DYNAMICS OF MODIFIED PREDATOR-PREY MODELS*

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Besides being structurally unstable, the Lotka-Volterra predator-prey model has another shortcoming due to the invalidity of the principle of mass action when the populations are very small. This leads to extremely large populations recovering from unrealistically small ones. The effects of linear modifications to structurally unstable continuous-time predator-prey models in a (small) neighbourhood of the origin are investigated here. In particular, it is shown that typically either a global attractor or repeller arises depending on the choice of coefficients.
The analysis is based on Poincaré mappings, which allow an explicit representation for the classical Lotka-Volterra equations.

Dedicted to the memory of Valeri Melnik

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1. Introduction

The Lotka-Volterra model has had a very influential role in the development of population dynamics. Its lack of structural stability has led to its being superceded by more suitable models, but it is nevertheless still useful for its instructive value.

The model has another shortcoming which is also present in many later models in population dynamics as well as in chemical dynamics. This is a consequence of the principle of mass action [Alo07, Mur01], which is based on the assumption of uniform mixing and uniform interaction probabilities that are used to deduce the product interaction terms. This assumption is clearly not satisfied when the populations are extremely small. In the Lotka-Volterra model it leads to extremely large populations growing from extremely small ones, the larger the smaller the population value is near the origin. This phenomenon is sometimes called the *atto-fox problem* (cf. [Mol91]).

The initial point for our analysis are two-species predator-prey models, which are structurally unstable in the sense that their solutions form a family of neutrally stable closed curves surrounding a nontrivial equilibrium. Indeed, such cycles have been observed in natural systems, like populations of small mammals, red grouse, and snowshoe hares (see [Edw06; p. 33] for a survey).

In this paper we investigate the effects of a linear modification to structurally unstable predator-prey models in a possibly small neighbourhood of the origin. It is not so much a linearization as a replacement of the nonlinear equations by linear ones with slightly different coefficients to account for the neglected nonlinearities. Our analysis is geometric in nature and our main tool is the Poincaré mapping. Essentially two new types of behaviour arise depending on the coefficients chosen for the linear modification, namely a bounded disk of periodic solutions which is either globally attracting or globally repelling.

For the classical Lotka-Volterra equations we are able to derive an explicit representation of the Poincaré map. Thus, our analysis reduces to the investigation of a scalar smooth mapping. Here, it is possible to observe also nongeneric phenomena, like the existence of isolated closed trajectories being either attractive or repelling.

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2. Predator-prey models

General Gause-type predator-prey models describing the continuous-time interaction of two species are of the form (see, e.g., [Hsu78, CFL08])

$$\begin{cases} \dot{x} = xg(x) - yp(x), \\ \dot{y} = (cp(x) - q(x))y, \end{cases}$$

where x represents the prey population (or its density) and y is the predator population (density). The growth rate $g(x)$ governs the growths of the prey in absence of predators and $q(x)$ is the death rate of the predator. Moreover, $p(x)$ can be interpreted as predator response function, which is weighted with a parameter $c > 0$ in the predator equation. Various concrete examples for the functions g, p and q have been discussed in, for instance, [May01] (see also Sec. 2.4).

2.1. The unmodified equation

In this paper, we restrict to a special case of the above model, namely to predator-prey equations

$$\begin{cases} \dot{x} = (a-y)p(x), \\ \dot{y} = (cp(x) - q(x))y \end{cases} \tag{1}$$

depending on real parameters $a, c > 0$.

Clearly, the system (1) is separable. We suppose throughout that $p, q : [0, \infty) \to \mathbb{R}$ are C^1-functions satisfying the standing assumptions

$(H)_1$ $p(0) = 0$, $p'(0) > 0$ and $p(x) > 0$ for all $x > 0$

$(H)_2$ $q(0) > 0$

$(H)_3$ the function $cp - q : [0, \infty) \to \mathbb{R}$ has a unique zero $x^* > 0$ with

$$cp'(x^*) > q'(x^*),$$
$$q(x^*)p'(x^*) > q'(x^*)p(x^*)$$

and define the function

$$R(x, x^*) := \int_{x^*}^{x} \frac{q(\xi)}{p(\xi)}\, d\xi.$$

The hypotheses $(H)_1$–$(H)_3$ are clearly met for the classical Lotka-Volterra equations (see Sec. 3) and for a further illustration we refer to Fig. 1.

