1$ and $D2$ in 18.1. In 18.2 we depict the rest of the dynamic.

Let us look at the dynamics at a point between the equilibrium and $D2$ but very close to $D2$. The orbits in (S1) and (S2) point towards this point and will collide in L. We now have to determine the angles to decide how the orbits will continue. Following the Filippov-approach we create a cone with the directions of these orbits as vectors. The orbit starting in (S2) will have a slope very close to $\bar{k}$ because we are very close to $D2$. The second orbit will point into (S2), but the slope of this vector will be further from $\bar{k}$, because we are not so close to $D1$. We look at the cone and we see that the only possible way left for the orbits is to continue towards the equilibrium. The same holds true if we would have started close to $D1$ instead of $D2$.

Let us take an arbitrary point between $D1$ and $D2$ and assume the dynamic there is away from the equilibrium. It can't leave L and would lead towards $D1$ or $D2$. Due to the continuity in the change of the slope we would get a new equilibrium which is obviously a contradiction. Hence the dynamics on the whole segment between $D1$ and $D2$ - segment D - points towards the equilibrium.

When we look at Figure 18.2 we have the following situation: We take the ω-limit of the points $D1$ and $D2$ which obviously spiral away from the equilibrium. Therefore the segment of attraction for the equilibrium increases the further we follow the ω-limits. Considering that the orbits at the edge also point inwards it seems very likely that all orbits in $\mathbb{R}^2_+$ will converge to the equilibrium. We can't rule out the existence of a limit cycle with the equilibrium in its interior though.

3.4.2 Case a

We remember: In case a is the refuge rather small, L lies below the equilibrium of (S2), which is the only equilibrium in $\mathbb{R}^2_+$. We will now have to distinguish between quite a few subcases here. As the first distinctions we will distinguish between cases where the forward-orbit of $D2$ intersects with L and cases where it does not. When it does not intersect we will look at the backward-orbit of $D2$. When the forward-orbit does intersect we will have to follow the orbit further and see where it ends up. In all these subcases we will also have to distinguish between cases where $D1$ lies to the "left" or "right" of $D2$.

Case a.1: The forward-orbit of $D2$ doesn't intersect with L; $D1$ is "left" of $D2$

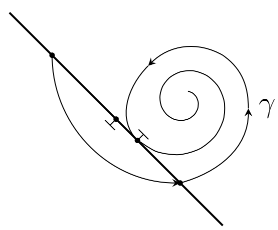

Figure 19: Everything as described in the title. The thick line is L. The "nails" stand for $D1$ and $D2$.

This subcase is rather simple. We see from the picture that all orbits will eventually end up in (S2) and won't return to (S1). In (S2) they underlie the dynamics there and will converge to the attractor of (S2) which is either an equilibrium or limit cycle. Which of these cases depends on the equations of (S2) and we have shown how one deals with that in Chapter 2.1. We will refer to the backwards-orbit of $D2$ as γ in the subcases a.1 to a.4. If we follow γ back in time we see that the area of attraction grows with each intersection of γ with L. It is possible that these intersections (restricting us to those to the "left" of $D1$) could converge to one point and then the area of attraction could only grow to a certain point and γ would converge to a limit cycle. We can't rule out this case but it seems far more likely that γ will at one point stop intersecting with L and it's α-limit will be the empty set. Then all of $\mathbb{R}^2_+$ would converge to the (S2)-attractor.

Case a.2: The forward-orbit of $D2$ doesn't intersect with L; $D1$ is "right" of $D2$; γ first intersects "right" of $D1$ then between $D1$ and $D2$

The long title of this paragraph already adumbrates the difficulties distinguishing all these subcases, but the picture makes the situation a lot clearer.

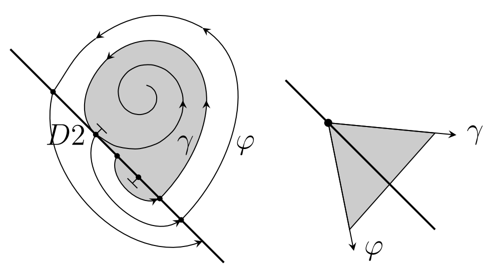

Figure 20: The shaded area in the first picture will converge towards the (S2)-attractor. The rest of $\mathbb{R}^2_+$ towards a Filippov cycle. The second picture shows the Filippov cone for a point between $D1$ and $D2$.

