The behaviour and attractiveness of the Lotka-Volterra equations

DOCTORAALSCRIPTIE WISKUNDE

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Contents

Chapter 1

Introduction

We live in a world which is replete with dynamical systems. When a grocery store decides to cut prices to become cheaper than its competitors, the management of that store is trying to influence the dynamical system of stores and customers. When adding several chemicals together to prepare, for instance, a cup of coffee or a hot meal, we create a system in which chemicals are competing, being created or destroyed, and eventually reach some kind of equilibrium. And during a walk trough the forest on a sunny afternoon, a careful observer can see all kinds of biological species compete for resources, territory, or mating partners. Even if someone would be locked up in an empty room with concrete walls, there are still hundreds of dynamical systems present inside this persons body.

For some of the examples mentioned above, it is possible to write down a mathematical model without much assumptions or simplifications. Take for example a system consisting of two chemicals in solution, which react to form a third. Typical assumptions that we need to model this system is that there are indeed only two initial chemicals present and that there is no interaction with the environment. These kind of assumptions are not only reasonable, they can also be made more accurate by improving the conditions of our chemical experiment.

For other systems, especially economical and biological ones, things are not always that clear. Simplifications are often necessary, since the complete system is too complex to put into a model. However, oversimplification may rob us of interesting dynamics that is present in the more complete system. Therefore, in dealing with these systems, it is useful to bear in mind the famous quote from Albert Einstein

> Everything should be made as simple as possible, but not simpler.

The model given by the Lotka-Volterra equations, which is studied in this thesis, seems to match this 'simplification-condition'. As is argued in the next section, making the model even simpler (which in effect means taking away all interactions) goes too far. On the other hand, much of the dynamical behaviour observed 'in the field' can be modeled accurately by these equations, so it seems that the Lotka-Volterra model itself is not an oversimplification.

However, there is still reason to be cautious. The Lotka-Volterra model still leaves quite some room for simplification or extension of the model. For example, the original predator-prey model[1] which was introduced by Volterra himself, turns out to be a conservative system.

[1] In this thesis, we shall use terminology taken from biological models (such as 'species' and 'predator-prey') to describe the dynamical systems. However, making the obvious substitutions, they apply to a far broader range, including for example chemical and economical systems.

The dynamics of such a system are completely understood, but rather unrealistic. In this example, only interactions between species were taken into account, neglecting the fact that specimens of the same species usually influence each other as well. This was of course realized by Volterra himself, who extended the model (but still keeping it within the 'Lotka-Volterra structure'), turning it into a dissipative system.

Another example of possible oversimplification is to include too few species in the model. As we will see later on, a competition model with only two species is generally not persistent, which means that at least one species will become extinct. However, including a third species (which we might naively expect not to have much influence on the situation), we find that periodic or almost periodic behaviour can occur.

The Lotka-Volterra model system allows for a surprisingly large number of generalizations, without changing the underlying structure of the model. Not only can we extend the model with additional interactions or species, it is also possible to include features like seasonal dependence, external interference and immaturity periods. While starting with simple autonomous, two-dimensional systems to get our bearings, we shall include all these effects, while trying to find a system that matches Einstein's criterion.

1.1 The Lotka-Volterra equations

The Lotka-Volterra equations were first introduced by Volterra himself in his 1931 book 'Leçons sur la théorie mathématique de la lutte pour la vie' [40]. Assuming that there is only quadratic interaction between the different species, a general system that gives the population of n different species is given by the following set of n coupled differential equations:

$$\dot{x}_j = \varepsilon_j x_j + \sum_{k=1}^{n} a_{jk} x_j x_k \qquad (j = 1, \ldots, n). \tag{1.1}$$

In this model, x_j is the number of individuals of species j, the ε_j's are the growth rates and the a_{jk}'s are the interaction coefficients of the species. For convenience, we also introduce the interaction matrix $A = (a_{jk})$, of which the elements are the interaction coefficients. We shall use the term 'coefficients' when we make a statement that is valid for both the growth rates and the interaction coefficients.

When we take as initial data for system (1.1) that all x_j's except one (say for $j = 1$) are zero, we get the single-species logistic growth model:

$$\dot{x} = \varepsilon x - a x^2. \tag{1.2}$$

The dynamics of this model (for both ε and a positive) are well-understood. For x small, the quadratic term is negligible and the population grows (almost) exponentially. However, as it gets larger, the quadratic term becomes significant, limiting the growth and providing an upper bound at $x = \frac{\varepsilon}{a}$. This feature models the effect that if the population gets to large, resources may get scarce and exponential growth is no longer possible.

The logistic model also already shows two features that we will try to find in many other systems. One is the existence of stable and unstable fixed or equilibrium points. As is easily checked, both $x = 0$ and $x = \frac{\varepsilon}{a}$ are equilibrium points of equation (1.2). However, $x = \frac{\varepsilon}{a}$ is stable, whereas $x = 0$ is unstable.

The other feature is the existence of an attractor. The stable equilibrium point $x = \frac{\varepsilon}{a}$ attracts

orbits: any solution of (1.2) with nonzero initial conditions will give an orbit that converges to $x = \frac{\varepsilon}{a}$. Such a point (or set) is called an attractor.
Of course, the concepts of (un)stable equilibrium points and attractors are common in mathematics and definitions can be found in many books. However, for completeness we include a short definition list in Appendix A and a list of useful theorems in Appendix B.

Obviously, the Lotka-Volterra equations, that allow for interactions between several coexisting species, are much more realistic than the single-species logistic model. Basically, it allows for two additional effects:

1. Competition between species: In the logistic model, the population of a single species is limited to a certain level because of 'internal competition' (there is, for example, only a limited amount of food available). Introducing inter-species competition allows for effects like the struggle for food or territory between species as well.

2. Predator and prey species. Certain (carnivorous) species can not sustain themselves at all if left alone. They might for instance be principal non-vegetarians and only consider other animals fitting food. For such a species, the growth rate ε is negative, and hence the species, if placed in a single-species environment, would simply become extinct. However, if we provide a prey species, the carnivorous predators have a chance of survival.

The abovementioned interaction effects are included in the Lotka-Volterra system by choosing an appropriate interaction matrix A. We can therefore classify the system by its interaction matrix.

1.2 A classification of Lotka-Volterra systems

Already in the previous section, we introduced the main classification of Lotka-Volterra systems used in the literature: a distinction is made between competitive and predator-prey models.

In any competition model, all interaction effects are negative. After all, we wish to model the struggle for survival, and in this case, having more others lessens your own chances. This gives a very simple condition on the interaction matrix: all its elements should simply be nonpositive. Although this is the case mostly studied, some authors also use the term competitive for a system in which only all inter-species interactions are nonpositive.

Of course, there could also be the complete opposite effect. In some utopian world, all interactions could be constructive, which would be reached by making all elements of the interaction matrix positive. As it turns out, this makes for a rather uninteresting system (much like Utopia would probably be a very dull place to live), but it is a valid possibility.

On the other hand, we have the predator-prey system. In its simplest form, the predators will have a negative effect on the prey, and the prey a positive effect on the predators. If we ignore all competition effects (so also the internal competition on the diagonal of A) and assume both interaction effects are equal in size, this gives us a perfectly skew-symmetric interaction matrix. In any physical system, such a symmetry always gives rise to a conserved quantity, which indeed is also the case here. In fact, this quantity is a Hamiltonian and can be considered to be an energy functional. Because of the existence of a conserved quantity, we will call such a system conservative.

As mentioned before, conservative systems are not very realistic and as such an example of oversimplification. If we, for example, eliminate the predator species, the prey will have unbounded growth (the system does not reduce to the logistic equation, because we did not include internal competition). Including competition both between specimens of a single species and between the different predator or prey species, of course destroys the symmetry of the interaction matrix. We are still able to define the same energy functional, but energy is no longer conserved. Because of the competition, there will effectively be dissipation of energy, which is why these kind of systems are called dissipative.

We are now in a position to define our main classification of Lotka-Volterra systems in three[2] main classes. Here the classification is made by giving conditions on the interaction matrix $A = (a_{ij})$, following [7]. In doing so, we do allow for the possibility that we need a change of variables to get our system in the proper form. As stated above, this is not the 'canonical' or only way. It does however have the advantage that it is valid for both autonomous and non-autonomous systems.

The main classes of Lotka-Volterra systems are called

1. **cooperative** (resp. **competitive**) if $a_{jk} \geq 0$ (resp. $a_{jk} \leq 0$) for all $j \neq k$,
2. **conservative** if there exists a diagonal matrix $D > 0$ such that AD is skew-symmetric,
3. **dissipative** if there exists a diagonal matrix $D > 0$ such that $AD \leq 0$.

By $A \leq 0$ we mean that A is negative definite in the sense of quadratic forms. See Appendix C for details on this formulation.

1.3 Outline

Before we can start out and investigate the properties of the different classes of Lotka-Volterra systems, we need a few general results on the internal equilibria one finds in such a system. These results are given in Chapter 2. After this, we study the properties of each of the three different types of Lotka-Volterra systems, in the case that all coefficients are independent of time (and the system is therefore autonomous). This is done in Chapters 3, 4 and 5. In each of these chapters, we begin with a simple planar example and then move on to the general (n-dimensional) system. In Chapter 3 we shall use semiflow and index theory to find conditions under which periodic orbits are possible in cooperative and competitive systems. In Chapters 4 and 5, we take a different approach, and use the concepts of the associated and reduced graph of a conservative or dissipative system to find the long-time dynamics.

In Chapter 6 we leave the autonomous systems and take the more realistic point of view that the coefficients can depend on time, letting go of another (over)simplification. Once again we look for (attracting) periodic orbits, and for conditions on the systems such that they can exist. Recent results in this direction show that in some cases, explicit conditions on the coefficients are not necessary, and we can suffice by giving conditions on the averages of the coefficients.

[2] The number of classes is a bit subjective here: one could call competitive and cooperative systems different classes. Of course, it is also possible to introduce another class, by adding cooperation instead of competition to a conservative system, creating a system for which the energy increases. However, as already follows from results on cooperative systems, such a system does not have any interesting dynamics.

Finally, in Chapter 7 we include the (also quite realistic) effect that newly-born animals do not immediately take part in the competition and neither are they immediately able to reproduce. From the stage-structured model studied in this chapter, we can derive possible ways to influence the system in such a way that a species might survive where it would otherwise perish, without directly harming the other species.

For completeness, there are three appendices in which we list some theorems and definitions which are used in this thesis. In Appendix A general definitions on dynamical systems, flows and equilibria are given. Some widely used tools that apply to dynamical systems (such as Lyapunov functions and index theory) are introduced in Appendix B. Some background on quadratic forms, which are used in our classification of Lotka-Volterra systems, can be found in Appendix C.

Chapter 2

Interior equilibria in Lotka-Volterra systems

In the previous chapter, we introduced the Lotka-Volterra system (1.1)

$$\dot{x}_j = \varepsilon_j x_j + \sum_{k=1}^{n} a_{jk} x_j x_k \qquad (j = 1, \ldots, n). \tag{1.1}$$

Since populations can not be negative, the vector $\mathbf{x} = (x_1, x_2, \ldots, x_n)$ is taken to be an element of $\mathbb{R}^n_+$, which is defined as

$$\mathbb{R}_+ = \{\mathbf{x} \in \mathbb{R}^n : x_j \geq 0 \text{ for } j = 1, \ldots, n\}.$$

Of course, any of the populations might be zero. However, if $x_j = 0$ holds at a certain point in time, it holds for all time. Therefore, if $m < n$ of the populations in system (1.1) are zero, the dynamics can be described by a system of dimension $n - m$. For nontrivial results, we should therefore take $\mathbf{x} \in \mathrm{Int}(\mathbb{R}^n_+)$, which is defined as

$$\mathrm{Int}(\mathbb{R}^n_+) = \{\mathbf{x} \in \mathbb{R}^n : x_j > 0 \quad \text{for} \quad j = 1, \ldots, n\}.$$

When we consider the two-dimensional (planar) Lotka-Volterra system, it is not hard to determine the dynamics of each of the three classes of systems introduced in Section 1.2. This is done in the first sections of the following three chapters.

When we proceed beyond the $n = 2$ case, the equations become considerably more complex. Already in the $n = 3$ case chaotic behaviour may occur[1]. In this chapter we shall derive some general results about the n-dimensional equations (1.1). Our main interest here are the (possible) internal equilibria of the system. These results can be found in many books and articles on dynamical or evolutionary systems, for instance in the books by Hofbauer and Sigmund [16] or by Sell and You [34].

We first introduce some terminology, using the general dynamical system

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

[1]Here chaotic behaviour means that a small variation in the initial conditions gives a totally different outcome. The standard model system for chaotic behaviour is given by the discrete system $x \to 4x(1-x)$. An example of a real-life chaotic system is a roulette wheel. In Section 3.6 we present an example of a three-dimensional Lotka-Volterra system that displays chaotic-like behaviour.

on any open subset $D \subset \mathbb{R}^n$ and with $\mathbf{f} \in C^1(D)$. An equilibrium point $\mathbf{p} \in D$ of this system is called *hyperbolic* if the Jacobian matrix of $\mathbf{f}$ at $\mathbf{p}$ has no purely imaginary eigenvalues. This makes the equilibrium point 'sturdy' in the sense that its stability type remains unchanged under small perturbations of the system. The *stable manifold* of $\mathbf{p}$, denoted $W^s(\mathbf{p})$ is the set of all initial conditions whose orbits approach $\mathbf{p}$ as $t \to \infty$. For an introduction about hyperbolic equilibria and stable manifolds, see the book by Strogatz [38].

The interior equilibria of equation (1.1) are the strictly positive solutions of

$$\varepsilon_i + \sum_{j=1}^{n} a_{ij} x_j = 0 \qquad (i = 1, \dots, n) \tag{2.1}$$

Theorem 2.1 $\mathrm{Int}(\mathbb{R}^n_+)$ *contains* α- *or* ω-*limit points if and only if (1.1) admits an interior equilibrium.*

Proof Obviously an equilibrium is its own α- and ω-limit. To prove the converse, we define $L : \mathrm{Int}(\mathbb{R}^n_+) \to \mathbb{R}^n$ by

$$y_i = L(x_i) = \varepsilon_i + \sum_{j=1}^{n} a_{ij} x_j \qquad (i = 1, \dots, n).$$

If equation (1.1) admits no internal equilibrium, the set $K = \mathrm{Im}(L(\mathrm{Int}(\mathbb{R}^n_+)))$ is disjoint from $\mathbf{0}$. Using a theorem from complex analysis (see Lang [19], Lemma IV.2.2), we know that this implies that there exists a hyperplane H through $\mathbf{0}$ which is disjoint from the convex set K. Thus there exists a vector $\mathbf{c} = (c_1, \dots, c_n) \neq \mathbf{0}$ which is orthogonal to H (i.e. $\mathbf{c} \cdot \mathbf{x} = 0$ for all $\mathbf{x} \in H$) such that $\mathbf{c} \cdot \mathbf{y}$ is positive for all $\mathbf{y} \in K$. Hence we can define a function $V : \mathrm{Int}(\mathbb{R}^n_+) \to \mathbb{R}$ by

$$V(\mathbf{x}) = \sum c_i \log x_i. \tag{2.2}$$

Now if $\mathbf{x}(t)$ is a solution of (1.1) in $\mathrm{Int}(\mathbb{R}^n_+)$, then the time derivative of $V(\mathbf{x}(t))$ satisfies

$$\dot{V} = \sum c_i \frac{\dot{x}_i}{x_i} = \sum c_i y_i = \mathbf{c} \cdot \mathbf{y} > 0.$$

So V is increasing along each orbit. But by Lyapunov's theorem (Theorem B.1) its derivative $\dot{V}$ should vanish at any ω-limit point. Hence there can be no such point. To exclude α-limit points, we use the Lyapunov function $-V$. □

From the proof it follows that if system (1.1) has no internal equilibrium, then the derivative of the Lyapunov function (2.2) is strictly positive. A system for which such a function exists is called 'gradient-like' by some authors.

Usually there will be at most one solution of equation (2.1). The only exception is the 'degenerate' case $\det(A) = 0$ (then we get a continuum of rest points). If there is a unique interior equilibrium $\mathbf{p}$ and the solution $\mathbf{x}(t)$ converges neither to the boundary nor to infinity, then its time average converges to $\mathbf{p}$.

Theorem 2.2 *If there exist positive constants* a *and* A *such that* $a < x_i(t) < A$ *for all* i *and all* $t > 0$, *and* $\mathbf{p}$ *is the unique rest point in* $\mathrm{Int}(\mathbb{R}^n_+)$, *then*

$$\lim_{T \to \infty} \frac{1}{T} \int_0^T x_i(t) dt = p_i \qquad (i = 1, \dots, n) \tag{2.3}$$

Proof We rewrite (1.1) as

$$\frac{d}{dt}\log x_i = \varepsilon_i + \sum_{j=1}^{n} a_{ij}x_j.$$

Integrating from 0 to T and dividing by T we get

$$\frac{\log x_i(T) - \log x_i(0)}{T} = \varepsilon_i + \sum_{j=1}^{n} a_{ij}z_j, \tag{2.4}$$

where

$$z_j = \frac{1}{T}\int_0^T x_j(t)dt.$$

Clearly we have $a < z_j(T) < A$ for all j and all $T > 0$.

We now take any sequence T_k in $\mathbb{R}_+$ that converges to $+\infty$. Since $z_j(T_k)$ is a bounded sequence, it must have a convergent subsequence of which we denote the limit by $\bar{z}_j$. The function $x_i(T)$ is also bounded, so the left-hand side of (2.4) vanishes if we take the limit of T to infinity. Hence this limit yields

$$0 = \varepsilon_i + \sum_{j=1}^{n} a_{ij}\bar{z}_j.$$

Thus the point $\bar{\mathbf{z}} = (\bar{z}_1, \ldots, \bar{z}_n)$ is an equilibrium. Since $\bar{z}_j > a$ for all j, it lies in $\mathrm{Int}(\mathbb{R}^n_+)$. By unicity it must therefore be equal to $\mathbf{p}$, which implies (2.3). □

Chapter 3

Cooperative and competitive systems

3.1 Rabbits and sheep

3.1.1 The dynamics of an example system

Since a planar system is much easier to visualize than a general one, it often helps to start by considering a 2-dimensional model. For the competitive case, this means we have two species competing for the same resource(s) and space, but neither one directly harming the other[1]. We denote the rabbit population by x and the sheep population by y. Assuming (obviously) that the rabbits multiply faster and that the sheep usually win the struggle for the resource (except when seriously outnumbered), a Lotka-Volterra model for the interaction between the two is given by[2]:

$$\begin{aligned} \dot{x} &= x(3 - x - 2y) \\ \dot{y} &= y(2 - x - y) \end{aligned} \tag{3.1}$$

The nullclines of this systems are the y-axis and the line $y = \frac{1}{2}(3 - x)$ for the first equation and the x-axis and the line $y = 2 - x$ for the second. In total this gives us four fixed points: the origin (which is an unstable node), the stable nodes (3,0) and (0,2) and the saddle point (1,1) where the nontrivial nullclines intersect. Its stable manifold separates the solution space $\mathbb{R}^2_+$ into two basins of attraction (see figure 3.1). Therefore, unless we happen to start on the stable manifold of the saddle point, we see that always one species grows (or declines) to its carrying capacity, while the other starves and perishes.

In the example above, there are two basins of attraction because the point where the nontrivial nullclines intersect lies inside the first quadrant (the only relevant one, because populations can not be negative). If it would lie outside the quadrant, one species would always be doomed, unless it starts out as the only one[3]. This result can be extended to higher dimensions, as was done by Zeeman (see Section 3.3).