By assumption, besides the trivial equilibrium $(0, 0)$, eqn. (1) also has a unique nontrivial equilibrium in the point (x^*, a). It turns out that the zero point is a saddle for

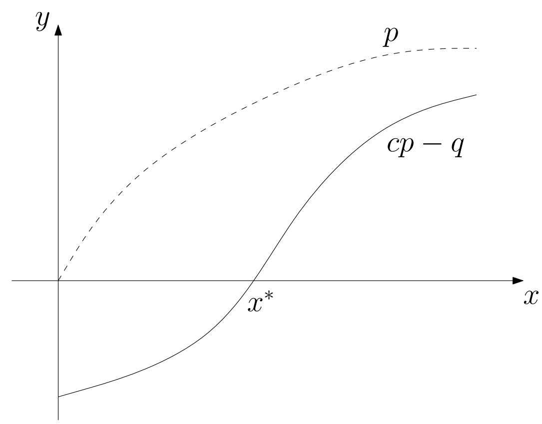

Fig. 1. Graphs of the two functions $cp - q$ and p (dotted)

(1) (cf. $(H)_1$ and $(H)_2$) and the coordinate axes are invariant. Moreover, by $(H)_3$ the linearization of (1) in (x^*, a) has the purely imaginary eigenvalues

$$\pm\sqrt{ap(x^*)(cp'(x^*) - q'(x^*))}i.$$

Therefore, (x^*, a) is a center, since the function $H : (0, \infty)^2 \to \mathbb{R}$,

$$\begin{aligned} H(x, y) &= \int_{x^*}^{x} c - \frac{q(\xi)}{p(\xi)}\, d\xi + \int_{a}^{y} \frac{\eta - a}{\eta}\, d\eta \\ &= c(x - x^*) - R(x, x^*) \\ &\quad + y - a\Big(1 + \ln \frac{y}{a}\Big) \end{aligned}$$

is constant along solution curves of (1), i.e., it is a first integral in the biologically relevant open first quadrant.

Proposition 2.1. *The function H achieves its global minimum 0 at the equilibrium (x^*, a) and its level sets are closed curves.*

Proof. It is easy to see that (x^*, a) is the unique critical point of H. Next we write $H(x, y) = H_1(x) + H_2(y)$,

$$H_1(x) := c(x - x^*) - R(x, x^*),$$

$$H_2(y) := y - a\Big(1 + \ln \frac{y}{a}\Big)$$

and obtain that by (H_3) the unique minimum 0 of H_1 and H_2 is attained at x^* resp. a. The additive structure of H guarantees that $H(x^*, a) = 0$ is the global minimum. With this at hand, as in the classical Lotka-Volterra case (cf., e.g., [Bra78; p. 415, Lemma 1]) one shows that the level curves of H are closed. ■

The constant $h(s) = H(sx^*, sa)$ for the trajectory of (1) through the point (sx^*, sa) as a function of $s \in (0, 1]$ is

$$\begin{aligned} h(s) &= \int_{x^*}^{sx^*} c - \frac{q(\xi)}{p(\xi)}\, d\xi + \int_a^{sa} \frac{\eta - a}{\eta}\, d\eta \\ &= (a + cx^*)(s-1) - a \ln s + R(sx^*, x^*). \end{aligned}$$

Thus, each trajectory of (1) in $(0, \infty)^2$ corresponds to a unique point (sx^*, sa) and therefore to a unique parameter value $s \in (0, 1]$.

We can summarize that the trajectories of (1) rotate counter-clockwise around the equilibrium (x^*, a) in the first quadrant. Each nontrivial trajectory has its turning points at $x = x^*$ and $y = a$. Consequently, as the phase portrait in Fig. 2 illustrates, from a modeling perspective, the above Gause-type model (1) exhibits a number of problems:

- The system is not structurally stable, which means that small perturbations (or discretizations, cf. [SH98]) destroy the scenario of exclusively periodic (and bounded) complete solutions. The introduction of an appropriate inner-specific competition rectifies this problem and the nontrivial equilibrium becomes globally asymptotically stable. In this setting, H serves as a global Lyapunov function (see [Hsu78; pp. 94ff]).