Technically we have here more than one possible forward-orbit for $D2$. We create the Filippov cone at $D2$ - one vector is pointing into (S1), one vector into (S2) - and see that the forward orbit(s) could either head into (S1), (S2) or stay on the discontinuity. If the orbit stays on the discontinuity, it could still head into (S1) or (S2) later on, because the Filippov cone for points between $D1$ and $D2$ would look like the one for $D2$. If the orbit stay on the discontinuity for a long time it will eventually hit the grey shaded area (Figure 20.1) and leave the discontinuity at the latest when it hits $D1$.

The γ-orbit we are always referring to in the title is the one, if the orbit at $D2$ continues directly into (S2). If the orbit continues into (S1) we call it φ. φ will eventually spiral outwards. If we understand the backward-orbit of $D2$ as part of γ, then γ intersects twice with L but then stops there due to the discontinuity of L. We can see that the interior of γ (adding a bit of L to close it of) will converge to the (S2)-attractor. The rest of $\mathbb{R}^2_+$ on the other hand doesn't. Looking at φ we see that it spirals outwards. Recalling that the dynamics close to the axes is inwards, we necessarily have a Filippov Cycle to which the rest of $\mathbb{R}^2_+$ converges to. We see that we have a dependency on the initial condition in case a.2. When an orbit starts in the interior of γ, convergence is towards the (S2)-attractor. When it starts in the complement, convergence is towards the Filippov cycle. Starting on γ itself is undecided.

Case a.3: The forward-orbit of $D2$ doesn't intersect with L; $D1$ is "right" of $D2$; γ first intersects "right" of $D1$ then "left" of $D2$

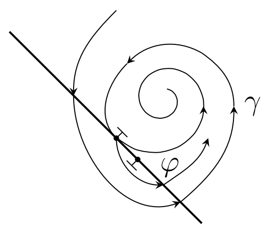

Figure 21: φ spirals inwards.

The main difference here to case a.2 is that the orbit φ also spirals inwards. Both φ and γ will converge towards the (S2)-attractor. If we can exclude a Filippov cycle like in case a.1, then all orbits will converge towards the (S2)-attractor.

Case a.4: The forward-orbit of $D2$ doesn't intersect with L; $D1$ is "right" of $D2$; γ first intersects "left" of $D1$

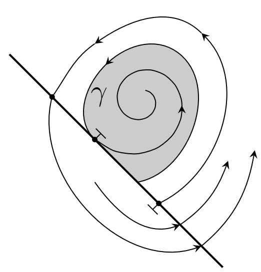

Figure 22: Again: The shaded area will converge towards the (S2)-attractor. The rest of $\mathbb{R}^2_+$ towards a Filippov cycle.

We see that the backward-orbit of $D2$ "stops" at the first intersection with L. The interior of the closure of γ (again adding a bit of L) will converge to the (S2)-attractor, while the rest of $\mathbb{R}^2_+$ will spiral outwards and therefore an attracting limit cycle has to exist. We see that, when we follow the orbit starting at $D1$ and see that its path leads away from γ. We have again a dependency on the initial condition to decide the convergence.

Case a.5: The forward-orbit of $D2$ does intersect with L; $D1$ is "right" of $D2$

We should note that we again have a situation where the orbits might split at $D2$. If we talk about the forward-orbit of $D2$ in case a.5 to a.8 we are referring to the orbit starting at $D2$ and continuing into (S2).

Case a.5 to a.8 will all be cases where the forward-orbit of $D2$ does intersect with L. This is obviously only possible when the dynamics at the equilibrium are spiraling outwards, which is only possible if the equilibrium in (S2) is unstable. We also know that L intersects with the limit cycle of (S2). If it wouldn't the limit cycle would lie completely above L and every orbit between L and the limit cycle had to get closer to the limit cycle. But the orbit starting at $D2$ gets further away from it. Contradiction. Therefore L cuts the limit cycle of (S2).