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[1]Though this kind of competition is often regarded as 'nice' and 'peaceful', here it means that one species might starve the other to death, so you can ask yourself in which system a rabbit would rather live: one with foxes (where he might be eaten) or one with sheep (where he is quite likely to starve). The foxes might be the least cruel...

[2]This model is based on the example in section 6.4 of Strogatz [38].

[3]Of course, in many biological systems one needs at least *two* specimens of any of the competing species to give it any chance of persisting, but mathematical mammals do not suffer this inhibition.

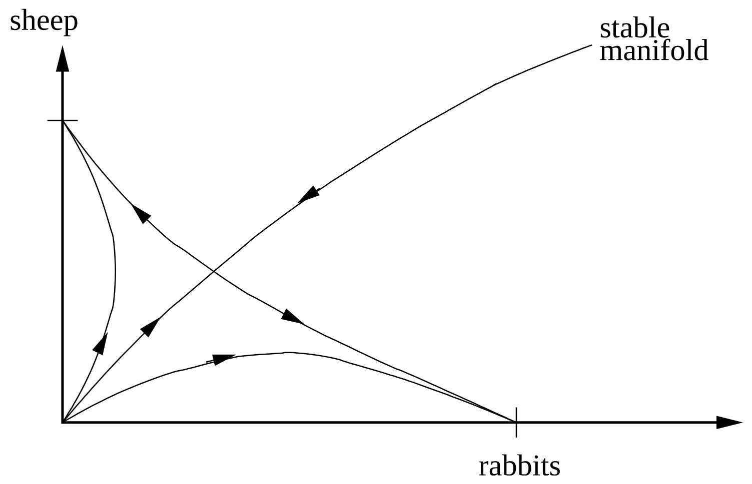

Figure 3.1: Two competitive species

A final possibility is that the roles of the saddle point and the stable nodes are reversed. In that case the only stable solution is a peaceful coexistence of both species. It is not hard to show that this is the case if the intersection point of the nontrivial nullclines lies above the line connecting the stable points on the axes (and, of course, in the first quadrant), and that we have the bistable case if it lies below this line.

3.1.2 Closed orbits

One might wonder if the world is really as harsh as is suggested in the previous section. There, only in very special cases a coexistence of species is possible, but most of the time one of them must become extinct. In other cases (like predator-prey systems), there is also the possibility of a periodic solution, represented in the phase plane by a limit cycle. In this section we present an argument using index theory that excludes this possibility for the system at hand. The basic definitions and theorem we need here are given in Appendix B.2. A more extensive introduction into index theory is given in Strogatz [38], Chapter 6.8.

Now suppose the system from the previous section has a periodic solution. Then it must enclose at least one stable node to satisfy the index condition from Theorem B.3. If the 'internal' equilibrium point is stable, it is a global attractor, so there can be no periodic orbit around it. In the case the stable nodes lie on the axes (so in all the cases in which one species dominates and the other perishes), any closed orbit around one of them would intersect an axis. But since the axes themselves are also solutions, this means that solutions would intersect, which is impossible. Hence there can be no periodic orbits.

3.2 General cooperative and competitive differential equations

Throughout this chapter, we consider the autonomous dynamical system described by the ordinary differential equations

$$\dot{x} = f(x) \tag{3.2}$$

on an open subset $D \subset \mathbb{R}^n$ and with $f \in C^1(D)$. In order for our system to be 'well-behaved', we assume the region D to be convex, i.e. that for all $t \in [0,1]$ and $x, y \in D$ we have $tx + (1-t)y \in D$. We denote by $\phi_t(x)$ the solution of (3.2) that starts at the point $x \in \mathbb{R}^n$ at $t = 0$. We call $\phi_t(x)$ the *flow* of (3.2) and consider f as the vector field that generates this flow.

In Appendix A some general terminology about equation (3.2) and the associated flow is defined and in Appendix B we list some basic results. As is done in these appendices, we consider the region D to be a subset of the Banach space $\mathbb{R}^n$. Furthermore, we define a partial ordering $\leq$ on D generated by the positive cone $\mathbb{R}^n_+$. This means that $x \leq y$ if for each component of x and y we have $x_i \leq y_i$ (see Appendix A.2). We also define the stronger ordering $\ll$ by saying that $x \ll y$ if $y - x \in \mathrm{Int}(\mathbb{R}^n_+)$, which means that $x_i < y_i$ for each component of x and y.

There is an intuitive way of defining the concepts of cooperative and competitive systems of differential equations using the concept of the semiflow (see Definition A.4), of which the solution $\phi_t(x)$ of (3.2) defined above is an example. Using this, we call a system of ordinary differential equations *cooperative* if it generates a monotone semiflow in forward time. Likewise, we call it *competitive* if it generates a monotone semiflow in backward time.

To be more rigorous, we take a closer look at the equation itself.

Definition 3.1 *The system of ordinary differential equations (3.2) is called* cooperative *if the region D on which it is defined is convex and the inequalities*

$$\frac{\partial f_i}{\partial x_j}(x) \geq 0 \qquad i \neq j, \quad x \in D \tag{3.3}$$

hold. If they hold with the inequalities reversed, the system is called competitive.

From this definition we immediately see that if system (3.2) is cooperative and generates a flow $\phi_t(x)$, then the system

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

is competitive with flow $\phi_{-t}(x)$ and vice versa. This means that, by changing the direction of time, we can change a cooperative system in a competitive one and vice versa. Moreover, in line with our intuitive idea about cooperative systems, by this definition they indeed are monotone dynamical systems.

We need to verify that Definition 3.1 is consistent with the definition of cooperative and competitive Lotka-Volterra systems given in Section 1.2. To do so we observe that we can write system (1.1) in the form of system (3.2) by defining

$$f_j(x) = x_j \left(\varepsilon_j + \sum_{k=1}^{n} a_{jk} x_k \right) \qquad j = 1, \ldots, n.$$

Taking the derivative of f as in equation (3.3) we find that

$$\frac{\partial f_j}{\partial x_k}(x) = a_{jk} x_j \qquad \text{for } j \neq k.$$

Thus, by Definition 3.1, the system is cooperative if all coefficients a_{jk} with $j \neq k$ are positive, and competitive if they are all negative. This is exactly the same requirement as given in Section 1.2.

In Section 3.1 we analyzed a two-dimensional competitive system and found that over time, the system necessarily relaxes to an equilibrium. Whether this equilibrium persisted for more than one species depended on the parameter values. This type of dynamics also appears in higher-order systems. Theorem 3.3 gives sufficient conditions on a Lotka-Volterra system of arbitrary dimension to relax to a single-species equilibrium, meaning that all except one species become extinct. However, for competitive systems with more than two species there are more possibilities, as they might allow periodic orbits. The key results in this direction are given in Sections 3.4 and 3.5. We illustrate these ideas with a three-dimensional example in Section 3.6.

3.3 Extinction

For competitive systems in arbitrary dimension, the following general theorem by Zeeman [43] holds:

Theorem 3.1 *If the competitive Lokta-Volterra system (1.1)*

$$\dot{x}_j = \varepsilon_j x_j + \sum_{k=1}^{n} a_{jk} x_j x_k \qquad (j = 1, \dots, n).$$

satisfies the inequalities

$$\frac{\varepsilon_j}{a_{jj}} > \frac{\varepsilon_i}{a_{ij}} \quad \forall i < j \qquad \text{and} \qquad \frac{\varepsilon_j}{a_{jj}} < \frac{\varepsilon_i}{a_{ij}} \quad \forall i > j \tag{3.4}$$

then the axial fixed point

$$R_1 = \left(-\frac{\varepsilon_1}{a_{11}}, 0, \dots, 0\right)$$

is globally attracting on $\mathbb{R}^n_+$.

Formulated in the language of Section 3.1, the theorem states that if there is no intersection of the nontrivial nullclines in $\mathbb{R}^n_+$, then one of the species is dominant. This means that all except one species die out, whereas the population of the remaining one goes to its carrying capacity.

3.4 Compact limit sets

3.4.1 Ordering

A key result in the theory of cooperative and competitive equations is that any compact limit set of such a system is incomparable with respect to $\ll$, i.e. there can not be two points x and y in the limit set that satisfy $x \ll y$. In the special case that the limit set is an ω-limit set and the system is cooperative (and hence generates a monotone flow), this is a consequence of the Nonordering of limit sets theorem (Theorem B.8). The more general case is stated in this section.

Theorem 3.2 *A compact limit set of a cooperative or a competitive system is incomparable with respect to $\ll$.*

Since a periodic orbit is a compact limit set, it must satisfy this theorem and therefore has no two points related by $\ll$. On the other hand, any Jordan curve in $\mathbb{R}^2$ must contain two such points. This gives an alternative proof for the statement made in Section 3.1.2, namely that there can be no periodic orbits for a system of two competing (or cooperating) species.

3.4.2 Topological equivalence

The next theorem (Theorem 3.3) states that the flow on a compact limit set of our system in $\mathbb{R}^n$ can be described by the flow of a system of dimension $n-1$. To formalize this, we need the concept of topological equivalence.

Let A be an invariant set for system (3.2) with flow ϕ_t (i.e. $\phi_t(a) \in A \quad \forall a \in A$) and let B be an invariant set for the flow ψ_t of the system

$$\dot{y} = F(y) \tag{3.5}$$

which is defined on the same open subset $D \subset \mathbb{R}^n$ as system (3.2) and also has $F \in C^1(D)$.

Definition 3.2 *The flow ϕ_t on A is* topologically equivalent *to the flow ψ_t on B if there is a homeomorphism $Q : A \to B$ such that $Q(\phi_t(x)) = \psi_t(Q(x))$ for all $x \in A$ and $t \in \mathbb{R}$.*

We call the system (3.5) Lipschitz if the function F is Lipschitz.

Theorem 3.3 *The flow on a compact limit set of a cooperative or competitive system in $\mathbb{R}^n$ is topologically equivalent to a flow on a compact invariant set of a Lipschitz system of differential equations in $\mathbb{R}^{n-1}$.*

The results in this section are originally due to Hirsch [12]. A complete and readable proof of Theorems 3.2 and 3.3 is given in the book by Smith [36].

3.5 The Poincaré-Bendixson theorem in three dimensions

Even in the plane, it is often difficult to show that a dynamical system admits a periodic orbit. One of the few results in that direction is the well-known Poincaré-Bendixson theorem (stated in Appendix B.3, Theorem B.4). However, the main result of the previous section, Theorem 3.3, tells us that for cooperative and competitive systems in dimension n we can describe the dynamics of a compact limit set by a system of dimension $n-1$. Since periodic orbits are compact limit sets, this suggest we might be able to extend the Poincaré-Bendixson theorem to cooperative or competitive systems in three dimensions. This is the basis of the following theorem.

Theorem 3.4 (3-dimensional Poincaré-Bendixson) *A compact limit set of a competitive or cooperative system in $\mathbb{R}^3$ that contains no equilibrium points is a periodic orbit.*

The first proof of this theorem was given by Hirsch in [14], using earlier partial results by himself [12] and Smith [35]. The complete proof can be found in the earlier mentioned book by Smith [36].

Since the (forward) flow of a cooperative system is monotone, it follows directly from Theorem B.7 that such a system can never have a nontrivial attracting periodic orbit[4]. However, a competitive system does not have such a limitation and therefore attracting periodic orbits are allowed. As was shown in Section 3.1.2, they do not exist in two-dimensional systems, but by the following theorem they do exist if the system is three-dimensional.

Theorem 3.5 *Suppose (3.2) is a competitive system in the region* $D \subset \mathbb{R}^3$ *and that* D *contains a unique and hyperbolic equilibrium point* p. *Suppose further that the stable manifold* $W^s(p)$ *of* p *is one-dimensional and tangent at* p *to a vector* $v \gg 0$. *If there is a point* $q \in D \backslash W^s(p)$ *such that* $\gamma^+(q)$ *has compact closure in* D, *then* $\omega(q)$ *is a nontrivial periodic orbit.*

Proof The theorem follows from Theorem 3.4 if we can show that $p \notin \omega(q)$. Because $q \notin W^s(p)$, we certainly have $\omega(q) \neq p$. Now suppose $p \in \omega(q)$. Then by the Butler-McGehee Lemma (see [5]) we have that $\omega(q)$ contains a point y on $W^s(p)$ with $y \neq p$. Because $\omega(q)$ is invariant, we can assume that y is a point of the local stable manifold and can be chosen arbitrarily close to p. Since $W^s(p)$ is tangent at p to a strictly positive vector, it follows that we have either $y \ll p$ or $p \ll y$. However, since both y and p are elements of the compact limit set $\omega(q)$, this contradicts Theorem 3.2. □

3.6 A three-dimensional example

The example we present in this section is based on the 1975 article by May and Leonard [24]. In their introduction they remark that they can not use the 'powerful, but 2-dimensional, Poincaré-Bendixson techniques'. However, the three-dimensional Poincaré-Bendixson theorem (which was proven in 1990), does apply to the region of interest of their system.

An interesting property of this example is that it exhibits what one might call 'alternating attractor' dynamics. For a certain choice of parameters, there are three equilibrium points (each corresponding to the situation that one species has reached its carrying capacity and the other two are extinct) which all seem to attract the orbit in turns. To the casual observer it might therefore seem for a long time that one species will certainly dominate the system forever, when suddenly Fortune's favor switches to another species and it seems to dominate. However, this species in turn will lose its dominance to the third over time as well, which once again loses it to the first. Even though the 'dominance period' of each becomes longer and longer as time increases, none of the species will gain the final overhand[5].

The example system is the following Lotka-Volterra system for three competing species:

$$\begin{aligned} \dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3) \\ \dot{x}_2 &= x_2(1 - \beta x_1 - x_2 - \alpha x_3) \\ \dot{x}_3 &= x_3(1 - \alpha x_1 - \beta x_2 - x_3) \end{aligned} \tag{3.6}$$

where we choose both α and β positive to make the system competitive.

[4]Smith also shows that if a cooperative system is irreducible (i.e. the Jacobian matrix is irreducible at each point in the domain), then the Perron-Frobenius theorem implies that any periodic orbit is linearly unstable (Smith [36], Proposition 4.3.4).

[5]This is of course a beautiful illustration of the well-known fact that Fortune never sticks to her decisions.

This system has eight equilibria. They correspond to the situations that there are no specimens at all (the origin); that there is only one species (the three equilibria $(1,0,0)$, $(0,1,0)$ and $(0,0,1)$); that there coexist two species, which are the three equilibria

$$\frac{1}{1-\alpha\beta}\begin{pmatrix}1-\alpha\\1-\beta\\0\end{pmatrix},\quad \frac{1}{1-\alpha\beta}\begin{pmatrix}0\\1-\alpha\\1-\beta\end{pmatrix} \text{ and } \frac{1}{1-\alpha\beta}\begin{pmatrix}1-\beta\\0\\1-\alpha\end{pmatrix}$$

and finally the situation that all three species coexist

$$\frac{1}{1+\alpha+\beta}\begin{pmatrix}1\\1\\1\end{pmatrix}. \tag{3.7}$$

The stability of all these equilibria, as well as the dynamics of the system, is of course dependent on the values of the parameters α and β. For the most interesting equilibrium (the 'internal' one (3.7) with the three coexisting species), the Jacobian matrix $\left(\frac{\partial f_i}{\partial x_j}\right)$ is given by

$$-\left(\frac{\partial f_i}{\partial x_j}\right) = \begin{pmatrix}1 & \alpha & \beta\\ \beta & 1 & \alpha\\ \alpha & \beta & 1\end{pmatrix}. \tag{3.8}$$

The eigenvalues of J are

$$\lambda_0 = 1+\alpha+\beta, \tag{3.9}$$

$$\lambda_\pm = 1-\frac{1}{2}(\alpha+\beta) \pm \frac{i}{2}\sqrt{3}(\alpha-\beta). \tag{3.10}$$

From which we see that this equilibrium is stable for $\alpha+\beta<2$. For $\alpha+\beta>2$ and both $\alpha\geq 1$ and $\beta\geq 1$ the three equilibria corresponding to the existence of a single species are all stable, and which one the system converges to is dependent on the initial conditions. The interesting dynamics occur when we choose (without loss of generality) $0<\alpha<1<\beta$ such that $\alpha+\beta\geq 2$. An overview of all these possibilities is given in Figure 3.2.

3.6.1 The special case $\alpha+\beta=2$.

In the special case that $\alpha+\beta=2$, both complex eigenvalues of the internal equilibrium point are purely imaginary. This means that the equilibrium is not hyperbolic and hence that we can not apply Theorem 3.5. However, it is still possible to show that in this case an attracting periodic orbit must exist.

We define the total population N by

$$N(t) \equiv x_1(t)+x_2(t)+x_3(t). \tag{3.11}$$

Summation of the three equations (3.6) immediately yields the following equation for N:

$$\dot{N} = N(1-N), \tag{3.12}$$

of which general solution is (using separation of variables)

$$N(t) = \frac{N(0)}{N(0)+(1-N(0))e^{-t}}. \tag{3.13}$$

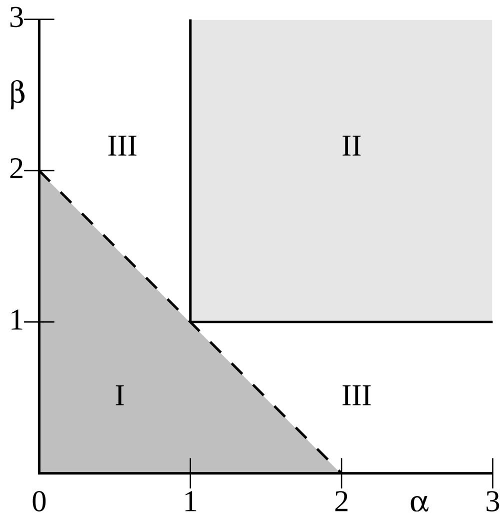

Figure 3.2: The three different possible dynamics: (I): $\alpha + \beta < 2$, the internal equilibrium (three-species coexistence) is stable; (II): $\alpha + \beta > 2$ and $\alpha, \beta \geq 1$, the three single-species equilibria are stable; (III) $\alpha + \beta \geq 2$, but α or β less than 1: there is no asymptotically stable equilibrium point, but there is a periodic orbit.

Hence we find for the asymptotic limit

$$\lim_{t \to \infty} N(t) = 1, \tag{3.14}$$

so the asymptotic solution of (3.6) lies in the plane $N = x_1 + x_2 + x_3 = 1$.

Of course, if we can find another surface which also contains the asymptotic solution, we are practically done. The asymptotic solution then must be (a subset of) the intersection of both surfaces.

To get such a second surface, we look at the product $P(t)$ of the three populations

$$P(t) \equiv x_1(t)x_2(t)x_3(t). \tag{3.15}$$

To translate a product to a sum, we use logarithms. We therefore rewrite equations (3.6) as

$$\frac{d \log x_1}{dt} = 1 - x_1 - \alpha x_2 - \beta x_3$$

for the first one and analogously for the second and third. Adding these three equations we find (using $\alpha + \beta = 2$):

$$\frac{d}{dt} \log(x_1 x_2 x_3) = 3 - 3N. \tag{3.16}$$

Combining (3.16) and (3.12) we find for the product $P(t)$

$$\frac{d \log P(t)}{dt} = 3 \frac{d \log N(t)}{dt}$$

which yields by integration

$$\frac{P(t)}{P(0)} = \left(\frac{N(t)}{N(0)} \right)^3.$$

From this we find for the asymptotic limit of $P(t)$:

$$\lim_{t\to\infty} P(t) = C \equiv \frac{P(0)}{(N(0))^3}, \tag{3.17}$$

so the asymptotic solution of (3.6) must also lie on the hyperboloid $P = x_1x_2x_3 = C$ in $\mathbb{R}^3$, where the constant C is determined by the initial conditions.