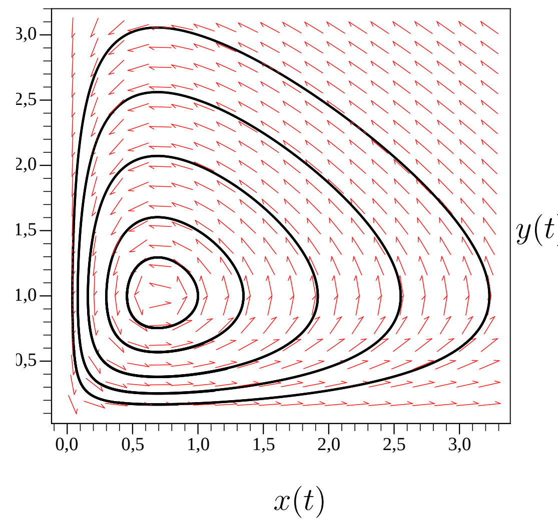

Fig. 2. Phase portrait of (1) for $a = 1$, $c = 1$, $p(x) = 1 - e^{-x}$ and $q(x) \equiv 0.5$

- Although the number of predators becomes unrealistically small it nevertheless recovers and achieves an extremely large value. More precisely, provided we start in a point (x^*, η) with $\eta \gg a$ predators, the corresponding minimal size of predators becomes extremely small as η grows. Hence, also for eqn. (1) we have an *atto-fox problem* (cf. [Mol91]) and a similar phenomenon occurs for the size of the prey population as well.

- If the number of predator or prey is small, their interactions become more rare. In such cases, we suggest that it could be more reasonable to assume that the growth of the two populations is independent from each other.

2.2. The modified equation

Let us therefore address the latter problem that predator-prey interactions become less frequent, if the density of one species is small. Let us suppose that in a rectangle

$$B := [0, \epsilon_1] \times [0, \epsilon_2]$$

with $\epsilon_1, \epsilon_2 > 0$, the predator-prey equations (1) are modified to a decoupled linear system

$$\begin{cases} \dot{x} = \delta_1 x, \\ \dot{y} = -\delta_2 y, \end{cases} \tag{2}$$

where $\delta_1, \delta_2 > 0$ are real parameters.

Note that eqn. (2) might be considered as linearization of (1) in $(0,0)$ describing the population growth without interaction, provided

$$\delta_1 = ap'(0), \qquad \delta_2 = q(0).$$

However, since we neglected the nonlinearities in (2) inside the box B, it might be advisable to consider parameters δ_1, δ_2 near the above values. We will come back to this aspect, when it comes to a biological interpretation of our assumptions. For our mathematical analysis, yet, no such restriction on $\delta_1, \delta_2 > 0$ is made in the following.

In order to make our geometrical arguments work, we suppose

$$\epsilon_1 < x^*, \quad \epsilon_2 < a,$$

i.e., the nontrivial equilibrium (x^*, a) is not contained in B.

Starting at the top of the rectangle at a point $(s\epsilon_1, \epsilon_2)$, where $0 < s < 1$, the linear eqn. (2) has the solution

$$x(t) = s\epsilon_1 e^{\delta_1 t}, \qquad y(t) = \epsilon_2 e^{-\delta_2 t}$$

which cuts the vertical right edge of the box (i.e. with $x = \epsilon_1$) after the time

$$T = -\frac{1}{\delta_1} \ln s > 0.$$

At this time (see Fig. 3)

$$y(T) = \epsilon_2 e^{-\delta_2 T} = \epsilon_2 s^{\delta},$$

where for notational convenience we abbreviate throughout

$$\delta := \frac{\delta_2}{\delta_1}.$$

2.3. Comparison of curves

Now the crucial question is for the dynamical effect of the above modification turning the well-understood eqn. (1) into a nonsmooth dynamical system. Does it stabilize the system or lead to unbounded trajectories? More geometrically, is the modified solution curve above or below the corresponding closed curve of the unmodified eqn. (1) through $(s\epsilon_1, \epsilon_2)$?