So we know we are in a rather specific situation. In turn these considerations show us that if the equilibrium is stable or it's unstable and L is away from the (S2)-limit cycle, we have one of the cases a.1 to a.4.

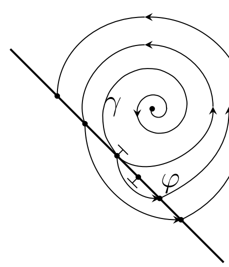

Figure 23: This is the first time that the orbit from $D2$ spirals outwards strong enough that it intersects with L. This also means that we can follow the orbit back in time and it will then approach the equilibrium. Because there is no limit cycle in (S2) left, the orbit even has to converge to the equilibrium.

In case a.5 we first look at the situation at $D2$. If we look at the ω-orbit we see that it converges to the equilibrium in (S2). There is nowhere else to go, considering that there is no other possible attractor due to the (S2)-limit cycle being cut by L. If we look at the forward-orbit of $D2$ (either γ or φ) it spirals outwards. Therefore there exists a limit cycle and all orbits have to converge to a Filippov cycle, due to the absence of every other possible attractor.

Case a.6: The forward-orbit of $D2$ does intersect with L; $D1$ is "left" of $D2$; γ first intersects between $D1$ and $D2$

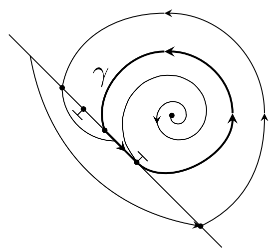

Figure 24: The orbit starting at $D2$ spirals outward again but this time it returns and creates a limit cycle.

If we start at $D2$ again we see that there is only one forward-orbit possible now, because of the dynamics in (S1). If we follow this orbit we land somewhere between $D1$ and $D2$ due to the assumptions. In both (S1) and (S2) the dynamics is towards L and therefore the orbit can't leave L. Following the Filippov-approach we instantly see that the orbit will continue on L until it hits $D2$ again. We have a closed orbit, therefore a limit cycle.

If we look at the interior of γ we see that the limit cycle is attracting. Also if we follow a point between $D1$ and $D2$ back in time - there is also an orbit from (S1) leading there - we see that it spirals outwards, therefore γ is also attracting there. In the absence of any other Filippov cycles it's area of attraction is all of $\mathbb{R}^2_+$. The difference to the cases before is that we now actually know the exact form of the limit cycle.

Case a.7: The forward-orbit of $D2$ does intersect with L; $D1$ is "left" of $D2$; γ first intersects "right" of $D1$ and then "left" of $D2$

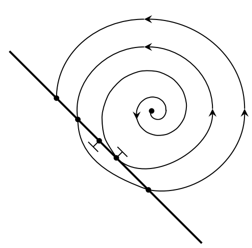

Figure 25: In proximity to the equilibrium as well as $D1$ and $D2$ this case looks like case a.1 with α- and ω-limit switched.

If we look at the graphic we see that the dynamic at the equilibrium is outwards and will eventually hit L. The segment between $D1$ and $D2$ shows the same dynamic as in the last case and the orbits there will lead to $D2$ from where it will spiral outwards, as will the other orbits anywhere near it. The outwards spiraling orbits will eventually stop, due to the inwards spiraling orbits at the edge of the plane and we have shown the existence of a Filippov cycle. Every orbit in $\mathbb{R}^2_+$ will eventually converge to a Filippov cycle.

Case a.8: The forward-orbit of $D2$ does intersect with L; $D1$ is "left" of $D2$; γ first intersects "right" of $D1$ and then between $D1$ and $D2$

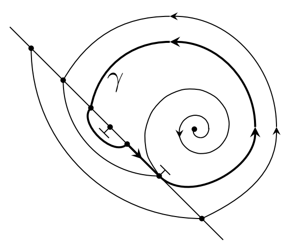

Figure 26: We know the exact form of the limit cycle. The difference to case a.6 is that it takes a short detour into (S1).