Combining the results we found for N and P, we find that all solutions[6] of system (3.6) with initial conditions in $\mathrm{Int}(\mathbb{R}^3_+)$ tend asymptotically to the intersection of the plane $N = 1$ and the hyperboloid $P = C$, which is a periodic orbit in the plane $N = 1$. We illustrate this in Figure 3.3.

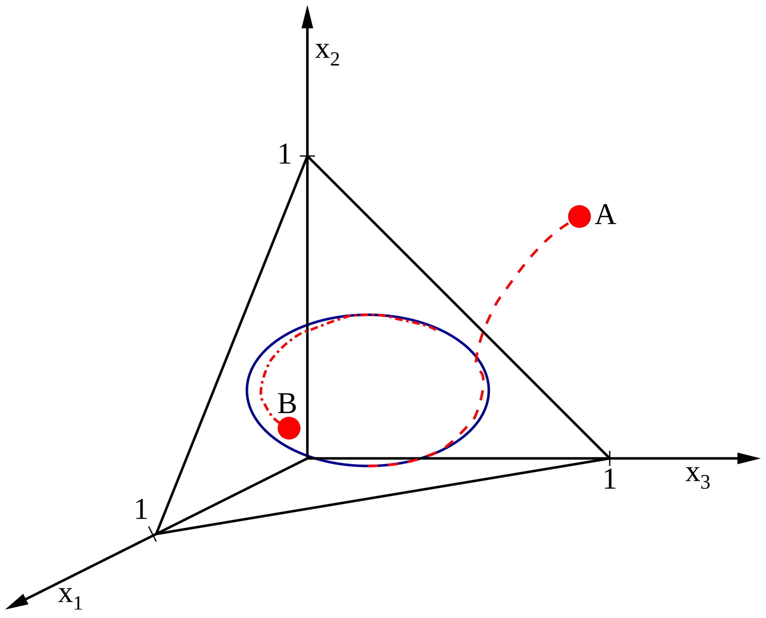

Figure 3.3: The phase space of system (3.6) for $\alpha + \beta = 2$. All non-trivial orbits converge to a periodic orbit in the plane $x_1 + x_2 + x_3 = 1$.

3.6.2 The case $\alpha + \beta > 2$, $0 < \alpha < 1 < \beta$.

When $\alpha + \beta > 2$ the internal equilibrium point $p = \frac{1}{1+\alpha+\beta}(1,1,1)$ is both unstable and hyperbolic. We need the extra assumption that either α or β is also less than 1 to make sure none of the other equilibria are stable. (This means that in this section we limit ourselves to region III of Figure 3.2. Of course, we can without loss of generality take $\alpha < 1$ and $\beta > 1$.) The equilibrium point p has a one-dimensional stable manifold, tangent to the eigenvector that is associated to the stable eigenvalue λ_0. From (3.8) and (3.9) it is immediately clear that this eigenvector is $(1,1,1)$. To be able to apply Theorem 3.5, it remains only to show that there is a point $q \in \mathrm{Int}(\mathbb{R}^3_+)$ that does not lie on the diagonal and of which the closure of the orbit is compact. Since we are working in a finite-dimensional space, compactness of a

[6] Except, of course, those solutions that have initial conditions that lie exactly on the (1-dimensional) stable manifold of the internal equilibrium.

subset is equivalent to the subset being closed and bounded. It is therefore sufficient to show that all orbits are bounded.

First we observe that, like in the two-dimensional case, the set $\mathrm{Int}(\mathbb{R}^3_+)$ is invariant. This holds because if we restrict the system to one of the planes that form the boundary of $\mathbb{R}^3_+$, we get a two-dimensional Lotka-Volterra system, which makes the boundary planes invariant and hence (because no orbits can cross) also the interior is invariant. Like in the case when $\alpha+\beta=2$, we define the total population N to be the sum of the three individual populations (equation (3.11)). In the case at hand, the time derivative of N becomes

$$\begin{aligned}\dot{N} &= N-(x_1^2+x_2^2+x_3^2)-(\alpha+\beta)(x_1x_2+x_2x_3+x_3x_1)\\ &= N(1-N)-(\alpha+\beta-2)(x_1x_2+x_2x_3+x_3x_1)\end{aligned}\tag{3.18}$$

and since the last term in (3.18) is strictly negative, we find that

$$\dot{N} \leq N(1-N). \tag{3.19}$$

Since populations cannot be negative, the value of their sum N is bounded from below. By equation (3.19) it is also bounded from above, because for any value $N>1$ the time derivative $\dot{N}$ is negative, and the value of N decreases. But that means that all orbits must be bounded, and therefore that their closure is compact. Hence we satisfy all conditions of Theorem 3.5 and can conclude that for any starting point $q \in \mathrm{Int}(\mathbb{R}^3_+)$ that does not lie on the diagonal, the ω-limit set $\omega(q)$ is a nontrivial periodic orbit.

Of course, we also want to find out what this periodic orbit looks like. To do this, we use P/N^3 as a Lyapunov function (where P, as in (3.15), is the product of the three populations; this Lyapunov function was suggested by Hofbauer and Sigmund in [16]). A straightforward calculation shows that

$$\frac{d}{dt}\left(\frac{P}{N^3}\right)=\frac{P}{N^4}\left(1-\frac{\alpha+\beta}{2}\right)\Big[(x_1-x_2)^2+(x_2-x_3)^2+(x_3-x_1)^2\Big]\leq 0. \tag{3.20}$$

Hence, by Lyapunov's theorem (Theorem B.1), the ω-limit set we are looking for is contained in the set $\{x\in\mathbb{R}^3_+ : P=0\}$, which is exactly the boundary of $\mathbb{R}^3_+$. As we observed before, on the boundary planes the system (3.6) reduces to a two-dimensional competitive system. For example, on the boundary plane where $x_3=0$:

$$\begin{aligned}\dot{x}_1 &= x_1(1-x_1-\alpha x_2)\\ \dot{x}_2 &= x_2(1-\beta x_1-x_2),\end{aligned}$$

which, by the 'Extinction theorem' (Theorem 3.1) has a single, global attracting fixed point $(1,0)$ in the plane $\{x\in\mathrm{Int}(\mathbb{R}^3_+) : x_3=0\}$. Hence there is an hetroclinic orbit from $(0,1,0)$ to $(1,0,0)$ in the region $\{x\in\mathbb{R}^3_+ : x_3=0\}$. Analogously, we find hetroclinic orbits from $(1,0,0)$ to $(0,0,1)$ and from $(0,0,1)$ to $(1,0,0)$ in the other boundary planes. Combining, we find that these three hetroclinic orbits together with the equilibrium points $(1,0,0)$, $(0,1,0)$ and $(0,0,1)$ form the ω-limit set of each point q in $\mathrm{Int}(\mathbb{R}^3_+)$, except those on the diagonal. See Figure 3.4.

We make a final observation on the behaviour of the orbits over time. Since $\omega(q)$ is a periodic orbit, none of the equilibrium points in the boundary can attract an orbit for all time (which

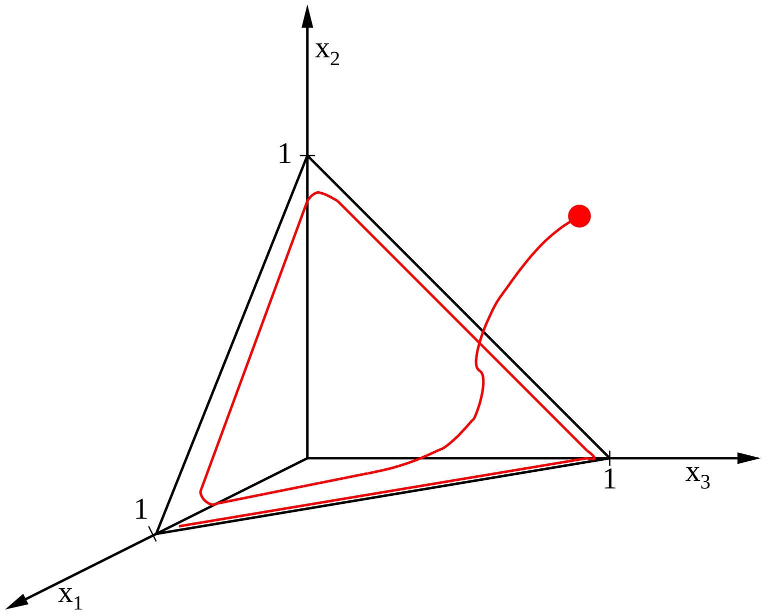

Figure 3.4: The phase space of system (3.6) for $\alpha+\beta>2$ and $0<\alpha<1<\beta$. All non-trivial orbits have the same ω-limit, that consists of the hetroclinic orbits and equilibrium points on the boundary.

is consistent with the observation that none of them is asymptotically stable, since each has both an incoming and an outgoing hetroclinic orbit). However, as is shown by May and Leonard for a certain choice of parameters[7], it is possible to make an estimate of the time the orbit stays 'in the neighbourhood' of one of these equilibrium points. It turns out that the duration of this period grows with time, so the longer we watch, the longer each species (when its turn comes) seems to dominate.

As a final remark, we note that this example shows that the lower limit on the values of x_i in Theorem 2.2 is essential. Here, the populations are bounded from above, but they approach 0 arbitrarily close for large enough time, so there is no value $a>0$ such that $x_i(t)>a$ for all t. As we have seen, the time averages of the population in this example do indeed not converge. On the other hand, in the case of the previous section where $\alpha+\beta=2$, the solutions stay away from the boundary and Theorem 2.2 holds, so the time average of the solution converges to the internal equilibrium point.

[7] May and Leonard assume that we can neglect the last term of the right-hand side of equation (3.18) for the derivative of N, in which case we find that in the limit that $t\to\infty$, we get $N\to 1$. Of course, whether or not this assumption holds depends on the values of α and β, but for both of them reasonably small it holds.

Chapter 4

Conservative systems

4.1 Rabbits and foxes

Again we start with a simple 2-dimensional example. Widely used, but perhaps a bit unrealistic, is the following predator-prey system for rabbits (x) and foxes (y):

$$\begin{aligned} \dot{x} &= x(4-2y) \\ \dot{y} &= y(-1+x) \end{aligned} \tag{4.1}$$

The nullclines of this system are the y-axis and the line $y = 2$ for the first equation and the x-axis and the line $x = 1$ for the second. In total this gives us two fixed points: the origin (which is a saddle point) and the 'center point' (1, 2) where the nontrivial nullclines intersect. Around this center point all orbits that start in the first quadrant cycle, so this model predicts the existence of infinitely many periodic solutions. See figure 4.1.

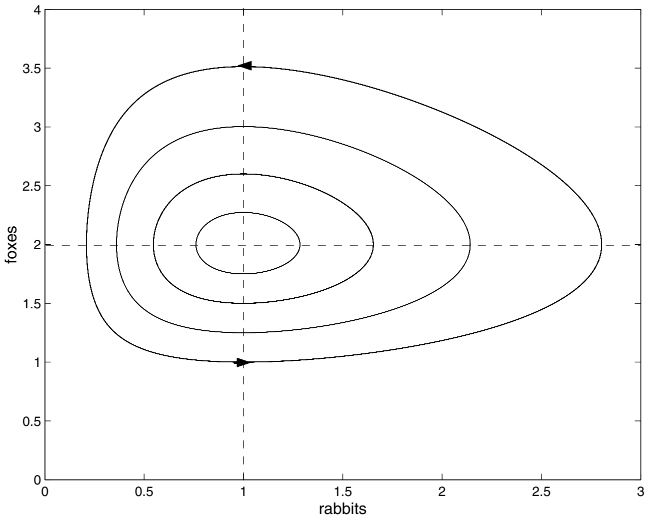

Figure 4.1: A (conservative) predator-prey system

4.2 Characterizations of conservative systems

In Chapter 1 we defined a Lotka-Volterra system to be conservative if there is a diagonal matrix $D > 0$ such that AD is skew-symmetric. Fortunately, the system has a gauge freedom which allows us to get rid of the matrix D. Defining

$$y_j = \frac{1}{d_j} x_j \qquad (j = 1, \ldots, n),$$

the system (1.1) with interaction matrix A is transformed into a new system with interaction matrix AD:

$$\dot{y}_j = \varepsilon_j y_j + \sum_{k=1}^{n} d_j a_{jk} y_j y_k \qquad (j = 1, \ldots, n).$$

All classes of Lotka-Volterra systems defined in Chapter 1 are invariant under this change of gauge. From now on, we assume the gauge of the conservative system to be chosen such that A itself is skew-symmetric.

The following proposition by Volterra himself [40] gives a necessary and sufficient condition for a system to be conservative:

Proposition 4.1 *A Lotka-Volterra system with a skew-symmetric interaction matrix $A = (a_{jk})$ is conservative if and only if the following are satisfied:*

1. $a_{jj} = 0 \qquad (j = 1, \ldots, n)$,
2. $a_{jk} \neq 0 \Rightarrow a_{jk} a_{kj} < 0 \qquad (j \neq k)$,
3. $a_{i_1 i_2} a_{i_2 i_3} \cdots a_{i_s i_1} = (-1)^s a_{i_s i_{s-1}} a_{i_{s-1} i_{s-2}} \cdots a_{i_1 i_s}$
   for every finite sequence of integers $(i_1, \ldots, i_s)$ with $1 \leq i_r \leq n$ for $r = 1, \ldots, s$.

We can visualize this rather technical proposition using the associated graph $G(A, \varepsilon)$ of the Lotka-Volterra system. This is a labeled graph, where with each species j we associate a vertex labeled ε_j and we draw an edge connecting vertex j to vertex k if $a_{jk} \neq 0$. The conditions in the above proposition then translate to the conditions that (1) $a_{jj} = 0$ and $a_{jk} \neq 0 \Rightarrow a_{kj} \neq 0$ and that (2) for each closed path in the graph with an even (resp. odd) number of vertices the product of the coefficients when we go around in one direction is equal to (resp. minus) the product when we go around in the other direction. For example, given the graph of Figure 4.2, this second condition would simply become

$$a_{23} a_{34} a_{42} = -a_{24} a_{43} a_{32}.$$

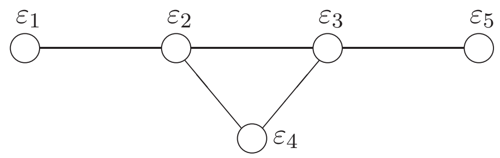

Figure 4.2: An example of the associated graph of a simple Lotka-Volterra system

4.3 Hamiltonian formulation of a conservative system

Exploiting the skew-symmetry of the interaction matrix, we can recast any conservative Lotka-Volterra system (1.1) in Hamiltonian form[1]. Defining new variables Q_j (called 'quantity of life' by Volterra) by

$$Q_j(t) = \int_0^t x_j(\tau)d\tau \qquad (j = 1, \dots, n), \tag{4.2}$$

we can rewrite (1.1) as a second-order ode system:

$$\ddot{Q}_j = \varepsilon_j \dot{Q}_j + \sum_{k=1}^{n} a_{jk}\dot{Q}_j\dot{Q}_k \qquad (j = 1, \dots, n). \tag{4.3}$$

We now introduce the Hamiltonian

$$H = \sum_{j=1}^{n}(\varepsilon_j Q_j - \dot{Q}_j). \tag{4.4}$$

Using the skew-symmetry of A, we find that this is a conserved quantity (or 'first integral'):

$$\dot{H} = -\sum_{j,k=1}^{n} a_{jk}\dot{Q}_j\dot{Q}_k = 0.$$

Restricting the Q_j's to $\mathbb{R}^+$, we can define another set of n variables:

$$P_j = \log \dot{Q}_j - \frac{1}{2}\sum_{k=1}^{n} a_{jk}Q_k \qquad (j = 1, \dots, n). \tag{4.5}$$

In terms of the variables Q_j and P_j, we can now write the Hamiltonian as

$$H = \sum_{j=1}^{n}\varepsilon_j Q_j - \sum_{j=1}^{n}\exp\left(P_j + \frac{1}{2}\sum_{k=1}^{n} a_{jk}Q_k\right) \tag{4.6}$$

Using this version of the Hamiltonian, it immediately follows that we can rewrite (4.3) in the following form[2]:

$$\begin{cases} \dot{P}_j &= \dfrac{\partial H}{\partial Q_j} \\ \dot{Q}_j &= -\dfrac{\partial H}{\partial P_j} \end{cases} \qquad (j = 1, \dots, n). \tag{4.7}$$

[1] In this section we follow the article by Duarte, Fernandes and Oliva [7], who in turn follow Volterra [40].

[2] This are the famous Hamilton equations from classical mechanics. There, Q is the generalized coordinate, P is the generalized momentum and the Hamiltonian H is the total energy of the system. These equations give an alternative formulation of Newton's equations of motion. However, they are also still valid in quantum mechanics, where a system is specified by giving its Hamiltonian, and the time evolution of the Hamiltonian itself is given by Schrödinger's equation.

4.4 Reducing the Hamiltonian system to the Lotka-Volterra equations

In the previous section, we wrote the n-dimensional Lotka-Volterra system (1.1) as a system of $2n$ Hamiltonian equations (4.7). This process can be reversed, in the sense that if we start out with the Hamiltonian system (4.7) and Hamiltonian (4.6), we can obtain the Lotka-Volterra equations (1.1). To do this, we define the map $\Psi : \mathbb{R}^{2n} \to \mathbb{R}^n_+$ by

$$\Big(\Psi(P_1, \ldots, P_n, Q_1, \ldots, Q_n)\Big)_j = \exp\left(P_j + \frac{1}{2}\sum_{k=1}^{n} a_{jk} Q_k\right) \tag{4.8}$$

(which, by substituting the expression (4.5) for P_j, can be seen to be nothing more than the time derivative of the defining equation (4.2) for Q_j). We can now recover the Lotka-Volterra equations by setting

$$x_j = \Big(\Psi(P_1, \ldots, P_n, Q_1, \ldots, Q_n)\Big)_j$$

and differentiating

$$\begin{aligned}
\dot{x}_j &= \left(\dot{P}_j + \frac{1}{2}\sum_{k=1}^{n} a_{jk}\dot{Q}_k\right) x_j \\
&= \left(\frac{\partial H}{\partial Q_j} - \frac{1}{2}\sum_{k=1}^{n} a_{jk}\frac{\partial H}{\partial P_j}\right) x_j \\
&= \varepsilon_j x_j + 2\cdot\frac{1}{2}\sum_{k=1}^{n} a_{jk}\exp\left(P_k + \frac{1}{2}\sum_{l=1}^{n} a_{kl} Q_l\right) x_j \\
&= \varepsilon_j x_j + \sum_{k=1}^{n} a_{jk} x_j x_k .
\end{aligned}$$

By going from the Hamiltonian back to the Lotka-Volterra system, what we are doing is essentially a symmetry reduction. That this is possible is due to the fact that the map Ψ is a Poisson bracket on $\mathbb{R}^{2n}$, giving this space the structure of a Poisson manifold. For a general introduction into Poisson manifolds and Hamiltonian systems we refer to the book by Olver [26]. The same reduction as sketched above, but using the Poisson manifold structure, can be found in [7].

4.5 Example

Using the symmetry reduction from the previous section, it is possible to start out with a Hamiltonian (which can, for example, be obtained by means of physical or biological considerations) and get a conservative Lotka-Volterra system which exhibits the same dynamics.