Suppose for given $s \in (0,1)$ we start in the point $(s\epsilon_1, \epsilon_2)$. Then the corresponding constant for the unmodified closed curve is

$$\begin{aligned} H(s\epsilon_1, \epsilon_2) &= c(s\epsilon_1 - x^*) - R(s\epsilon_1, x^*) \\ &\quad + \epsilon_2 - a\Big(1 + \ln \frac{\epsilon_2}{a}\Big) \end{aligned}$$

and at the exit point of the modified dynamics in B the constant is

$$\begin{aligned} H(\epsilon_1, \epsilon_2 s^{\delta}) &= c(\epsilon_1 - x^*) - R(\epsilon_1, x^*) \\ &\quad + \epsilon_2 s^{\delta} - a\Big(1 + \ln \frac{\epsilon_2 s^{\delta}}{a}\Big). \end{aligned}$$

Consequently, defining the difference function $\Delta : (0,1] \to \mathbb{R}$,

$$\Delta(s) := H(s\epsilon_1, \epsilon_2) - H(\epsilon_1, \epsilon_2 s^{\delta}) \tag{3}$$

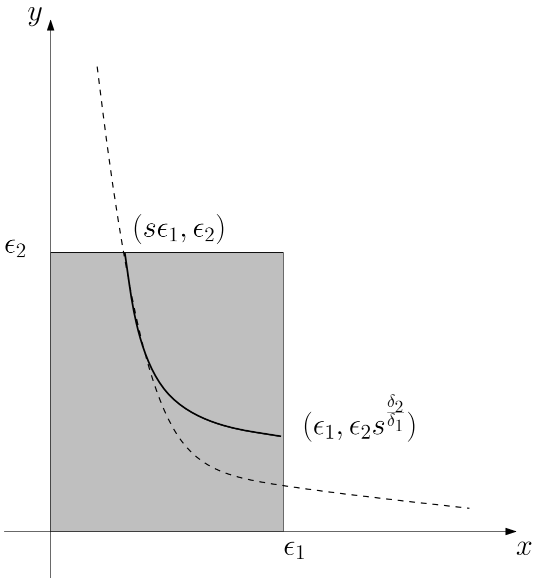

Fig. 3. Trajectories of the modified and original (dotted) predator-prey equations (1)

we obtain $\Delta(1) = 0$ and the representation

$$\begin{aligned}\Delta(s) &= c\epsilon_1(s-1) + \epsilon_2(1 - s^\delta) \\ &\quad + R(\epsilon_1, \epsilon_1 s) + a\delta \ln s.\end{aligned}$$

Furthermore, its derivative is given by

$$\Delta'(s) = \epsilon_1 \left(c - \frac{q(\epsilon_1 s)}{p(\epsilon_1 s)} \right) + \frac{\delta}{s} \left(a - \epsilon_2 s^\delta \right)$$

and we obtain the following behavior:

Lemma 2.2. *One has the limit relation*

$$\lim_{s \searrow 0} \Delta'(s) = \begin{cases} \infty, & a\delta p'(0) > q(0), \\ -\infty, & a\delta p'(0) < q(0). \end{cases}$$

Proof. We write $\Delta'(s) = n(s)/d(s)$ with numerator

$$\begin{aligned} n(s) :=& \epsilon_1 c p(\epsilon_1 s) s - \epsilon_1 q(\epsilon_1 s) s + \delta a p(\epsilon_1 s) \\ &- \delta \epsilon_2 p(\epsilon_1 s) s^\delta \end{aligned}$$

and denominator $d(s) := p(\epsilon_1 s)s$. Our assumptions guarantee

$$\lim_{s \searrow 0} n(s) = \lim_{s \searrow 0} d(s) = 0,$$

and due to $\lim_{s \searrow 0} \frac{p(\epsilon_1 s)}{s^{1-\delta}} = 0$ (cf. $(H)_1$) we have

$$\lim_{s \searrow 0} n'(s) = \epsilon_1 (a\delta p'(0) - q'(0)).$$

This yields

$$\lim_{s \searrow 0} \frac{n'(s)}{d'(s)} = \begin{cases} \infty, & a\delta p'(0) > q(0), \\ -\infty, & a\delta p'(0) < q(0) \end{cases}$$