The dynamics at the equilibrium is again outwards. If we start at $D2$ we have only one possible orbit to follow forward and observing the assumptions it will intersect with L "right" of $D1$. From there it will take a little detour in (S1) until it hits L, in the segment between $D1$ and $D2$, again. Like the case before the dynamics in (S1) and (S2) will force the orbit to stay on L until it hits $D2$ again. We have a limit cycle which is attracting its entire interior, and, like in case a.6, also from the rest of the plane. The main difference to a.6 is that the limit cycle is also partly in (S1).

We have now finally finished classifying the possible situations of the dynamics depending on L and the equations determining $D1$ and $D2$. From this we have seen that if we know the relation of $D1$ and $D2$ and know the behaviour of γ we can understand the dynamics that are happening. We also see that we can classify the cases differently depending on their attractors:

- a.2, a.4, a.5, a.7: There is a Filippov cycle as an attractor, but it is not close to $D1$ and $D2$.
- a.1, (a.2), a.3, (a.4): They underlie (at least partly) the dynamics of (S2). In the case of a.1 and a.3 L doesn't influence the system enough

to actually disturb the dynamics at all. The orbits will eventually converge to the (S2)-attractor.

- a.2, a.4: The ω-limit of an orbit depends on its starting point. L has disturbed the system in a way that initial conditions are actually relevant. In the case of (S1) or (S2) alone it didn't matter what the amount of predators or prey in the beginning was, to determine the future of the system. Here it can either lead to a "big" Filippov cycle like in a.5 and a.7 or to the "smaller" attractor of (S2).

- a.6, a.8: Here we actually know how the limit cycle looks like. We can easily find it by following γ.

It seems that there could be a crossover between these cases depending alone on the slope of L. First case a.1/a.3 which switch to a.2/a.4 if the slope reaches a certain level and from there to a.5/a.7 and then a.6/a.8. However some of these cases need a stable/unstable equilibrium in (S2) to actually be possible. Therefore we can't reduce the cases due to such a simple rule.

We have a surprisingly rich pool of possible behaviours, but we also see that some of these cases aren't so different from each other. It looks like we can subsume case a.1 and a.3, because they have pretty much the same limit-behaviour. Likewise it seems one can also subsume case a.2 with a.4 as well as case a.5 with a.7 and a.6 with a.8. This would noticeably decrease the amount of cases. There are some arguments for these subjugations. If we look, for example, at case a.5 and a.7: The only difference here is that $D1$ has moved a bit from being "right" of $D2$ to being just a bit "left" of it and stop somewhere before the intersection of γ and L. But if we move too far towards the intersection of γ and L with $D1$, then the γ-orbit wouldn't move far enough and we'd land up in case a.8. So, we see that there needs to be a distinction between these cases, at least as long we can't find a proper expression for distinguishing where the intersections of γ and L happen in relation to $D1$ and $D2$. If this were possible we would easily be aware in which case we are and would know the behaviour of the dynamics. Now, for the behaviour of $D1$ and $D2$ we found a criterion (or, at least, an easy way to calculate it) to find out the relation of $D1$ and $D2$. For the behaviour of the γ-orbit we would need an explicit solution of the system which seems too much to ask for, but for explicit parameters it can be done numerically without too much effort.

4 Conclusion

We have now finished what we have anticipated in the introduction. We have analyzed and classified the equations for the constant refuge, have seen how the orbits roughly behave and know their ω-limits. We have especially seen that there is no more unbounded growth possible as was in the paper of Křivan. We have also seen that not much changes if we let the assumptions of our special version of the Gause-model drop and switch to the general case. The only thing that needs to be borne in mind is the number of limit cycles and their position relative to $\hat{x}$. When this is done the dynamics can be analyzed without much trouble. What is needed though is the explicit form of the limit cycles in (S2).