As an example system, we take the Hamiltonian

$$H = 4Q_1 - Q_2 - e^{P_1 - \frac{1}{2}Q_2} - e^{P_2 + \frac{1}{2}Q_1}, \tag{4.9}$$

for which the Hamilton equations (4.7) give

$$
\begin{aligned}
\dot{Q}_1 &= -\frac{\partial H}{\partial P_1} = e^{P_1 - \frac{1}{2}Q_2} \\
\dot{Q}_2 &= -\frac{\partial H}{\partial P_2} = e^{P_2 + \frac{1}{2}Q_2} \\
\dot{P}_1 &= \frac{\partial H}{\partial Q_1} = 4 - \frac{1}{2}e^{P_2 + \frac{1}{2}Q_1} \\
\dot{P}_2 &= \frac{\partial H}{\partial Q_2} = 1 + \frac{1}{2}e^{P_1 - \frac{1}{2}Q_2}
\end{aligned}
$$

If we now define x_1 and x_2 using the map (4.8), we find

$$
\begin{aligned}
\dot{x}_1 &= \frac{d}{dt}e^{P_1 - \frac{1}{2}Q_2} \\
&= e^{P_1 - \frac{1}{2}Q_2} \cdot \left(\frac{\partial P_1}{\partial t} - \frac{1}{2}\frac{\partial Q_2}{\partial t} \right) \\
&= e^{P_1 - \frac{1}{2}Q_2} \cdot \left(4 - \frac{1}{2}e^{P_2 + \frac{1}{2}Q_1} - e^{P_2 + \frac{1}{2}Q_2} \right) \\
&= x_1(4 - x_2),
\end{aligned}
$$

and analogously

$$x_2 = x_2(1 + x_1).$$

Thus, starting out from the Hamiltonian (4.9), we have recovered the example system (4.1) from Section 4.1. This example illustrates the fact that the Hamiltonian contains all information about the system, and that, given the Hamiltionian, the dynamics can be obtained in two ways: using the Hamilton equations, or by a symmetry reduction to the Lotka-Volterra system.

4.6 A criterion for Hamiltonialism

It is obvious that not all Lotka-Volterra systems allow for a Hamiltonian formulation. Take for example $\varepsilon_j = 1$ and $a_{jk} = 0$ for all j and k in (1.1). Then we get a system with a single source (the origin), in which every population grows exponentially.

In order to prevent this exceptional cases, we therefore must impose an additional condition on our system, to make sure it stays bounded. By Theorem 2.1 it is sufficient to demand that it has at least one internal fixed point. Combining this with the requirements to be conservative (Proposition 4.1), we arrive at the following criterion

Corollary 4.2 *If system (1.1) satisfies the following three conditions:*

1. *The system has an equilibrium point in* $\mathrm{Int}(\mathbb{R}^n_+)$*;*
2. *The matrix associated to the system satisfies* $a_{jj} = 0$ *and* $a_{jk} \neq 0 \Rightarrow a_{jk}a_{kj} < 0$*;*
3. *The graph associated to the system is a forest (a collection of disjoint trees);*

then it has a Hamiltonian formulation.

Chapter 5

Dissipative systems

5.1 Rabbits and humans

In the previous chapter we introduced the 2-dimensional system (4.1) as a (predator-prey) model for the populations of rabbits and foxes. This model does allow solutions in which only one of the two species is present. If there are only foxes, they will die out exponentially, for there is no food to keep them alive. However, if there are only rabbits, they will multiply exponentially (as rabbits do...), since there is no predator present to eat them. This is of course a somewhat unrealistic feature, for at a certain point the number of rabbits will be so large that they too will feel the agony of having insufficient resources to sustain their hordes of offspring. To compensate for this, we postulate that the growth is not exponential but instead logistic, meaning that there is a maximum carrying capacity for both species.

In the next example model x can once again be considered the number of rabbits. They reproduce rapidly if there are not many of them, but the negative x^2-term limits their number to a maximum. Furthermore, they are eaten by species y, hence a larger number of y specimens diminishes their number.

Species y in this example can eat both the natural ('vegetable') resource and the rabbits, so both the linear term and the xy term have positive coefficient. The species is therefore both herbivorous and carnivorous - an example of such a species would be the humans. However, there are also dissipative systems for which the growth rate of the prey species (y) is negative. Of course, they too have a maximum carrying capacity, so the y^2 term has a negative coefficient.

This dissipative system is a possible generalization of the (oversimplified) predator-prey model of the previous chapter. In the literature these models are therefor referred to as the 'generic' predator-prey model, in which the species (in the two-dimensional case) are usually taken to be rabbits and foxes.

$$\begin{aligned} \dot{x} &= x(4 - 2x - 2y) \\ \dot{y} &= y(1 + x - 2y) \end{aligned} \tag{5.1}$$

This system has two nontrivial nullclines, given by the lines

$$\begin{aligned} 4 - 2x - 2y &= 0, \\ 1 + x - 2y &= 0. \end{aligned}$$

The fixed points in $\mathbb{R}^2_+$ are the origin (which is an unstable node), the saddle points $(2,0)$ and $(0,\frac{1}{2})$ on the axes and the stable spiral point $(1,1)$ in the interior of $\mathbb{R}^2_+$.

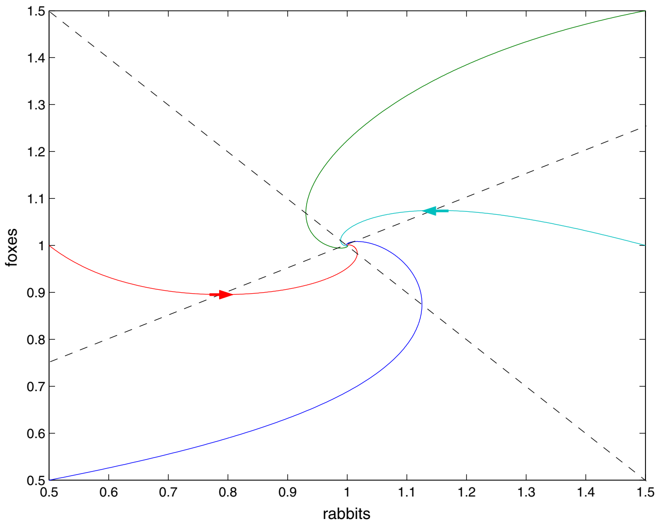

Figure 5.1: A spiral node in the dissipative system.

The interaction matrix associated with the Lotka-Volterra system (5.1) is given by

$$A = \begin{pmatrix} -2 & -2 \\ 1 & -2 \end{pmatrix}. \tag{5.2}$$

Using the positive diagonal matrix[1]

$$D = \begin{pmatrix} 1 & 0 \\ 0 & 4 \end{pmatrix},$$

we find that $AD \leq 0$, meaning that AD is negative definite (this is quickly verified by computing the eigenvalues of AD, which are -4 and -6). Hence we can classify system (5.1) to be dissipative.

As before, we can make a gauge transformation to new variables based on the matrix D such that the interaction matrix of the resulting system becomes AD (and hence is negative definite 'by itself'). In this example, this is done by taking $\tilde{x} = x$ and $\tilde{y} = \frac{1}{4}y$. Dropping the tildes again, the system after the transformation is given by

$$\begin{aligned} \dot{x} &= x(4 - 2x - 8y) \\ \dot{y} &= y(1 + x - 8y) \end{aligned} \tag{5.3}$$

The interior fixed point of the transformed system (5.3) is $(\bar{x},\bar{y}) = (1,\frac{1}{4})$. To show that this point is stable, we use the following Lyapunov function (see Section 5.3.1)

$$V(x,y) = (x - \bar{x}\log x) + (y - \bar{y}\log y).$$

[1]With 'positive matrix' here we mean that the matrix is positive definite in the sense of quadratic forms, see Appendix C. If the matrix is diagonal, this is equivalent to demanding that all entries are positive.

The time derivative of this function is

$$\begin{aligned}\dot{V}(x,y) &= \frac{\dot{x}}{x}(x-\bar{x}) + \frac{\dot{y}}{y}(y-\bar{y}) \\ &= (4-2x-8y)(x-\bar{x}) + (1+x-8y)(y-\bar{y}) \\ &= (-2(x-\bar{x}) - 8(y-\bar{y}))\,(x-\bar{x})\,((x-\bar{x}) - 8(y-\bar{y}))\,(y-\bar{y}) \\ &= -2(x-\bar{x})^2 - 7(x-\bar{x})(y-\bar{y}) - 8(y-\bar{y})^2\end{aligned}$$

which has exactly one zero (at $(\bar{x},\bar{y})$) and is concave. Hence we have $\dot{V}(x,y) \leq 0$ for all $(x,y) \in \mathbb{R}^2_+$. The point $(\bar{x},\bar{y})$ is therefore stable by Lyapunov's theorem (Theorem B.1), and the set $\{(x,y) : \dot{V}(x,y) = 0\} = \{(\bar{x},\bar{y})\}$ is the ω-limit set of any orbit that starts in $\mathrm{Int}(\mathbb{R}^2_+)$.

5.2 Dissipative and stably dissipative systems

As stated in Chapter 1, a dissipative system is characterized by the fact that its interaction matrix satisfies $AD \leq 0$, where $D > 0$ is a diagonal matrix. The class was first introduced by Volterra himself as a generalization of predator-prey systems [40].

Aside from the technical characterization in terms of the interaction matrix, we can also define dissipative systems in a more visual way. This definition holds for general systems of arbitrary (or even infinite) dimension.

Definition 5.1 *A dissipative system is one for which phase space*[2] *volumes are contracted by the time evolution.*

Thus the system of the previous section is dissipative, since we have shown that all orbits in $\mathrm{Int}(\mathbb{R}^2_+)$ converge to the internal equilibrium. Hence, as time goes forward, the set of points in phase space that can be reached by a particular orbit contracts and eventually reduces to this single equilibrium point.

It is possible to construct a system which does fit the definition of a dissipative one, but changes class under a small perturbation. To exclude these cases we introduce the concept of a stably dissipative system.

Definition 5.2 *A Lotka-Volterra system with interaction matrix A is called* stably dissipative *if we still get a dissipative system for any interaction matrix $\tilde{A} = (\tilde{a}_{jk})$ that can be obtained from A by a sufficiently small perturbation on the nonzero coefficients.*

Put down into a mathematical expression, the requirement of Definition 5.2 reads

$$\exists \delta > 0 : \max_{jk} |a_{jk} - \tilde{a}_{jk}| < \delta \Rightarrow \tilde{A} \text{ is dissipative.}$$

By allowing only perturbations on the nonzero coefficients of A, we get that the elements of A and $\tilde{A}$ satisfy

$$a_{jk} = 0 \Leftrightarrow \tilde{a}_{jk} = 0.$$

Thus the graphs of the systems with interaction matrices A and $\tilde{A}$ are identical.

[2] The *phase space* of a system of n odes is the $2n$-dimensional space spanned by all possible vectors $(x_1, \ldots, x_n, \dot{x}_1, \ldots, \dot{x}_n)$.

Remark Not all authors use the same term for these types of systems. The notion of a stably dissipative system was first introduced by Redheffer in [28], but there it is called a stably admissible system. However, in the original work of Volterra, the systems Redheffer calls admissible were called dissipative [40]. Duarte, Fernandes and Oliva, who wrote an article combining results of all three types of systems [7], therefore chose to use the term stably dissipative, a convention we will follow here.

5.3 The dynamics of the attractor of a stably dissipative system

In this section we show that, for a stably dissipative system with a nontrivial fixed point, the system has a globally attracting subset and the dynamics on this attractor are Hamiltonian. To do so, we first introduce a Lyapunov function V for the system (which immediately gives the attracting subset $\dot{V} = 0$) and subsequently show that this set satisfies Corollary 4.2. For this we use the concept of the reduced graph which was first introduced by Redheffer. The solution presented in this section is from [29].

For this section, our system of interest is the stably dissipative Lotka-Volterra system (1.1) with equilibrium point $\mathbf{q} = (q_1, \ldots, q_n) \in \mathrm{Int}(\mathbb{R}^n_+)$:

$$\begin{cases} \dot{x}_j &= \varepsilon_j x_j + \sum_{k=1}^{n} a_{jk} x_j x_k \\ 0 &= \varepsilon_j + \sum_{k=1}^{n} a_{jk} q_k \end{cases} \tag{5.4}$$

The following lemma will be useful when we are characterizing the set $\dot{V} = 0$ later on.

Lemma 5.1 *For a stably dissipative Lotka-Volterra system with interaction matrix A, there exists a positive diagonal matrix $D = \mathrm{diag}(d_1, \ldots, d_n)$ such that $AD \leq 0$ and*

$$\sum_{j,k=1}^{n} d_k a_{jk} w_j w_k = 0 \Rightarrow a_{jj} w_j = 0 \qquad (j = 1, \ldots, n). \tag{5.5}$$

Proof For a stably dissipative Lotka-Volterra system with interaction matrix $A = (a_{ij})$ we define the following perturbation:

$$\tilde{a}_{jk} = a_{jk} \qquad (j \neq k), \qquad \tilde{a}_{jj} = (1 - \delta) a_{jj}.$$

The matrix $\tilde{A}$ again is associated to a dissipative Lotka-Volterra system. Hence we can choose a diagonal matrix $D > 0$ such that $\tilde{A}D \leq 0$. Since we already have $a_{jj} \leq 0$ and because for any vector $\mathbf{w} = (w_1, \ldots, w_n) \in \mathbb{R}^n$ we have

$$\sum_{j,k=1}^{n} d_k a_{jk} w_j w_k = \sum_{j,k=1}^{n} d_k \tilde{a}_{jk} w_j w_k + \delta \sum_{j=1}^{n} d_j a_{jj} w_j^2,$$

we find that $AD \leq 0$ and

$$\sum_{j,k=1}^{n} d_k a_{jk} w_j w_k = 0 \Rightarrow a_{jj} w_j = 0 \qquad (j = 1, \ldots, n). \tag{5.6}$$

□

5.3.1 The Lyapunov function

Now making the gauge transformation to new variables $y_j = \frac{1}{d_j} x_j$ (which we shall call x_j again), we get a system with an interaction matrix satisfying $A \leq 0$ and equation (5.6).

We are now well-enough equipped to introduce the Lyapunov function given by

$$V = \sum_{j=1}^{n} (x_j - q_j \log x_j), \tag{5.7}$$

which satisfies

$$\dot{V} = \sum_{j,k=1}^{n} a_{jk}(x_j - q_j)(x_k - q_k) \leq 0. \tag{5.8}$$

This shows that V is indeed a Lyapunov function and that all orbits of the system (5.4) must converge on the set $\dot{V} = 0$. Combining (5.4), (5.6) and (5.7) we find that solutions for the equation $\dot{V} = 0$ must satisfy

$$\begin{cases} \dot{x}_j &= x_j \sum_{k=1}^{n} a_{jk}(x_k - q_k) \\ 0 &= a_{jj}(x_j - q_j) \qquad\qquad (j = 1, \ldots, n). \end{cases} \tag{5.9}$$

We therefore have either $a_{jj} = 0$ or $a_{jj} < 0$ with $x_j = q_j$ on the attractor.

5.3.2 The reduced graph

In section 4.2 we introduced the concept of the associated graph of a Lotka-Volterra system. We now add some additional information to it by discerning three types of vertices. We shall put a crossed circle $\oplus$ at vertex j if either $a_{jj} < 0$ or $a_{jj} = 0$ and we have shown that $x_j = q_j$ on the attractor. As an intermediate case, we put a 'dotted' circle $\odot$ on a vertex j where we can only show that x_j is constant (but not equal to q_j) on the attractor. If we can show neither of the above, we put an open circle $\bigcirc$ on the vertex. By repeatedly applying (5.9) we find the following propagation rules for the vertices (see [33]):

Lemma 5.2 *For the graph of a stably dissipative Lotka-Volterra system with fixed point the following propagation rules hold:*

1. *If there is a $\oplus$ or a $\odot$ at vertex j and a $\oplus$ at all neighbours of j except at one vertex l, then we can put a $\oplus$ at vertex l.*
2. *If there is a $\oplus$ or a $\odot$ at vertex j and a $\oplus$ or $\odot$ at all neighbours of j except at one vertex l, then we can put a $\odot$ at vertex l.*
3. *If there is a $\bigcirc$ at vertex j and a $\oplus$ or $\odot$ at all neighbours of j, then we can put a $\odot$ at vertex j.*

The graph obtained from the original graph by repeated application of these propagation rules is called the *reduced graph* of the system. See Figure 5.2 for an example of a graph and its reduced graph.

The following proposition about the reduced graph shall be useful in the proof of the central theorem of this chapter:

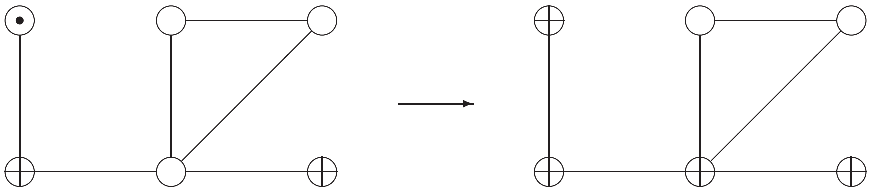

Figure 5.2: A graph $G(A)$ and its reduced graph $R(A)$.

Proposition 5.3 *Define K to be the subgraph of the reduced graph of a stably dissipative Lotka-Volterra system formed by the vertices with a $\bigcirc$ or a $\odot$ and the connections between them. Then K is a forest, i.e. a set of disjoint trees.*

Proof All we have to do is to check that the reduced graph has no closed paths of which the vertices are all of type $\bigcirc$ or $\odot$. Assume such a closed path exists and label its vertices from 1 to m. Then we have $a_{jj} = 0$ for each $j \in (1, \ldots, m)$, so given two adjacent vertices j and k on this closed path we must have

$$a_{jk} + a_{kj} = 0$$

since for a dissipative system we have $A \leq 0$. This means that if we consider the Lotka-Volterra system that consists of only this closed path, it is conservative. By Proposition 4.1 this means that we must have

$$a_{12} \cdots a_{m-1,m} a_{m1} = (-1)^m a_{1m} a_{m,m-1} \cdots a_{21},$$

a condition that is not preserved under small perturbations. Hence the original system is not stably dissipative. $\square$

We can now prove the claim, made earlier in this section, that the stably dissipative Lotka-Volterra system (5.4) has a global attractor with Hamiltonian dynamics on that attractor. The existence of the attractor was already shown by constructing the Lyapunov function (5.7). What remains is to show that this attractor has Hamiltonian dynamics. This theorem is the central result of the article by Duarte, Fernandes and Oliva [7].

Theorem 5.4 *Consider the stably dissipative Lotka-Volterra system (5.4) with fixed point* $\mathbf{q}$ *and the Lyapunov function V given by (5.7). Then the dynamics on the set $\dot{V} = 0$ are Hamiltonian. Moreover, they can be described by a Lotka-Volterra system of dimension $m \leq n$.*

Proof Consider the system restricted to $\dot{V} = 0$. We split the set of all variables x_j into two groups labeled by sets $J_\bigcirc$ and $J_\oplus$. In the first group $\{x_j\}_{j \in J_\bigcirc}$ we gather all the x_j's corresponding to vertices with a $\bigcirc$ or a $\odot$ in the reduced graph $R(A)$. In the second group $\{x_j\}_{j \in J_\oplus}$ we put all the x_j's that correspond to vertices with a $\oplus$ in $R(A)$. For $j \in J_\oplus$ we have $x_j = q_j$; hence the restricted system satisfies

$$\left\{ \begin{array}{lcll} \dot{x}_j &=& \left(\varepsilon_j + \sum_{k \in J_\oplus} a_{jk} q_k\right) x_j + \sum_{k \in J_\bigcirc} a_{jk} x_j x_k & \text{if} \quad j \in J_\bigcirc, \\ x_j &=& q_j & \text{if} \quad j \in J_\oplus. \end{array} \right. \tag{5.10}$$

Defining $\tilde{\varepsilon}_j = \varepsilon_j + \sum_{k\in J_\oplus} a_{jk}q_k$ and $\tilde{a}_{jk} = a_{jk}$ for $j,k \in J_\bigcirc$ we obtain the Lotka-Volterra system

$$\dot{x}_j = \tilde{\varepsilon}_j x_j + \sum_{k\in J_\bigcirc} \tilde{a}_{jk} x_j x_k \qquad (j \in J_\bigcirc). \tag{5.11}$$

The graph associated with the interaction matrix $\tilde{A} = (\tilde{a}_{jk})_{j,k\in J_\bigcirc}$ of system (5.11) is the subgraph K of the reduced graph $R(A)$ of the original system that is formed by the vertices with a $\bigcirc$ or a $\odot$ and the connections between them. The matrix $\tilde{A}$ satisfies $\tilde{a}_{jj} = 0$ and there is a diagonal matrix $D > 0$ such that $\tilde{A}D \leq 0$. Therefore we have

$$d_j\tilde{a}_{jk} + d_k\tilde{a}_{kj} = 0,$$

and hence

$$a_{jk} \neq 0 \Rightarrow a_{jk}a_{kj} < 0.$$

Finally we note that the $(q_j)_{j\in J_\bigcirc}$ are a solution of the system

$$\tilde{\varepsilon}_j + \sum_{k\in J_\bigcirc} \tilde{a}_{jk}q_k = 0 \qquad (j \in J_\bigcirc).$$

By Proposition 5.3 we therefore satisfy the conditions of Corollary 4.2, so system (5.11) has a Hamiltonian formulation. □

Summarizing, the proof shows that the dynamics on the attractor can be described by a Lotka-Volterra system of dimension $m \leq n$, whose associated graph is a tree, which is conservative and has a fixed point in $\mathbb{R}^n_+$. Hence by Corollary 4.2 the system has a Hamiltonian formulation. Conversely, any such system describes an attractor, because any system of which the associated graph is a tree (or a forest) is stably dissipative.