and the claim follows from l'Hospital's rule. ■

We denote the set of critical points of Δ in the interval $(0, 1)$ by

$$\Gamma := \{ s \in (0,1) : \Delta'(s) = 0 \}.$$

In case $\Delta(s) > 0$ the modification from Sec. 2.2 has a stabilizing effect in the sense that trajectories move towards the domain where (1) has not been modified. On the other hand, $\Delta(s) < 0$ yields a destabilization and one obtains solutions approaching the coordinate axes with increasingly larger amplitudes.

2.3(A). Stabilizing case

Due to the integral occurring in the definition of Δ it might be hard to verify $\Delta(s) > 0$ directly. Thus, we impose a condition based on the derivative Δ' which ensures that Δ is strictly positive.

We begin by considering the case

$$\begin{aligned} \epsilon_1 \delta_1 \left(\frac{q(\epsilon_1)}{p(\epsilon_1)} - c \right) &> \delta_2 (a - \epsilon_2), \\ \inf_{s \in \Gamma} \Delta(s) &> 0, \\ q(0) &> a\delta p'(0) \end{aligned} \tag{4}$$

which guarantees, as we will see below, $\Delta(s) > 0$ for all $s \in (0,1)$. This means that the modified solutions cuts the vertical boundary above the cut point for the corresponding closed curve of the unmodified solution.

Hence all solutions passing through the box will asymptote towards the unmodified closed curve which passes through the corner (ϵ_1, ϵ_2) of the box, i.e. the disk enclosed by this curve is asymptotically stable (see Fig. 4). This behaviour does not depend on the size of the box and we can summarize:

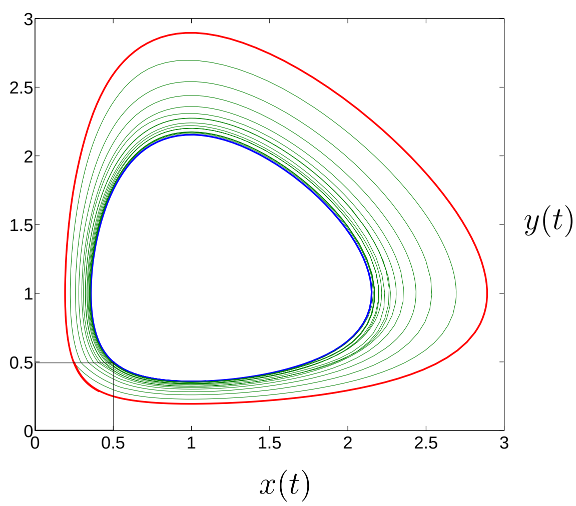

Fig. 4. Stabilizing case: Trajectories of the unmodified (red, blue) and modified equation (green) for $a = 1$, $\epsilon_1 = \epsilon_2 = 0.5$, $\delta_1 = 1.5$, $\delta_2 = 1.1$ with c, p, q as in (8)

Proposition 2.3. *Under the assumptions* (4) *the sublevel set* $H^{-1}((-\infty, H(\epsilon_1, \epsilon_2)])$ *is a global attractor.*

Proof. It remains to show that Δ is strictly positive on $(0,1)$. This, however, follows directly from assumption (4), whose first inequality guarantees $\Delta'(1) < 0$, while Lemma 2.2 yields $\lim_{s\searrow 0} \Delta'(s) = -\infty$. Together with $\Delta(1) = 0$ we therefore have $\Delta(s) > 0$ for all $s \in (0,1)$. ∎

The present stabilizing case enforced by the assumptions (4) is the realistic one from a biological perspective. Indeed, inside the box B there is no predator-prey interaction. This has a positive effect on the growth rate for the prey, i.e. it is reasonable to assume

$$\delta_1 > ap'(0).$$

Provided the death rate of the predator is not severely affected while the prey is absent, we have $\delta_2 \approx q(0)$ and therefore

$$\delta_1 q(0) > a\delta_2 p'(0).$$

This condition, however, is just the last inequality of (4). Thus, our modification prevents the atto-fox problem.