The change to the non-constant refuge has caused a few more challenges. But nevertheless we know that only one equilibrium is in the interior of the $\mathbb{R}^2_+$-plane and the limit cycle, if existing, is around it. There might be more than one Filippov cycle though. We have never explicitly disproved the existence of one and there doesn't seem to be an easy way to do it. When we consider the history of the Gause model in regards to the existence of multiple limit cycles we see that it took quite some time to solve that question. It seems therefore presumptuous to attempt to solve this question for a system - even though it is only a special case - which might be even more difficult to handle because of the discontinuity. This problem is one that I have to leave to others or future works to solve.

Another difficulty left is the behaviour of the γ-orbit. We have stated that it can be easily calculated numerically but this leaves one somewhat unsatisfied. Without knowing the behaviour of the γ-orbit we can't completely distinguish between all of the subcases. At the present state we can easily differentiate with basic geometry if we are in case a or b and we can differentiate the subcases of b with the criterion in 3.3 but we have no complete solution for a. We can exclude some subcases with the stability of the equilibrium and some with the relative placement of $D1$ and $D2$ but for a complete distinction we would need to know the behaviour of the orbits at $D2$. Like we mentioned, this can easily be done numerically but an explicit analytical solution would be preferred. When we ignore this problem we can say that all cases have been completely solved and analyzed.

What is left is to consider what could be done following this work. The obvious thing is to drop the assumptions of the special version of the Gause model and switch to the general case with a non-constant refuge. One could immediately transfer the results for S2an and S2ab. They can be reached without any reference to the equations (2) and (3) by using graphical arguments. The same holds true for S1ab and S1an. We have used the equations from (2) and (3) for these results, but we would get the same results without any use of those equations, by using a graphical method. For the criterion in 3.3 we have used the equations but we haven't done much with them. We have just shown the way one would have to use them and this way is the same way for any different version of the Gause model or the general case. Analogous results can easily be reached. The classifications of the subcases were mainly geometric arguments which would also hold for the general case. One would mainly have to keep in mind the possible multiple limit cycles in (S2). We see that this generalization probably wouldn't be too complicated, but one would have to deal with a lot of different subcases.

Another assumption that I had to make for the sake of simplicity was that the discontinuity is a line. It might be more realistic for the discontinuity to follow a strictly monotonically decreasing function instead. The Filippov-approach would become a bit more difficult because we would have to work with the derivative of this function to create the cone and there might be multiple equilibria on the discontinuity then. If that were to be true one would probably get even more subcases than before and we already had quite a few to consider.

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Zusammenfassung:

Diese Masterarbeit beschäftigt sich mit dem Gause Räuber–Beute Modell unter der zusätzlichen Annahme, dass die Beute nur bis zu einem gewissen Grad erlegt werden kann.

Für die Beute existiert eine Art Schutzgebiet in welches sich eine gewisse Anzahl von Tieren zurückziehen und Sicherheit finden kann. In diesem Schutzgebiet können sie sich nun vermehren bis es zu viele Tiere für das Schutzgebiet gibt und einige es verlassen müssen. Nun können sich wiederum die Raubtiere vermehren, da sie wieder Beute finden.

Diese Dynamik wurde nach Vorbild des Gause Räuber–Beute Modells in Gleichungen gegossen und analysiert. Die Schwierigkeit liegt darin, dass die nun entstandenen Differential-Gleichungen unstetig sind. Um das Verhalten der Gleichungen zu verstehen, musste auf das Lösungskonzept von Filippov für unstetige Gleichungen zurückgegriffen werden. Damit ist es gelungen diese Dynamiken vollständig zu analysieren und klassifizieren.

Als weiterer Schritt wurde die Annahme einer konstanten Schutzgebietgrösse, die unabhängig ist von der Anzahl der Raubtiere, fallengelassen. Eine hohe Anzahl von Raubtieren bedeutet nun ein kleineres Schutzgebiet für die Beutetiere. Die so modifizierten Gleichungen wurden ebenfalls klassifiziert und beinahe vollständig analysiert. Lediglich die Problematik der möglichen Existenz von multiplen periodischen Orbits konnte nicht zufriedenstellend gelöst werden.

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