5.4 A six-dimensional example

We illustrate the theorems in this chapter using the following six-dimensional example system:

$$\left\{ \begin{array}{rcl} \dot{x}_1 &=& x_1(2 - 2x_2) \\ \dot{x}_2 &=& x_2(1 + 2x_1 - x_2 - 2x_3) \\ \dot{x}_3 &=& x_3(4 + 2x_2 - 2x_4 - 2x_5 - 2x_6) \\ \dot{x}_4 &=& x_4(-1 + 2x_3 - x_5) \\ \dot{x}_5 &=& x_5(-3 + 2x_3 + x_4) \\ \dot{x}_6 &=& x_6(-1 + 2x_3 - x_6) \end{array} \right. \tag{5.12}$$

This system has interaction matrix

$$A = \begin{pmatrix} 0 & -2 & 0 & 0 & 0 & 0 \\ 2 & -1 & -2 & 0 & 0 & 0 \\ 0 & 2 & 0 & -2 & -2 & -2 \\ 0 & 0 & 2 & 0 & -1 & 0 \\ 0 & 0 & 2 & 1 & 0 & 0 \\ 0 & 0 & 2 & 0 & 0 & -1 \end{pmatrix} \tag{5.13}$$

of which the quadratic form is given by

$$\mathbf{x}^T A\mathbf{x} = -x_2^2 - x_6^2.$$

This form is clearly negative definite and therefore system (5.12) is dissipative. It has a single equilibrium point $\mathbf{q}$ in $\mathrm{Int}(\mathbb{R}^6_+)$ given by

$$\mathbf{q} = (1, 1, 1, 1, 1, 1).$$

Thus the system is of the form of system (5.4).

The Lyapunov function of this system, defined by equation (5.7), is given by

$$V = \sum_{j=1}^{n}(x_j - q_j \log x_j) = \sum_{j=1}^{n}(x_j - \log x_j) \tag{5.14}$$

and has time derivative

$$\begin{aligned}
\dot{V} &= \sum_{j=1}^{n} \frac{\dot{x}_j}{x_j}(x_j - 1) \\
&= \sum_{j=1}^{n}(x_j - 1)\left(\varepsilon_j + \sum_{k=1}^{n} a_{jk}x_k\right) \\
&= \sum_{j=1}^{n}(x_j - 1)\left(\sum_{k=1}^{n} a_{jk}(x_k - 1)\right) \\
&= \sum_{j,k=1}^{n} a_{jk}(x_j - 1)(x_k - 1) \\
&= -2(x_1 - 1)(x_2 - 1) \\
&\quad +2(x_2 - 1)(x_1 - 1) - (x_2 - 1)^2 - 2(x_2 - 1)(x_3 - 1) \\
&\quad +2(x_3 - 1)(x_2 - 1) - 2(x_3 - 1)(x_4 - 1) - 2(x_3 - 1)(x_5 - 1) - 2(x_3 - 1)(x_6 - 1) \\
&\quad +2(x_4 - 1)(x_3 - 1) - (x_4 - 1)(x_5 - 1) \\
&\quad +2(x_5 - 1)(x_3 - 1) + (x_5 - 1)(x_4 - 1) \\
&\quad +2(x_6 - 1)(x_3 - 1) - (x_6 - 1)^2 \\
&= -(x_2 - 1)^2 - (x_6 - 1)^2.
\end{aligned}$$

which is clearly less than or equal to zero. V is therefore indeed a suitable Lyapunov function and the system has an attractor in the set $\{\mathbf{x} \in \mathrm{Int}(\mathbb{R}^6_+) : \dot{V}(\mathbf{x}) = 0\}$. By equation (5.9) we already know that we must have $x_2 = 1$ and $x_6 = 1$ on the attractor, since a_{22} and a_{66} are nonzero. Using this information, we can draw the associated graph of system (5.12), in which there are already two vertices of type $\oplus$. The propagation rules of Lemma 5.2 allow us to construct a reduced graph, in which four of the six vertices are of type $\oplus$. This graph and reduced graph are drawn in Figure 5.3.

The reduced graph illustrates Proposition 5.3: the subgraph formed by the vertices with a $\bigcirc$ (or a $\odot$, which are not present here) and the connections between them form a forest consisting of a single tree. For each of the four vertices that now have a $\oplus$ we know that on the attractor, the variable associated to the vertex goes to the equilibrium value. By

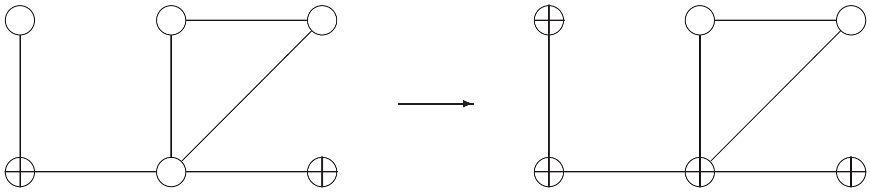

Figure 5.3: The graph and reduced graph of the example system (5.12).

Theorem 5.4 the dynamics of the system reduced to the variables associated with the two remaining vertices of type ○ (x_4 and x_5) are Hamiltonian on the attractor. In fact, the system on the attractor is the following two-dimensional conservative Lotka-Volterra system:

$$\begin{aligned} \dot{x}_4 &= x_4(1 - x_5) \\ \dot{x}_5 &= x_5(-1 + x_4) \end{aligned} \tag{5.15}$$

of which all orbits in $\mathrm{Int}(\mathbb{R}^2_+)$ are periodic around the equilibrium point $(1,1)$ (which can be characterized as a central node). See Figure 5.4.

Summarizing, we find that system (5.12) has an attractor given by the set $\dot{V} = 0$, where $V(\mathbf{x})$ is the Lyapunov function given by (5.14). On the attractor, four of the six components of $\mathbf{x}$ go to their equilibrium values, and the other two form a conservative Hamiltonian system, of which the solutions are periodic orbits.

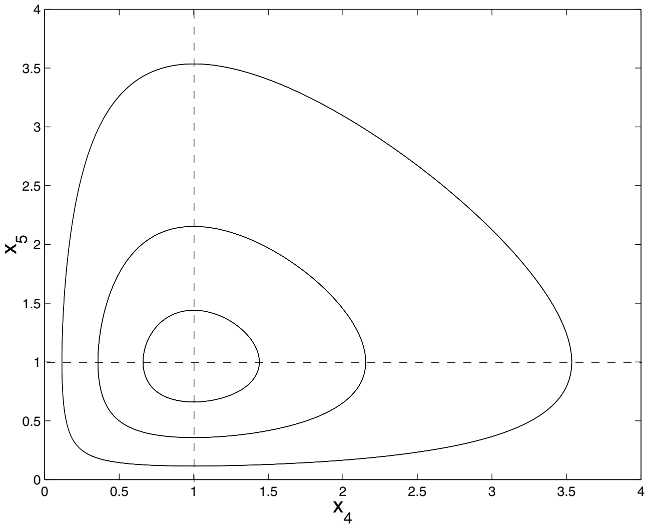

Figure 5.4: The dynamics on the attractor of system (5.12).

Chapter 6

Nonautonomous Lotka-Volterra systems

In the previous three chapters we discussed the three different types of autonomous Lotka-Volterra systems. However, there is no reason why the coefficients of the system could not be time-dependent[1]. In fact, if the equations are regarded as a model for a biological system, time-dependence comes in naturally. There might for instance be dependence on the season (which gives a periodic dependence on time). Systems that have such periodic or almost periodic coefficients are the subject of this chapter. In the first section we will consider systems of which only the growth rates (the ε_j's) are time-dependent. After that we widen our view and also allow for time-dependent interaction coefficients.

Another time-dependent feature of real-life systems is the fact that newly born animals are not immediately able to reproduce. To account for this, we introduce what is known as stage structure, effectively resulting in a time delay. This is done in the next chapter.

As in the autonomous case, a species living in a competitive Lotka-Volterra system is either permanent or will become extinct. The results in this chapter generalize those in Chapter 3 in that respect. However, when the system becomes nonautonomous, also systems that would be conservative in the time-independent case (simple predator-prey systems) can now have extinction or an attractor.

A basic introduction into the subject of this chapter is given in two articles [30] and [31] by Redheffer. As he states in the introduction of the first article, Redheffer had become interested in the subject due to Ahmad and Lazer. Their main interest is on average conditions on the system to be permanent or leading to extinction. Their article [1] (together with the response [32] from Redheffer) is the basis of the first section of this chapter. Important results in the direction of the full time-dependent competitive system were obtained by Gopalsamy [8, 9], Tineo and Alvarez [39], Montes de Oca and Zeeman [25] and again Ahmad and Lazer [2]. The main results from these articles are included in Section 6.2. Finally, the recent articles by Pinghua and Rui [27], Zhao and Cheng [45] and Zhao and Jiang [46] give conditions on general nonautonomous predator-prey systems to be permanent and attractive (Section 6.3).

[1] Introducing time-dependence in the coefficients, as we do here, is one possible generalization that can be made to make the system more realistic. Of course, there are also other possibilities, for instance introducing diffusion (modelling the feature that not all specimens live at exactly the same location in space). Results on those kind of systems are given in a recent article by Hutson, Lou and Mischaikow [17].

6.1 Competitive systems with constant interaction coefficients

In this section, following Ahmad and Lazer [1] and Redheffer [32] we look at the Lotka-Volterra system with time-dependent growth rate, but constant interaction coefficients:

$$\dot{x}_j = \varepsilon_j(t)x_j - \sum_{k=1}^{n} a_{jk}x_j x_k \qquad (j = 1, \dots, n). \tag{6.1}$$

where the minus sign before the summation indicates that we are dealing with a competitive system. It is implicitly assumed that $a_{jk} \geq 0$ for all j, k in order to really have a competitive system. Ahmad and Lazer initially assume that the interaction matrix $A = (a_{jk})$ also satisfies $A \geq 0$, by which assumption the system is also dissipative. However, as they already hint at and as is shown by Redheffer, the result holds for general 'dissipative competitive' systems, meaning that it is sufficient that there is a matrix $D > 0$ such that $AD \geq 0$.

Notation We denote by $\mathbf{d}$ the vector consisting of the diagonal elements of the diagonal matrix D, so $D = \operatorname{diag}(\mathbf{d})$. As before, for any two vectors $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n$ we have a partial ordering by

$$\mathbf{x} \leq \mathbf{y} \quad \text{meaning} \quad x_i \leq y_i, \qquad \mathbf{x} < \mathbf{y} \quad \text{meaning} \quad x_i < y_i \qquad \text{for} \quad i = 1, \dots, n.$$

Finally, for any number $a \in \mathbb{R}$ we define

$$a^+ = \max(a, 0), \qquad a^- = \min(a, 0).$$

6.1.1 Existence and uniqueness of solutions

There is a single, straightforward (though on first glance somewhat technical) condition on the coefficients of equation (6.1) for it to have a unique solution. In a hand waving manner, the condition can be simply stated that the growth rates should at all time be bounded away from both zero and infinity. More rigorously, it reads:
For all $t > 0$ (or $t \in \mathbb{R}$, as the case may be), let there be constant vectors $\mathbf{d} > 0$ and $\tilde{\mathbf{d}} > 0$ such that

$$a_{ii}\tilde{d}_i + \sum_{j \neq i} a_{ij}^+ d_j \leq \varepsilon_i(t) \leq a_{ii}d_i + \sum_{j \neq i} a_{ij}^- d_j \qquad i = 1, \dots, n \tag{6.2}$$

The following theorem is a special case of Theorem 1 of [30] and the proof can be found there.

Theorem 6.1 *If conditions (6.2) hold, then for any solution $\mathbf{x}(t)$ of (6.1) we have*

1. $\tilde{\mathbf{d}} \leq \mathbf{x}(0) \leq \mathbf{d}$ *implies* $\tilde{\mathbf{d}} \leq \mathbf{x}(t) \leq \mathbf{d}$ *for all* $t > 0$.
2. *There exists a solution* $\mathbf{x}^*(t)$ *satisfying* $\tilde{\mathbf{d}} \leq \mathbf{x}^*(t) \leq \mathbf{d}$ *for all* $t \in \mathbb{R}$.
3. *The solution* $\mathbf{x}^*(t)$ *is the only one bounded away from zero and infinity on* $\mathbb{R}$.
4. *Every solution satisfies* $\tilde{\mathbf{d}} \leq \liminf \mathbf{x}(t) \leq \limsup \mathbf{x}(t) \leq \mathbf{d}$.
5. *Every pair of solutions* $\mathbf{x}$, $\tilde{\mathbf{x}}$ *satisfies* $\lim |\mathbf{x}(t) - \tilde{\mathbf{x}}(t)| = 0$.

6. *If the vector $\varepsilon(t)$ of growth rates is periodic, there exists exactly one periodic solution $\mathbf{x}(t)$ on $\mathbb{R}$.*

7. *If the vector $\varepsilon(t)$ of growth rates is almost periodic, there exists exactly one almost periodic solution $\mathbf{x}(t)$ on $\mathbb{R}$.*

Remark In the case that all $a_{ij} \geq 0$ (so, using the classification of Section 1.2, for competitive systems) there is a simpler way to express conditions (6.2). In this special case we can take $d_i = \sup(\varepsilon_i(t)/a_{ii})$. Then there is a $\tilde{\mathbf{d}}$ such that (6.2) holds if

$$\inf \varepsilon_i(t) > \sum_{j \neq i} \frac{a_{ij}}{a_{jj}} \sup \varepsilon_j(t).$$

6.1.2 Example

We consider the following example system

$$\begin{array}{rcl} \dot{x}_1(t) & = & x_1(t)(1 + \frac{1}{2}\sin(t) - x_1(t) - \frac{1}{8}x_2(t)) \\ \dot{x}_2(t) & = & x_2(t)(1 + \frac{1}{2}\cos(t) - \frac{1}{8}x_1(t) - x_2(t)) \end{array} \tag{6.3}$$

which satisfies equation (6.2) for $d = (2, 2)$ and $\tilde{d} = (\frac{1}{4}, \frac{1}{4})$. By Theorem 6.1 it therefore has a unique periodic solution that satisfies $\frac{1}{4} \leq x_i(t) \leq 2$ for $i = 1, 2$. This solution is illustrated by the plot in Figure 6.1.

The most important difference between this system and system (3.1) in Section 3.1 is that here the periodic orbit is the unique solution, whereas in the original two-dimensional competitive system a periodic orbit was impossible (see Section 3.1.2). We can visualize why as follows: even though at any given point in time the situation is exactly as in Section 3.1 (with an internal saddle point and two basins of attraction), the saddle point and its stable manifold now move in time. As a consequence, an orbit starting in the basin of attraction of one of the axial equilibria, can be 'run over' by the stable manifold of the saddle point and end up in the other attraction basin. Since the motion of the saddle point (and hence its stable manifold, the separation line between the two basins) is periodic, this allows for a periodic movement. Theorem 6.1 states that, given conditions (6.2), this is exactly what will happen.

6.2 Nonautonomous competitive systems

As seasons change, some species might feel less (or more) encouraged to reproduce, resulting in a time-dependent growth rate. Of course, this indirectly influences the other species in the system; after all, if there are less sheep to compete, the rabbits will have more to eat.

Apart from this indirect effects (which are included in the time-dependent growth rate model of the previous section), there is also the possibility of direct effects. For instance, if one of the species hibernates, they will temporarily disappear from the field, but return in spring with a healthy appetite. To include such kind of time-dependent behaviour into our

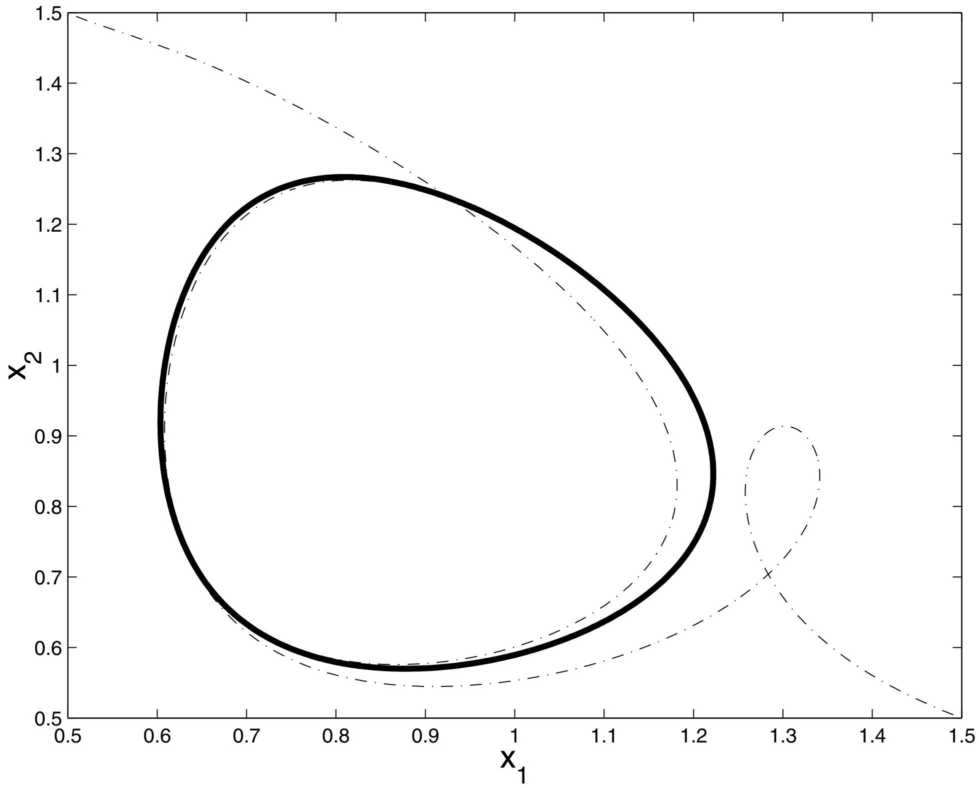

Figure 6.1: A periodic solution of a nonautonomous competitive system.

model, we also need to make the interaction coefficients time dependent. Not surprisingly, the resulting system becomes

$$\dot{x}_j = \varepsilon_j(t)x_j - \sum_{k=1}^{n} a_{jk}(t)x_jx_k \qquad (j = 1, \ldots, n). \tag{6.4}$$

All functions $\varepsilon_j(t)$ and $a_{jk}(t)$ are taken to be continuous in time. Since we are still looking at competitive systems, we take $a_{jk}(t) \geq 0$ for all j, k and all time.

There are two main results in the direction of nonautonomous competitive systems. One is by Montes de Oca and Zeeman [25], who generalize Theorem 3.1. They give sufficient and necessary conditions (similar, of course, to those of Theorem 3.1) on the coefficients such that exactly one species survives (and its number of specimens converges on its carrying capacity) and all others become extinct.

The other main result is more general and somewhat similar to an 'ordinary' uniqueness theorem. The precise statement is given in the next subsection. There are two different ways to approach this theorem, giving different sets of conditions under which it holds. If the time-dependence is (almost) periodic, the results by Gopolsamy [8, 9] and Tineo and Alvarez [39] give sufficient conditions on the coefficients for the theorem to be true. Their way of looking at the problem thus resembles the approach by Montes the Oca and Zeeman.

Based on their results on the simpler system (6.1), Ahmad and Lazer found not conditions on the coefficients themselves, but on their time averages [2]. Because the coefficients do not have to be (almost) periodic for their results to hold, they are a generalization of the earlier statements that give conditions on the coefficients.

6.2.1 Conditions on the coefficients

In order to simplify the next statement, we introduce the following notation for any scalar function $g(t)$ of time:

$$\begin{aligned} g^M &= \sup\{g(t) : t \geq 0\} \\ g^L &= \inf\{g(t) : t \geq 0\} \end{aligned}$$

We assume all coefficients of (6.4) are nonnegative and bounded from above. For the growth rates $\varepsilon_j(t)$ and 'diagonal elements' $a_{jj}(t)$ we also assume strict positivity. Given these basic assumptions, the sufficient conditions on the coefficients of (6.4) for the next theorem to hold are

$$\varepsilon_j^L > \sum_{\substack{k=1 \\ k\neq j}}^{n} \frac{a_{jk}^M \varepsilon_k^M}{a_{kk}^L} \quad \forall j = 1, \ldots, n. \tag{6.5}$$

Theorem 6.2 *If conditions (6.5) hold, then the following two statements are true:*

1. *If* $\mathbf{x}(t)$ *is a solution of system (6.4) with initial conditions in* $\mathrm{Int}(\mathbb{R}_+^n)$, *then*

$$0 < \inf_{t\geq 0} x_j(t) \leq \sup_{t\geq 0} x_j(t) < \infty$$

   for all $j = 1, \ldots, n$.

2. *If* $\mathbf{x}(t)$ *and* $\mathbf{y}(t)$ *are two solutions of system (6.4) with initial conditions in* $\mathrm{Int}(\mathbb{R}_+^n)$, *then*

$$\lim_{t\to\infty} (x_j(t) - y_j(t)) = 0$$

   for all $j = 1, \ldots, n$.

The first statement tells us that any solution that starts in $\mathrm{Int}(\mathbb{R}_+^n)$ stays bounded for all time (so no species can grow to infinite size - a rather realistic feature). Furthermore, once in $\mathrm{Int}(\mathbb{R}_+^n)$, a solution stays there forever (though it can of course approach any boundary plane arbitrarily close). This is in line with the results on the autonomous problem, where also the boundary planes (and hence also the interior of $\mathbb{R}_+^n$) were invariant.

The second statement of Theorem 6.2 can be considered a uniqueness result: no matter which initial conditions we choose, the final behaviour of the system will always be the same.

A proof of this theorem can be found in the article by Tineo and Alvarez [39].

6.2.2 Conditions on the averages

As stated in the introduction of this section, Ahmad and Lazer [2] found that instead of looking at the coefficients themselves, it can be sufficient to look only at their time averages, resulting in weaker conditions for Theorem 6.2 to hold. To average over time, we use the following functional of any function $g(t)$ of time:

$$A(g, t_1, t_2) = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} g(s)ds,$$

which allows us to introduce lower and upper averages of g (denoted $L(g)$ and $M(g)$ respectively):

$$\begin{aligned} L(g) &= \lim_{s\to\infty} \inf\{A(g,t_1,t_2) : (t_2 - t_1) \geq s\}, \\ M(g) &= \lim_{s\to\infty} \sup\{A(g,t_1,t_2) : (t_2 - t_1) \geq s\}. \end{aligned}$$

That the limits exist easily follows from the fact that the set $\{A(g,t_1,t_2) : (t_2 - t_1) \geq s\}$ gets smaller with increasing s.

The Ahmad-Lazer 'average conditions' to replace conditions (6.5) are given by

$$L(\varepsilon_j) > \sum_{\substack{k=1\\k\neq j}}^{n} \frac{a_{jk}^M M(\varepsilon_k)}{a_{kk}^L} \qquad (j = 1, \ldots, n). \tag{6.6}$$

To see that conditions (6.5) imply conditions (6.6), we note that for any function $g(t)$ of time

$$g_L \leq A(g,t_1,t_2) \leq g^M,$$

and hence

$$g^L \leq L(g) \leq M(g) \leq g^M.$$

On the other hand, as the example in the next subsection will show, there are systems for which conditions (6.6) hold, but conditions (6.5) do not.

6.2.3 Example

An example system supporting the claim in the last section is given by

$$\begin{aligned} \dot{x}_1(t) &= x_1(t)\Big(5 + 4\cos t - (3+\cos t)x_1(t) - x_2(t) - x_3(t)\Big) \\ \dot{x}_2(t) &= x_2(t)\Big(4 + 3\sin t - x_1(t) - (3+\sin t)x_2(t) - x_3(t)\Big) \\ \dot{x}_3(t) &= x_3(t)\Big(3 + 2\cos 2t - x_1(t) - \tfrac{1}{5}x_2(t) - (4+\cos 2t)x_3(t)\Big) \end{aligned} \tag{6.7}$$

which clearly satisfies the boundedness and positivity conditions on the coefficients. For this system we have

$$\varepsilon^L = \begin{pmatrix} 1\\1\\1 \end{pmatrix} \qquad \varepsilon^M = \begin{pmatrix} 9\\7\\5 \end{pmatrix} \qquad A^L = \begin{pmatrix} 2 & 1 & 1\\ 1 & 2 & 1\\ 1 & \frac{1}{5} & 3 \end{pmatrix} \qquad A^M = \begin{pmatrix} 4 & 1 & 1\\ 1 & 4 & 1\\ 1 & \frac{1}{5} & 5 \end{pmatrix}$$

so conditions (6.5) do not hold in any of the three cases (for instance, for $j = 1$, we have that the left hand side is 1 and the right-hand side is $\frac{31}{6}$). However, we also have

$$L(\varepsilon_1) = M(\varepsilon_1) = 5, \quad L(\varepsilon_2) = M(\varepsilon_2) = 4, \quad L(\varepsilon_3) = M(\varepsilon_3) = 3,$$

which gives for conditions (6.6):

$$5 > \tfrac{4}{2} + \tfrac{3}{3}, \quad 4 > \tfrac{5}{2} + \tfrac{3}{3}, \quad 3 > \tfrac{5}{2} + \tfrac{1}{5}\tfrac{4}{2},$$

so these conditions are satisfied. We can therefore conclude that Theorem 6.2 holds. To illustrate this, we plot the numerical solution in Figure 6.2.

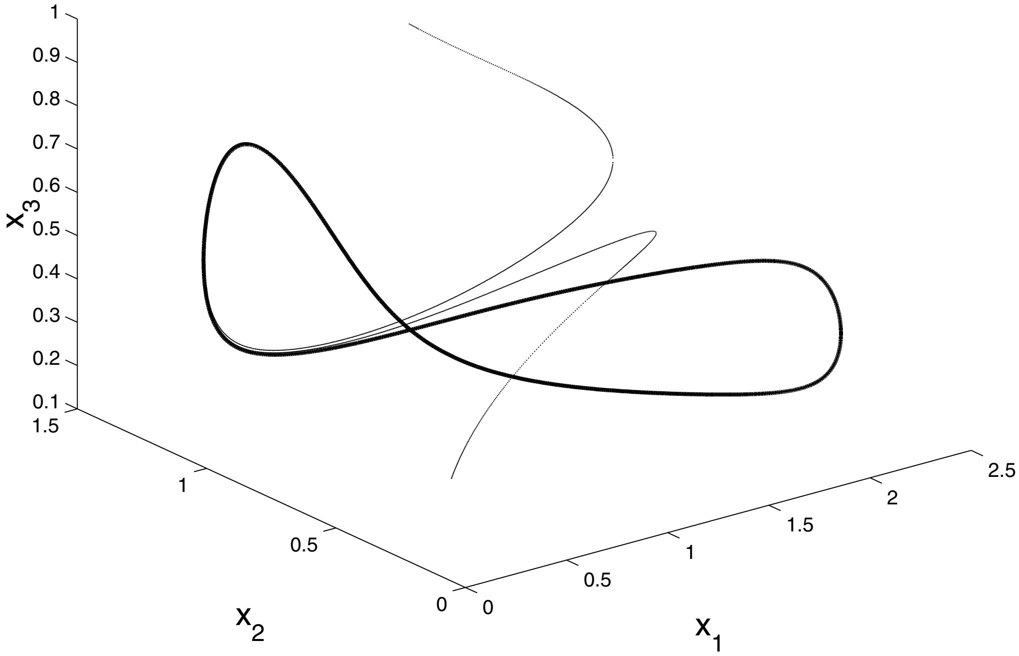

Figure 6.2: A periodic and attractive solution of the three dimensional nonautonomous competitive example system (6.7).

6.3 Nonautonomous predator-prey systems

In three recent articles, the two different approaches of the previous section were applied to (dissipative) predator-prey Lotka-Volterra systems. Pinghua and Rui [27] and Zhao and Cheng [45] followed the 'conditions on the coefficients' approach and were able to prove existence, uniqueness and global attractivity for periodic solutions. Following the ideas of Ahmad and Lazer, Zhao and Jiang [46] instead give average conditions on the system which ensure permanence without requiring that the solutions are periodic.

For m predator and n prey species, the nonautonomous Lotka-Volterra equations are given by

$$\begin{cases} \dot{x}_i(t) = x_i(t)\left(\varepsilon_i(t) - \sum_{k=1}^{n} a_{ik}(t)x_k(t) - \sum_{k=1}^{m} c_{ik}(t)y_k(t)\right) & (i = 1, \ldots, n), \\ \dot{y}_j(t) = y_j(t)\left(-\gamma_j(t) + \sum_{k=1}^{n} d_{jk}(t)x_k(t) - \sum_{k=1}^{m} b_{jk}(t)y_k(t)\right) & (j = 1, \ldots, m). \end{cases} \tag{6.8}$$

As before, we assume that for all time, all coefficients are bounded from above and nonnegative; the growth and death rates (the ε_i's and γ_j's) and 'self-interactions' (the a_{ii}'s and b_{jj}'s) are also assumed to be strictly positive.

In this section we use the same notation for infima, suprema and time averages as in section 6.2.

6.3.1 Conditions on the coefficients

In the article by Pinghua and Rui all coefficients of system (6.8) are assumed to be periodic in time with period T. To simplify notation, they introduce the following quantities (for $i = 1, \ldots, n$ and $j = 1, \ldots, m$):

$$\begin{aligned}
p_i &= \frac{\varepsilon_i^M}{a_{ii}^L}, \\
q_j &= \frac{1}{b_{jj}^L}\left(\sum_{k=1}^{n} d_{jk}^M p_k - \gamma_j^L\right), \\
\alpha_i &= \frac{1}{a_{ii}^M}\left(\varepsilon_i^L - \sum_{\substack{k=1\\k\neq i}}^{n} a_{ik}^M p_k - \sum_{k=1}^{m} c_{ik}^M q_k\right), \\
\beta_j &= \frac{1}{b_{jj}^M}\left(-\gamma_j^M + \sum_{k=1}^{n} d_{jk}^M \alpha_k - \sum_{\substack{k=1\\k\neq i}}^{m} e_{jk}^M q_k\right).
\end{aligned}$$

Assuming that for all i and j the inequalities $\alpha_i > 0$, $\beta_j > 0$ and $q_j > 0$ hold, Pinghua and Rui proceed to prove the following two inequalities on the populations:

$$\begin{array}{ccccccc}
\alpha_i & \leq & x_i & \leq & p_i & (i = 1, \ldots, n) \\
\beta_j & \leq & y_j & \leq & q_j & (j = 1, \ldots, m)
\end{array} \tag{6.9}$$

Denoting by $(\mathbf{X}(t, \mathbf{x}_0), \mathbf{Y}(t, \mathbf{y}_0))$ any solution $(\mathbf{x}(t), \mathbf{y}(t))$ of system (6.8) with initial conditions $\mathbf{x}(0) = \mathbf{x}_0, \mathbf{y}(0) = \mathbf{y}_0$, we can use inequalities (6.9) to construct an invariant set S in $\text{Int}(\mathbb{R}_+^{n+m})$:

$$S = \{(\mathbf{X}, \mathbf{Y}) \in \text{Int}(\mathbb{R}_+^{n+m}) : \alpha_i \leq x_i \leq p_i (i = 1, \ldots, n), \beta_j \leq y_j \leq q_j (j = 1, \ldots, m)\}.$$

We now use the Poincaré map (or 'shift operator') $\sigma : \mathbb{R}^{n+m} \to \mathbb{R}^{n+m}$ defined by

$$\sigma(\mathbf{X}(t, \mathbf{x}_0), \mathbf{Y}(t, \mathbf{y}_0)) = (\mathbf{X}(t + T, \mathbf{x}_0), \mathbf{Y}(t + T, \mathbf{y}_0)). \tag{6.10}$$

Obviously, any fixed point of σ would be a T-periodic solution of system (6.8). The existence of such a fixed point is guaranteed by Brouwer's Fixed Point Theorem (Theorem B.10). Summarizing, we find the following existence theorem:

Theorem 6.3 *If the coefficients of system (6.8) satisfy $\alpha_i > 0$, $\beta_j > 0$ and $q_j > 0$ for all $i = 1, \ldots, n$ and $j = 1, \ldots, m$, then the system has at least one strictly positive T-periodic solution.*

In order for the solution provided by Theorem 6.3 to be unique and globally attractive, we need a additional requirements on the coefficients. These requirements turn out to be quite sensible. For the prey species, they are that the intra-species competition should outweigh the cumulative effect of competition with other prey species and the cumulative consumption rates by all the predators of their species. This means that the dominant (though maybe only slightly so) time evolution effect for them is their own logistic growth (which is, after all, the best they could hope for, even if all other species would become extinct). For the predators on the other hand, the requirement should be that for their favourite prey species, their own benefit from eating it should outweigh the cumulative effects of other predator species eating this prey and the direct competitive effects between the predator species (for example, the fight for territory). If this requirement were not met, either the other predators would eat all the prey (leaving nothing for the species we are looking at) or the others would easily win the inter species competition. Both cases would lead to the extinction of the species at hand.

Put down into formula, the abovementioned requirements read:

$$\begin{aligned} a_{ii}(t) &> \sum_{\substack{k=1\\k\neq i}}^{n} a_{ki}(t) + \sum_{k=1}^{m} d_{ki}(t) \quad (i=1,\ldots,n),\\ b_{jj}(t) &> \sum_{k=1}^{n} c_{kj}(t) + \sum_{\substack{k=1\\k\neq j}}^{m} b_{kj}(t) \quad (j=1,\ldots,m). \end{aligned} \tag{6.11}$$

Theorem 6.4 *If the coefficients of system (6.8) satisfy $\alpha_i > 0$, $\beta_j > 0$ and $q_j > 0$ for all $i = 1,\ldots,n$ and $j = 1,\ldots,m$ and inequalities (6.11), then the system has a unique and strictly positive T-periodic solution which is globally attracting.*

To prove this theorem, Pinghua and Rui use that there is a T-periodic solution $(\mathbf{U}(t),\mathbf{V}(t))$ and introduce the following Lyapunov function for any solution $(\mathbf{X}(t),\mathbf{Y}(t))$:

$$L(t) = \sum_{i=1}^{n} |U_i(t) - X_i(t)| + \sum_{j=1}^{m} |V_j(t) - Y_j(t)|.$$

Some basic algebra then shows that all solutions indeed converge to the periodic one.

6.3.2 Conditions on the averages

Like in the competitive case, the same results as in the previous section can be obtained using only average conditions on the coefficients. The advantage of this approach is that the coefficients no longer need to be periodic in time. In their recent article, Zhao and Jiang [46] showed that for existence of a strictly positive, bounded solution[2] average conditions are sufficient. If we also want to make sure that the system is globally attractive, additional conditions on the coefficients like (6.11) are still necessary. In the article by Zhao and Jiang, those additional conditions are taken from the article by Zhao and Chen [45].

To find the average conditions, Zhao and Jiang start with looking at the logistic equations for the prey obtained from system (6.8) by taking all other populations equal to zero:

$$\dot{x}_i(t) = x_i(t)(\varepsilon_i(t) - a_{ii}(t)x_i(t)) \qquad (i=1,\ldots,n) \tag{6.12}$$

For any solution $\bar{x}_i(t)$ of (6.12) with $\bar{x}_i(0) > 0$ they deduce that, for any solution $(\mathbf{x}(t),\mathbf{y}(t))$ of system (6.8), the following statement holds:

[2] Zhao and Jiang use the terminology that system (6.8) is called permanent if there is a solution that is both strictly positive and bounded for all time.

For any $\bar{\varepsilon} > 0$ there is a $T_1 > 0$ such that for each component x_i of $\mathbf{x}$ and any time $t > T_1$ we have

$$x_i(t) \leq \bar{x}_i(t) + \bar{\varepsilon}.$$

Based on this observation, they define the constant ζ_1 as

$$\zeta_1 = \sup\{\bar{x}_i(t) + \bar{\varepsilon} : t \geq 0, i = 1, \ldots, n\},$$

which satisfies $0 < \zeta_1 < \infty$ and is independent of the solution $\bar{x}_i(t)$ of equation (6.12). Hence we find

$$x_i(t) \leq \zeta_1 \qquad (i = 1, \ldots, n), \tag{6.13}$$

which suggests the following as a first average condition on the system:

$$M\left(-\gamma_j + \sum_{k=1}^{n} d_{jk}\zeta_1\right) > 0 \qquad (j = 1, \ldots, m). \tag{6.14}$$

Using condition (6.14), Zhao and Jiang proceed to show that a similar construction is possible for the predator species. This gives rise to a constant ζ_2, defined analogously to ζ_1 and a time $T_2 \geq T_1$, for which we have for all $t > T_2$

$$y_j(t) \leq \zeta_2 \qquad (j = 1, \ldots, m). \tag{6.15}$$

Based on this, their second average condition is

$$M\left(\varepsilon_i - \sum_{\substack{k=1\\k\neq i}}^{n} a_{ik}\zeta_1 - \sum_{k=1}^{m} c_{ik}\zeta_2\right) > 0 \qquad (i = 1, \ldots, n). \tag{6.16}$$

Assuming (6.14) and (6.16) to hold, Zhao and Jiang find that there is also a constant $\mu_1 > 0$ and a time $T_3 \geq T_2$ such that for $t > T_3$

$$x_i(t) \geq \mu_1 \qquad (i = 1, \ldots, n). \tag{6.17}$$

This gives rise to a third average condition

$$M\left(-\gamma_j + \sum_{k=1}^{n} d_{jk}\mu_1 - \sum_{\substack{k=1\\k\neq j}}^{m} b_{jk}\zeta_2\right) > 0 \qquad (j = 1, \ldots, m). \tag{6.18}$$

Finally it turns out that also assuming (6.18), there is yet another constant $\mu_2 > 0$ and time $T_4 \geq T_3$ such that we have for $t > T_4$

$$y_j(t) \leq \mu_2 \qquad (j = 1, \ldots, m). \tag{6.19}$$

Hence, using the three average conditions (6.14), (6.16) and (6.18), Zhao and Jiang have shown that, for initial conditions in $\mathrm{Int}(\mathbb{R}_+^{n+m})$, any solution of system (6.8) is both strictly positive and bounded. Combined with the conditions provided by Zhao and Chen in [45] for a solution to be globally attractive, we find the following result.

Theorem 6.5 *If conditions (6.14), (6.16) and (6.18) are met, system (6.8) is permanent. If there also exist strictly positive real numbers λ_i, ω_j and κ ($i = 1, \ldots, n$, $j = 1, \ldots, m$) such that*

$$\begin{aligned}
\lambda_i a_{ii}(t) &> \sum_{\substack{k=1\\k\neq i}}^{n} \lambda_k a_{ki}(t) + \sum_{k=1}^{m} \omega_k d_{ki}(t) + \kappa \qquad (i = 1, \ldots, n),\\
\omega_j b_{jj}(t) &> \sum_{k=1}^{n} \lambda_k c_{kj}(t) + \sum_{\substack{k=1\\k\neq j}}^{m} \omega_k b_{kj}(t) + \kappa \qquad (j = 1, \ldots, m),
\end{aligned}$$

then system (6.8) is permanent and globally attractive.

6.3.3 Example

To illustrate both approaches in this section, we use the following example system:

$$\begin{aligned}
\dot{x}(t) &= x(t)\Big((5+\sin(t)) - (13+\cos(t))x(t) - (5+\cos(t))y(t)\Big)\\
\dot{y}(t) &= y(t)\Big(-\frac{1}{100}(2+\sin(t)) + \frac{1}{4}(3+\sin(t))x(t) - (3-\sin(t))y(t)\Big)
\end{aligned} \tag{6.20}$$

where y represents the number of predators and x the number of prey. From the coefficients of equation (6.20) we can compute the quantities defined in Section 6.3.1

$$p = \frac{1}{2} \qquad q = \frac{49}{200} \qquad \alpha = \frac{253}{1400} \qquad \beta = \frac{211}{5600}.$$

Thus all of these are positive, and by equation (6.9) we have

$$\begin{aligned}
\frac{253}{1400} &\leq x \leq \frac{1}{2}\\
\frac{211}{5600} &\leq y \leq \frac{49}{200}
\end{aligned}$$

so our system is permanent. Since the inequalities (6.11) are also satisfied, Theorem 6.4 holds and system (6.20) has a unique, globally attracting periodic orbit.

Of course, we also want to check if the average conditions hold. However, finding the exact values of ζ_1, ζ_2, μ_1 and μ_2 as defined above can be cumbersome. Fortunately, all we need is to find bounds on the values of x and y, and we already did that. Simplifying even a little more to make the computations of the average conditions simpler (but still valid), we take as upper limits

$$\zeta_1 = \frac{1}{2} \qquad \zeta_2 = \frac{1}{4} > \frac{49}{200},$$

and as lower limits

$$\mu_1 = 18 < \frac{253}{1400} \qquad \mu_2 = \frac{3}{8} < \frac{211}{5600}.$$

Using these, we can compute if the three average conditions hold. From (6.14) we have

$$M\left(-\frac{1}{100}(2+\sin(t)) + \frac{1}{8}(3+\sin(t))\right) = M\left(\left(\frac{3}{8}-\frac{1}{50}\right) + \left(\frac{1}{8}-\frac{1}{100}\right)\sin(t)\right) > 0,$$

so the first condition is satisfied. The second one (6.16) requires

$$M\left(5+\sin(t)-\frac{1}{4}(5+\cos(t))\right)=M\left(\frac{15}{4}+\sin(t)-\frac{5}{4}\cos(t)\right)>0,$$

so this condition is also met. Finally, to satisfy (6.18) we need

$$M\left(-\frac{1}{100}(2+\sin(t))+18\cdot\frac{1}{4}(3+\sin(t))\right)=M\left(\left(\frac{27}{2}-\frac{1}{50}\right)+\left(\frac{9}{2}-\frac{1}{100}\right)\sin(t)\right)>0,$$

which clearly also holds. Hence all three average conditions are met, and Theorem 6.5 tells us that system (6.20) is permanent. To see that it is also globally attractive, we observe that

$$\begin{aligned} 13+\cos(t) &> \frac{1}{4}(3+\sin(t)) \\ 3\cdot\left(3-\sin(t)\right) &> 5+\cos(t) \end{aligned}$$

so the additional conditions for global attractivity are met as well. Therefore, both approaches tell us that system (6.20) must have an attracting periodic orbit, which is illustrated in Figure 6.3.

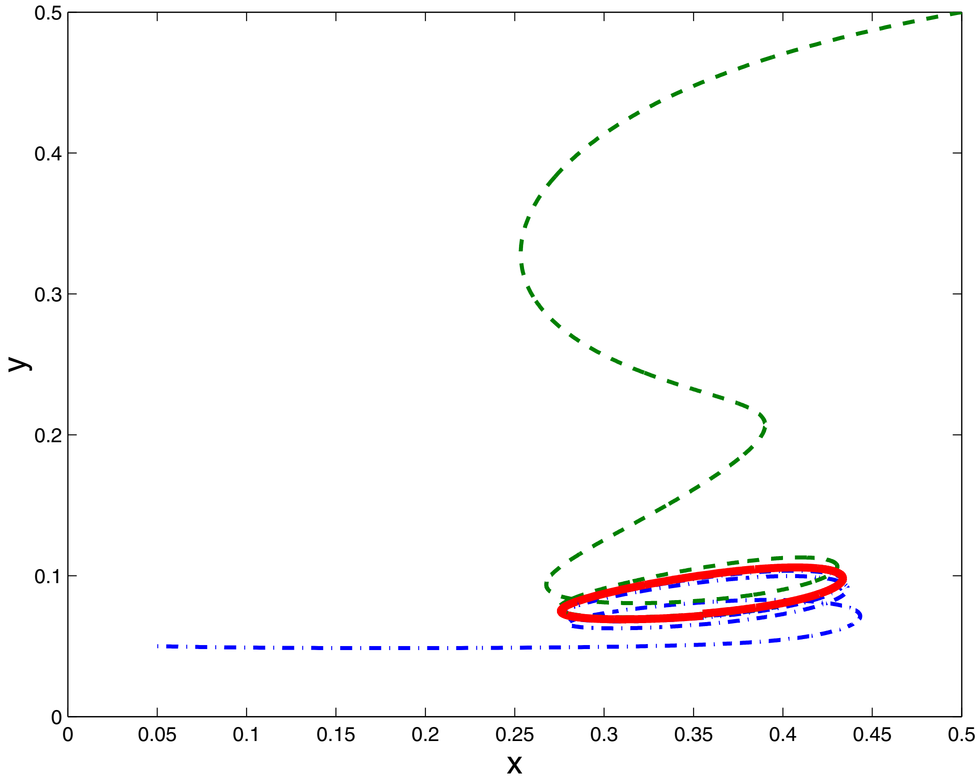

Figure 6.3: A periodic and globally attractive solution of the nonautonomous predator-prey example system (6.20).

Chapter 7

Lotka-Volterra systems with stage structure

In this chapter, we finally get rid of the extremely unrealistic feature exhibited by the systems studied so far, namely that newly born specimens of any species are immediately able to compete and reproduce (and indeed do so). In order to include the effect that in real life, newly born first have to grow up, we introduce what is known as stage structure into our system. This means that the population of each species is divided into two subgroups, consisting of the immature and the mature specimens. Based on the growth rate of the species, new immature specimens are born. During the first period τ of their life, they do not reproduce and do not compete with other species (i.e. they are taken care of by their parents). If they survive the immature period τ, they become mature, which in our model means that an immature specimen dies and a mature one is born. For the mature specimens, life is just like in the case without stage structure: they reproduce (producing, of course, new immature specimens), they compete for resources or try to outwit predators, and finally they die.

This kind of stage structure was applied to a single species by Aiello and Freedman [3]. They found that the introduction of stage structure has no effect on the permanence of the species, but, by choosing appropriate variables, it might maximize the total carrying capacity of the population.

Following this result, Wang and Chen [42] studied the predator-prey system with stage structure for the predator species, whereas Zhang [44] studied the system with stage structure for both predator and prey[1]. In both cases, it turns out that the introduction of stage structure might change the dynamics of the system from a single equilibrium attractor (when there is no stage structure) to an attracting periodic orbit. However, in line with the result for the single species model, if the system was permanent without the time delay, it still is after we add it.

In three recent papers, Liu, Chen et al. [23, 22, 21] found results on general (i.e. n-dimensional) competitive systems with stage structure. As usual, they looked at conditions for permanence, and, using monotone semiflow theory[2], global attractivity. In this chapter, we mainly follow their most recent article [21], in which the complete model is discussed.

[1] In both articles, the system exists of a single predator and a single prey species.

[2] See, for instance, the previously mentioned book by Smith [36].

7.1 A nonautonomous competitive model with stage structure

In this chapter, we shall denote by x_i the number of mature specimens of the i-th species, and by y_i the number of immature ones. The length of the immature stage of species i is denoted by τ_i. Immature specimens neither reproduce nor compete. However, we do allow for the possibility that they die before reaching the mature stage. Hence, apart from the birth rate ε_i we had before, we also need a death rate, which we denote by γ_i. Any immature specimen that survives for a time τ_i is of course immediately granted promotion to the ranks of the mature. All mature do compete amongst themselves and with the other species, just like in the previously discussed models[3], which is modeled using the interaction coefficients a_{ij}. All coefficients (the birth and death rates and interaction coefficients) are again assumed to be functions of time, but all periodical with a common period ω. We also assume (like in the previous chapter) that they all are both strictly positive for all time. Because of the periodicity, we do not have to enforce boundedness in this case.

The only part of the model which is not completely obvious from the definitions above is how we compute the growth rate of the number of mature specimens of a certain species. First of all, all specimens of species i that become mature at time t were born at time $t-\tau_i$. The number of born individuals at that time is $I_i(t-\tau_i) = \varepsilon_i(t-\tau_i)x_i(t-\tau_i)$. However, not all of them reach the mature state. To compute which fraction survives, we use that the quantity $I(s)$ satisfies the differential equation

$$\begin{cases} \dfrac{dI_i(s)}{ds} &= -\gamma_i(s)I_i(s), \qquad s \in [0,\tau_i] \\ I_i(s=0) &= \varepsilon_i(t-\tau_i)x_i(t-\tau_i). \end{cases}$$

The solution to this equation gives the rate we are looking for:

$$I(t) = \varepsilon_i(t-\tau_i)x_i(t-\tau_i)\exp\left(-\int_{t-\tau_i}^{t}\gamma_i(s)ds\right).$$

The complete nonautonomous n-species competitive model with stage structure is therefore given by

$$\begin{aligned} \dot{x}_i(t) &= \varepsilon_i(t-\tau_i)e^{-\int_{t-\tau_i}^{t}\gamma_i(s)ds}x_i(t-\tau_i) - x_i(t)\sum_{k=1}^{n}a_{ik}(t)x_k(t) \qquad (i=1,\ldots,n) \\ \dot{y}_i(t) &= \varepsilon_i(t)x_i(t) - \gamma_i(t)y_i(t) - \varepsilon_i(t-\tau_i)e^{-\int_{t-\tau_i}^{t}\gamma_i(s)ds}x_i(t-\tau_i) \quad (i=1,\ldots,n) \end{aligned} \tag{7.1}$$

To simplify notation we introduce for $i=1,\ldots,n$:

$$B_i(t) = \varepsilon_i(t-\tau_i)\exp\left(-\int_{t-\tau_i}^{t}\gamma_i(s)ds\right).$$

These functions $B_i(t)$ are also ω-periodic and strictly positive. Like in the previous chapter, we denote by g^L and g^M the infimum and supremum of any time-dependent scalar function $g(t)$ over all time.

[3]Apparently the simpler models taught them nothing; do they ever learn?

7.2 Extinction and permanence in the stage-structured model

Like in Section 6.2, it is possible to generalize Zeeman's result on the autonomous n-species competitive system (Theorem 3.1) to system (7.1). The proof of this theorem can be found in the article by Liu, Chen et al. [21].

Theorem 7.1 *If the coefficients of system (7.1) satisfy*

$$\begin{aligned} B_1^L &> \sum_{k=2}^{n} \frac{B_k^M a_{1k}^M}{a_{kk}^L} \\ \frac{B_1^L}{a_{11}^M} &> \frac{B_j^M}{a_{j1}^L} \qquad (j = 1, \ldots, n) \end{aligned} \tag{7.2}$$

then for $j = 1, \ldots, n$ we have $\lim_{t\to\infty} x_j(t) = \lim_{t\to\infty} y_j(t) = 0$ and $\lim_{t\to\infty} x_1(t) = x^*(t)$, $\lim_{t\to\infty} y_j(t) = y^*(t)$, where $(x^*(t), y^*(t))$ is the solution to system (7.1) when taking $x_j(t) = y_j(t) = 0$ for all $j = 2, \ldots, n$.

Theorem 7.1 essentially states that all but one (which we give number 1) species become extinct and the remaining one goes to its single-species solution. This solution is now no longer simply going to the carrying capacity, but $(x^*(t), y^*(t))$ is the globally attracting, ω-periodic solution of system (7.1) when only species 1 is present.

Of course, we would also like to know when system (7.1) is permanent. Fortunately, Liu, Chen et al. also give a result in that direction (which is also proven in [21]).

Theorem 7.2 *If the coefficients of system (7.1) satisfy*

$$\frac{B_i^L}{a_{ii}^M} > \sum_{\substack{k=1 \\ k\neq i}}^{n} \frac{B_k^M a_{ik}^M}{a_{kk}^L} \qquad (i = 1, \ldots, n) \tag{7.3}$$

then the system is permanent.

7.3 The influence of stage structure on the long-time behaviour

Theorems 7.1 and 7.2 in the previous section tell us what the long-time behaviour of system (7.1) will be. However, it would be interesting to see if we can influence the outcome by tuning the parameters. As it turns out, this is quite possible, and allows us to shift between full coexistence and single-species domination.

A useful quantity to consider in this respect is the stage-structured degree of species i, defined as

$$D_i(t) = \int_{t-\tau_i}^{t} \gamma_i(s) ds,$$

which measures the number of specimens that dies before reaching maturity. It therefore also measures how strong the effects of the introduction of stage structure are.

If we now suppose that conditions (7.3) are met (and hence Theorem 7.2 holds and the system is permanent) and we gradually increase the stage-structured degree of all but one (say with number 1) species. This means that the numbers $B_i(t)$ of those species will become smaller, so the number of specimens that survives to reach the mature stage decreases. Not surprisingly, this aids the competitive position of species 1. If the stage-structured degrees of all other species have sufficiently increased, we therefore should leave the regime of Theorem 7.2 and enter into the regime of Theorem 7.1, which is indeed what happens.

Based on this observation, we can conclude that a large stage-structured degree for species i is both directly harmful to it's own chances of survival and helpful to those of the competitors. If, for some reason, we want to mingle with nature to protect a certain species, one 'natural' way[4] to do so, would be by increasing the competitor's stage-structured degree[5]. There are essentially two ways to achieve this. The simplest one is by enlarging the immature death rates γ_i of the competitors (for instance, by shooting a number of infants). The other is to increase the time they spend as immature specimens. This sounds more impossible than it is: in this model, reaching maturity is essentially not a matter of reaching a simple age limit, but reaching the point where a specimen starts to participate in the life of the mature, which means that he starts competing and reproducing. Delaying that point, using proper measures, might well be the best way to preserve endangered species.

7.4 Example

To illustrate the ideas from this chapter, we look at the following two-species competition model:

$$\begin{array}{rcl} \dot{x}_1(t) & = & (4+\sin(t-\frac{1}{4}\pi))e^{-\frac{1}{4}\pi}x_1(t-\frac{1}{4}\pi) - x_1(t)((\frac{2}{9}+\frac{1}{9}\sin(t))x_1(t)+\frac{1}{5}x_2(t)) \\ \dot{y}_1(t) & = & (4+\sin(t))x_1(t) - y_1(t) - (4+\sin(t-\frac{1}{4}\pi))e^{-\frac{1}{4}\pi}x_1(t-\frac{1}{4}\pi) \\ \dot{x}_2(t) & = & (2+\cos(t-\frac{1}{4}\pi))e^{-\frac{1}{4}\pi}x_2(t-\frac{1}{4}\pi) - x_2(t)(\frac{1}{2}x_1(t)+(\frac{3}{2}+\frac{1}{2}\cos(t))x_2(t)) \\ \dot{y}_2(t) & = & (2+\cos(t))x_2(t) - y_2(t) - (2+\cos(t-\frac{1}{4}\pi))e^{-\frac{1}{4}\pi}x_2(t-\frac{1}{4}\pi) \end{array} \tag{7.4}$$

The common frequency of all periodic functions is 2π and the time delay in both cases is $\frac{1}{4}\pi$. Both stage-structure constants are equal to $\frac{1}{4}\pi$ as well.

For system (7.4) we have the following infima and suprema:

$$\begin{array}{llll} B_1^L = 3e^{-\frac{1}{4}\pi} & B_1^M = 5e^{-\frac{1}{4}\pi} & a_{11}^L = \frac{1}{9} & a_{11}^M = \frac{1}{3} \\ B_2^L = 1e^{-\frac{1}{4}\pi} & B_2^M = 3e^{-\frac{1}{4}\pi} & a_{22}^L = 1 & a_{22}^M = 2 \end{array}$$

from which we have

$$\begin{array}{rcl} B_1^L = 3e^{-\frac{1}{4}\pi} & > & \dfrac{B_2^M a_{12}^M}{a_{22}^L} = \dfrac{3e^{-\frac{1}{4}\pi}\cdot\frac{1}{5}}{1} = \dfrac{3}{5}e^{-\frac{1}{4}\pi} \\ \dfrac{B_1^L}{a_{11}^M} = 9e^{-\frac{1}{4}\pi} & > & \dfrac{B_2^M}{a_{21}^L} = 6e^{-\frac{1}{4}\pi} \end{array}$$

so conditions (7.2) are met and therefore Theorem 7.1 holds. This means that species 2 will become extinct, whereas the dynamics of species 1 will be determined by it's associated single-species system.

[4]As opposed to, for instance, simply killing off all competitors.

[5]It is of course not necessary to increase those degrees so much that our favored species is the sole survivor, but we can temper with them in such a way that we make coexistence possible.

Now if we are very fond of species 2, the previous section told us what to do to save it: simply enlarge the stage-structure constant of species 1. It turns out that if we increase it to $\frac{1}{2}\pi$ (for instance, if we are in a violent mood, by doubling the immature death rate of species 1, or, for a more peaceful approach, by lengthening the time it spends as an immature to $\frac{1}{2}\pi$), both species will live out their live in coexistence. To show that this is true, we once again compute the relevant quantities:

$$\begin{array}{llll} B_1^L = 3e^{-\frac{1}{2}\pi} & B_1^M = 5e^{-\frac{1}{2}\pi} & a_{11}^L = \frac{1}{9} & a_{11}^M = \frac{1}{3} \\ B_2^L = 1e^{-\frac{1}{4}\pi} & B_2^M = 3e^{-\frac{1}{4}\pi} & a_{22}^L = 1 & a_{22}^M = 2 \end{array}$$

and see that we now have

$$\begin{array}{ccc} \dfrac{B_1^L}{a_{11}^M} = 9e^{-\frac{1}{2}\pi} & > & \dfrac{B_2^M a_{12}^M}{a_{22}^L} = \dfrac{3}{5}e^{-\frac{1}{4}\pi} \\ \dfrac{B_2^L}{a_{22}^M} = \dfrac{1}{2}e^{-\frac{1}{4}\pi} & > & \dfrac{B_1^M a_{21}^M}{a_{11}^L} = \dfrac{5}{18}e^{-\frac{1}{2}\pi} \end{array}$$

so now conditions (7.3) hold. Therefore we are now in the regime of Theorem 7.2 and the system is now permanent.

An example an application of a Lotka-Volterra model with time delay to a real-life system is given in the article by Wang, Ma and Shao [41]. There the effect of introducing time delay in a system consisting of several HIV mutants is studied, using both analytical and numerical methods. It turns out that a small delay does not affect the behaviour of the system, but a large delay may cause a Hopf bifurcation, resulting in the creation of a periodic orbit (instead of a stable equilibrium point). These results are consistent with the earlier results mentioned in the introduction of this chapter.

What Wang, Ma and Shao are effectively doing is the same as we did in the artificial example in this section: by tuning the system parameters (in this case, by adjusting the length of the delay), we wish to alter the final state of the system. This approach may help us understand real-life dynamical systems better, and someday result in new techniques to safely influence them.

Appendix A

General definitions

In this first appendix, we list the definitions of some of the concepts used in this thesis. They are often used in texts about differential equations and the reader is therefore probably already familiar with them; they are listed here for completeness.

A.1 Flows, orbits and limit points of dynamical systems

Throughout this appendix we shall consider the dynamical system described by the ode

$$\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x}) \tag{A.1}$$

where $\mathbf{x} \in \mathbb{R}^n$ and $\mathbf{f} : \mathbb{R}^n \to \mathbb{R}^n$ is Lipschitz continuous, such that we always have existence and uniqueness of solutions[1].
We denote by $\phi_t(\mathbf{x})$ the solution of (A.1) that starts at the point $\mathbf{x} \in \mathbb{R}^n$ at $t = 0$. We call $\phi_t(\mathbf{x})$ the *flow* of (A.1) and consider $\mathbf{f}$ as the vector field that generates this flow. The (positive) *orbit* of $\mathbf{x}$ is defined as $\gamma^+(\mathbf{x}) = \{\phi_t(\mathbf{x}) : t \geq 0\}$. Analogously we define the negative orbit $\gamma^-(\mathbf{x})$ by taking $t \leq 0$. The *equilibrium points* or *fixed points* of (A.1) are those points $\mathbf{x}$ for which $\gamma(\mathbf{x}) = \{\mathbf{x}\}$. The orbit is said to be *T-periodic* if for some $T > 0$ we have[2] $\phi_T(\mathbf{x}) = \phi_0(\mathbf{x})$.

It is often impossible to obtain explicit solutions for a system of (ordinary) differential equations. However, we can usually tell something about the qualitative behaviour of the solutions. This we do by looking at their asymptotic behaviour.

Definition A.1 *Let $\phi_t(\mathbf{x})$ be the solution of the time-independent ode (A.1) that is defined for all $t \geq 0$ and has initial condition $\phi_0(\mathbf{x}) = \mathbf{x}$. Then the ω-limit of $\mathbf{x}$ is defined as the set of all accumulation points of $\phi_t(\mathbf{x})$ for $t \to \infty$, so*

$$\omega(\mathbf{x}) = \{\mathbf{y} \in \mathbb{R}^n : \phi_{t_k}(\mathbf{x}) \to \mathbf{y} \textit{ for some sequence } t_k \to \infty\}. \tag{A.2}$$

Alternatively, we could write

$$\omega(\mathbf{x}) = \cap_{t \geq 0} \overline{\cup_{s \geq t} \phi_s(\mathbf{x})}.$$

[1] We also call the system (A.1) Lipschitz if f is Lipschitz.

[2] Because of uniqueness of solutions of (A.1), this condition implies $\phi_{t+T}(\mathbf{x}) = \phi_t(\mathbf{x})$ for all $t \in [0, T]$.

Analogously we define the α-limit by taking $t \to -\infty$. Note that α- and ω-limits may be empty sets. However, in the case the orbit is contained in some compact set, there must be accumulation points and the ω-limit set is nonempty. Moreover, it is easy to verify that $\omega(\mathbf{x})$ is both closed (being a set of accumulation points) and invariant.

A.2 Ordering and monotonicity

Definition A.2 *A partial order relation (written suggestively as $\leq$) on a Banach space X is a relation on X satisfying*

1. *reflexivity: $x \leq x$ for all $x \in X$;*
2. *antisymmetry: $x \leq y$ and $y \leq x$ implies $x = y$;*
3. *transitivity: $x \leq y$ and $y \leq z$ implies $x \leq z$ for all $x, y, z \in X$.*

Definition A.3 *A* positive cone *Y_+ in a Banach space Y is a nonempty closed subset of Y satisfying:*

1. *$\mathbb{R}_+ \cdot Y_+ \subset Y_+$;*
2. *$Y_+ + Y_+ \subset Y_+$;*
3. *$Y_+ \cap (-Y_+) = \varnothing$.*

For $x, y \in Y$, the relation defined by $x \leq y$ if and only if $y - x \in Y_+$ is a closed partial order relation. We say this relation is generated by the positive cone Y_+.

Definition A.4 *A* semiflow *on a Banach space X is a continuous map $\Phi : X \times \mathbb{R}^+ \to X$ which satisfies:*

1. *$\Phi_0 = \mathrm{id}_X$;*
2. *$\Phi_s \circ \Phi_t = \Phi_{s+t}$ for $s, t \geq 0$.*

Here $\Phi_t(x) = \Phi(x, t)$ for $x \in X$ and $t \geq 0$ and id_X is the identity map on X.

Of course, the solution $\phi_t(\mathbf{x})$ of (A.1) in the previous section is an example of a semiflow.

Combining, we consider a Banach space X with a partial order relation $\leq$ generated by a positive cone X_+ and with a semiflow Φ. This semiflow is said to be *monotone* if it satisfies

$$\Phi_t(x) \leq \Phi_t(y) \text{ whenever } x \leq y.$$

A dynamical system is called monotone if all the flows it generates are monotone semiflows.

The flow Φ is called *strongly order preserving* if it is monotone and if whenever $x < y$ (i.e. $x \leq y$ and $x \neq y$) there exist open subsets $U, V \subset X$ with $x \in U$, $y \in V$ and $t_0 > 0$ such that

$$\Phi_{t_0} U \leq \Phi_{t_0} V.$$

Monotonicity of Φ then implies that $\Phi_t U \leq \Phi_t V$ for all $t \geq t_0$.

Appendix B

Some basic theorems about differential equations

All the statements made in this appendix are basic results in the theory of (ordinary) differential equations. There are numerous introductory books on the subject that all cover these items. A not so mathematically rigorous, but very readable and intuitively clear reference is the book by Strogatz [38]. A more mathematical introduction is the book by Arnold [4]. The books by Hirsh and Smale [15], Jordan and Smith [18] and Cesari [6] go somewhat deeper into the theory and provide proofs for most of the fundamental results.
Throughout this appendix, as in appendix A, we shall consider the dynamical system described by the ode (A.1)

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

where $\mathbf{x} \in \mathbb{R}^n$ and $\mathbf{f} : \mathbb{R}^n \to \mathbb{R}^n$ is Lipschitz continuous, such that we always have existence and uniqueness of a solution $\mathbf{x}(t)$ of (A.1).

B.1 Lyapunov functions

In Appendix A we defined the concept of the ω-limit of any starting point $\mathbf{x}$ of (A.1). The following theorem tells us where to look for the ω-limit without knowing the solution of the differential equation. This allows us to tell something of the asymptotic behaviour of the system without explicitly solving it.

Theorem B.1 (Lyapunov) *Let $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ be a time independent ode defined on some subset $G \subset \mathbb{R}^n$ and $V : G \to \mathbb{R}^n$ a continuously differentiable function. If for some solution $\mathbf{x}(t)$ the derivative $\dot{V}$ of the map $t \to V(\mathbf{x}(t))$ satisfies the inequality $\dot{V} \geq 0$ (or $\dot{V} \leq 0$), then $\omega(\mathbf{x}) \cap G$ (and $\alpha(\mathbf{x}) \cap G$) is contained in the set $\{\mathbf{x} \in G : \dot{V}(\mathbf{x}) = 0\}$.*

Proof Take $\mathbf{y} \in \omega(\mathbf{x}) \cap G$. Then there exists a sequence $t_k \to \infty$ with $\mathbf{x}(t_k) \to \mathbf{y}$. Since $\dot{V} \geq 0$ along the orbit of $\mathbf{x}$, we have by continuity that $V(\mathbf{y}) \geq 0$. Now suppose that $\dot{V}(\mathbf{y}) > 0$. This means that the value of V must increase along an orbit, so

$$V(\mathbf{y}(t)) > V(\mathbf{y}) \tag{B.1}$$

for $t > 0$. The function $V(\mathbf{x}(t))$ is also monotonically increasing. Because V is continuous, $V(\mathbf{x}(t_k))$ must converge to $V(\mathbf{y})$ and hence

$$V(\mathbf{x}(t)) \leq V(\mathbf{y}) \tag{B.2}$$

for all $t \in \mathbb{R}$. On the other hand, we have $\mathbf{x}(t_k) \to \mathbf{y}$, which implies $\mathbf{x}(t_k + t) \to \mathbf{y}(t)$ and therefore

$$V(\mathbf{x}(t_k + t)) \to V(\mathbf{y}(t)),$$

so that by (B.1)

$$V(\mathbf{x}(t_k + t)) > V(\mathbf{y})$$

for k sufficiently large. But this contradicts (B.2), and hence we must have $\dot{V}(\mathbf{y}) = 0$. □

Remark The function V in Theorem B.1 is called the *Lyapunov function*. Unfortunately, there is no general way to construct such a function, so we need to find one by trial and error.

B.2 Index theory in two dimensions

In this section we only list a few basic results that are of use in Chapter 3. A more extensive introduction into index theory is given in Strogatz [38], chapter 6.8.

The system (A.1) of odes defines a vector field $\dot{\mathbf{x}} = (\dot{x}, \dot{y})$ on $\mathbb{R}^2$. For any simply closed curve C in $\mathbb{R}^2$ we want to measure the winding of this vector field when we travel along the curve once. For this we define the angle θ by

$$\theta = \arctan\left(\frac{\dot{y}}{\dot{x}}\right)$$

and denote by $[\theta]_C$ the net change in θ over one (counterclockwise) rotation along C. Then the index of the curve C with expect to the vector field is defined as

$$I_C = \frac{1}{2\pi}[\theta]_C \tag{B.3}$$

One verifies immediately that a curve that does not enclose any fixed points has index 0. This allows us to define the index of any fixed point as the index of a curve that contains that fixed point and no others. It turns out that saddle points have index -1, and all other types have index $+1$. Furthermore, we have the following relation of the index of a curve and that of the points it encloses:

Lemma B.2 *If a closed curve C surrounds n isolated fixed points with indices I_1 to I_n, then*

$$I_C = I_1 + I_2 + \ldots + I_n$$

Now observing that a curve that is a trajectory in the phase plane must have index $+1$, we conclude

Theorem B.3 *Any closed orbit in the phase plane must enclose fixed points whose indices sum to $+1$.*

B.3 The Poincaré-Bendixson theorem in two dimensions

One possibility for the dynamics of a two-dimensional system is the existence of a closed orbit in the plane. The following theorem is often used when one tries to prove that such an orbit exists.

Theorem B.4 (Poincaré-Bendixson) *Let $G \in \mathbb{R}^2$ be a closed subset of the plane and suppose that*

1. *System (A.1) is continuously differentiable on an open set containing G;*
2. *G does not contain any fixed points of system (A.1);*
3. *There exists a trajectory $C = \{\mathbf{x}(t) : t \geq 0\}$ that is confined in G;*

then either C is itself a closed orbit, or it approaches a closed orbit as $t \to \infty$. In either case, the set G contains a closed orbit of (A.1).

More compactly stated, this theorem tells us that a compact limit set of a dynamical system in $\mathbb{R}^2$ that contains no equilibrium points is a periodic orbit. The proof of this theorem can be found in for instance [15] or [6].

The usual way to apply the Poincaré-Bendixson theorem is to construct a *trapping region* G in the plane. By this we mean a closed connected set that contains no fixed points and is constructed such that the vector field points 'inward' everywhere on the boundary of G. Such a region satisfies the conditions of the theorem and therefore contains a closed orbit.

B.4 A convergence criterion

In this section we assume the dynamical system (A.1) to be monotone and denote the monotone semiflow it generates by $\Phi_t(x)$. We take the space X of all possible starting points to be a metric space which is contained in some Banach space Y and has a partial ordering generated by a positive cone $Y_+ \subset Y$. We also assume the cone to have a nonempty interior. In the applications in this thesis Y is a Banach space of real-valued functions on the set $\Omega = \{1, 2, \ldots, n\}$. This means we can identify Y with $\mathbb{R}^n$ and Y_+ with $\mathbb{R}^n_+$.

The following lemma is the first step to proving convergence of $\Phi_t(x)$.

Lemma B.5 *A monotone sequence contained in a compact subset of X converges in X.*

Based on this lemma, we also assume the closure $\overline{\gamma^+(x)}$ of each orbit $x \in X$ to be a compact subset of X. We are now ready to state the following convergence criterion which is due to Hirsch [13].

Theorem B.6 (Convergence criterion) *Suppose $\Phi_T(x) \geq x$ for some $T > 0$. Then the ω-limit set $\omega(x)$ of x is a T-periodic orbit. If $\Phi_t(x) \geq x$ for $t \in (a, b)$ with $a, b \in \mathbb{R}^+ (a \neq b)$ then there is an equilibrium point p with $\Phi_t(x) \to p$ as $t \to \infty$. In particular, if Φ is strongly order preserving and $\Phi_T(x) > x$ for some $T > 0$ then $\Phi_t(x) \to p$ as $t \to \infty$.*

One of the most useful consequences of this criterion is the fact that a monotone dynamical system cannot have an attracting periodic orbit[1].

[1] A periodic orbit O is attracting if there is an open set U containing O such that $\omega(x) = O$ for each $x \in U$.

Theorem B.7 *If X is open in Y and Φ is monotone, then there does not exist a non-trivial, attracting periodic orbit.*

This theorem implies immediately that cooperative systems of arbitrary dimension can never have attracting periodic orbits.

Another consequence of the convergence criterion tells us how an ω-limit set is imbedded in the space X. In this theorem $x < y$ means $y - x \in \mathrm{Int}(Y_+)$, or (equivalently) that $x \leq y$ and $x \neq y$.

Theorem B.8 (Nonordering of limit sets) *If Φ is monotone, it is not possible to find two points x, y in an ω-limit set such that there exists neighbourhoods U of x and V of y with the property that $U \leq V$. If Φ is strongly order-preserving, it is not possible to find two points x, y in an ω-limit set such that $x < y$.*

We conclude by noting that an ω-limit set cannot contain a maximal or minimal element.

Corollary B.9 *If Φ is strongly order-preserving, $a \in \omega(x)$ and $\omega(x) \leq a$ or $\omega(x) \geq a$, then $\omega(x) = \{a\}$.*

Proofs of all statements in this section can be found in the book by Smith [36]. More about convergent monotone sequences (including Lemma B.5) can be found in the book by Hess [11]. Theorem B.7 (for ordinary differential equations) is originally due to Hadeler and Glas [10]. The other theorems are due to Hirsch [13], who also proved a stronger version of Theorem B.7. However, he makes the stronger assumption that the flow Φ is strongly monotone. Smith and Thieme [37] showed that the results also hold under the weaker assumption that Φ is only strongly order-preserving.

B.5 Brouwer's Fixed Point Theorem

A very useful theorem from basic topology is the famous Fixed Point Theorem:

Theorem B.10 (Brouwer) *Let σ be a continuous operator that maps a closed, bounded and convex set $\overline{\Omega} \subset \mathbb{R}^n$ into itself. Then $\overline{\Omega}$ contains at least one fixed point of the operator σ, that is, there is a point $\mathbf{x}^* \in \overline{\Omega}$ that satisfies $\sigma(\mathbf{x}^*) = \mathbf{x}^*$.*

Appendix C

Quadratic forms

The classification of Lotka-Volterra systems given in the introduction (Chapter 1) is made by specifying conditions on the interaction matrix A. One of the conditions states that $A \leq 0$, which is clarified to mean that 'A is negative definite in the sense of quadratic forms'. In this appendix, we briefly explain what quadratic forms are and what this statement means for A. Since quadratic forms are a part of elementary linear algebra, the reader is probably already familiar with them; this appendix, like Appendix A, is included for completeness. More on this subject can, among others, be found in the book by Lang [20].

C.1 Definition of a quadratic form

First introduced by Chauchy in 1829, the following definition of a quadratic form can be found in (almost) any book on linear algebra:

Definition C.1 *A* quadratic form $f(\mathbf{x})$ *in n variables is a homogenous*[1] *polynomial of degree 2 that can be written as*

$$f(\mathbf{x}) = \sum_{i,j=1}^{n} A_{ij} x_i x_j. \tag{C.1}$$

Obviously, for any square $n \times n$ matrix A there is an associated quadratic form, given by

$$f(\mathbf{x}) = \mathbf{x}^T A \mathbf{x}. \tag{C.2}$$

On the other hand, a quadratic form does not uniquely specify an associated matrix. For example, the following two matrices have the same associated quadratic form:

$$\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} \qquad \begin{pmatrix} 1 & 1 \\ -1 & 1 \end{pmatrix}.$$

However, in some cases we get a unique associated matrix if we specify the type of matrix we want to work with. It is for example easy to verify that each quadratic form has a uniquely defined upper triangular matrix, and the same holds for a symmetric matrix.

[1] 'Homogenous' here means that every term in the polynomial contains the product of the same number of variables, which in this case is 2.

In fact, using the feature that each matrix can be written as the sum of a symmetric and an antisymmetric matrix

$$A = A^S + A^{AS}$$

and noticing that the antisymmetric component does not contribute to the quadratic form, we only need to look to the symmetric component of a matrix to get all information about the associated quadratic form.

Since the matrices we are interested in have real components (complex interaction coefficients would be a bit strange), we can make use of the well-know theorem form linear algebra that all real symmetric matrices are diagonalizable. Moreover, all their eigenvalues are real. We can therefore write

$$A^S = C^{-1}DC$$

where D is a diagonal matrix of which the diagonal elements are the eigenvalues of A^S and C is an orthogonal transformation. Thus, for any (real) quadratic form, it is possible to rewrite equation (C.2) as

$$f(\mathbf{x}) = \mathbf{x}^T A\mathbf{x} = \lambda_1 y_1^2 + \lambda_2 y_2^2 + \ldots + \lambda_n y_n^2 \tag{C.3}$$

where $\lambda_1, \ldots, \lambda_n$ are the eigenvalues of the symmetric component of A, and $\mathbf{y} = C\mathbf{x}$.

C.2 Negative definiteness of a quadratic form

Definition C.2 *A quadratic form $f(\mathbf{x})$ associated to an $n \times n$ matrix A is called* negative definite *if for any $\mathbf{x} \in \mathbb{R}^n$*

$$f(\mathbf{x}) = \mathbf{x}^T A\mathbf{x} \leq 0. \tag{C.4}$$

Condition (C.4) can be hard to check for a general matrix. Fortunately, we can make use of equation (C.3) to find a much easier condition. After all, since each component of $\mathbf{y}$ in equation (C.3) is squared, it is immediately clear that $f(\mathbf{x})$ in that equation is nonpositive for any $\mathbf{y} \in \mathbb{R}^n$ if and only if all eigenvalues of A^S are nonpositive. Computing the eigenvalues of the quadratic component of a matrix is therefore sufficient to find out whether or not its associated form is negative definite, as is stated in the next theorem.

Theorem C.1 *The quadratic form associated to an $n \times n$ matrix A with real coefficients is negative definite if and only if all eigenvalues of the symmetric component of A are nonpositive.*

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