2.3(B). Destabilizing case

The dual assumption to (4) is

$$\begin{aligned} \epsilon_1\delta_1\left(\frac{q(\epsilon_1)}{p(\epsilon_1)} - c\right) &< \delta_2(a-\epsilon_2), \\ \sup_{s\in\Gamma} \Delta(s) &< 0, \\ q(0) &< a\delta p'(0) \end{aligned} \tag{5}$$

and an analogous analysis to the previous Sec. 2.3(A) tells us that $\Delta(s) < 0$ holds for $s \in (0,1)$ and the modification destabilizes our system. The modified solution cuts the vertical boundary below the cut point for the corresponding closed curve of the unmodified solution. Hence all solutions passing through the box will asymptote away from the unmodified closed curve which passes through the corner (ϵ_1, ϵ_2) of the box, i.e. the disk enclosed by this curve is asymptotically unstable (see Fig. 5). This behaviour is analogous to spurious solutions in numerical dynamics (cf. [SH98]).

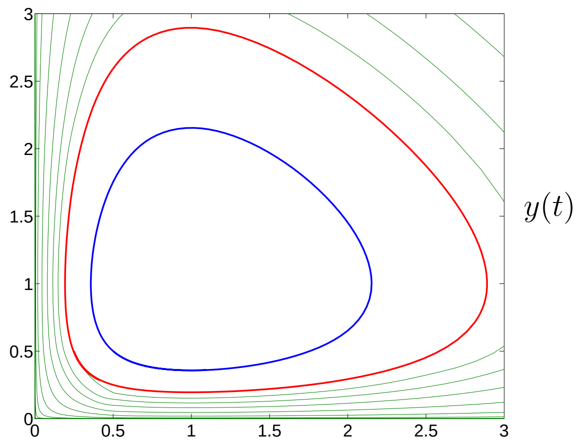

Fig. 5. Destabilizing case: Trajectories of the unmodified (red, blue) and modified equation (green) for $a = 1$, $\epsilon_1 = \epsilon_2 = 0.5$, $\delta_1 = 1.1$, $\delta_2 = 1.5$ with c, p, q as in (8)

We conclude this situation and obtain

Proposition 2.4. *Under the assumptions* (5) *the sublevel set* $H^{-1}((-\infty, H(\epsilon_1, \epsilon_2)])$ *is a global repeller.*

Proof. The proof follows as above, since we are in a dual situation to Proposition 2.3. ■

Similarly to the above interpretation in the stabilizing situation, the last inequality in (5) can be motivated on basis of the dual inequality

$$\delta_1 < ap'(0).$$

This, nevertheless, hardly reflects a biologically reasonable behavior, when a prey lowers its growth in absence of predators.

2.4. Specific and further models

In the literature (cf., e.g., [May01] various typical explicit examples for the functions p, q occurring in (1) can be found. They include

$$p_1(x) := \alpha x, \qquad q_1(x) := \bar{\alpha},$$
$$p_2(x) := \frac{\alpha x}{\beta + x}, \qquad q_2(x) := \frac{\bar{\alpha}x + \bar{\beta}}{\bar{\gamma}x + \bar{\delta}}$$
$$p_3(x) := \alpha x^{1+\beta},$$
$$p_4(x) := \alpha(1 - e^{-\beta x})$$

and for parameters $\alpha, \beta, \bar{\alpha}, \bar{\beta}, \bar{\gamma}, \bar{\delta} > 0$ these functions clearly satisfy both the assumptions $(H)_1$ and $(H)_2$. It is not difficult to formulate appropriate further conditions on the parameters such that also $(H)_3$ is fulfilled. A phase portrait for the functions p_4, q_1 can be found in Fig. 2.

Furthermore, we point out that the above approach also applies to predator-prey models, whose unmodified equation is not a special case of (1). For instance, consider the normalized system (cf. [CFL08])

$$\begin{cases} \dot{x} = (a - y)x, \\ \dot{y} = (f(x) - 1)y \end{cases} \tag{6}$$

where $a > 0$ is the growth rate of the prey and $f(x)$ determines the influence of the prey on the predator growth.

For the C^1-function $f : [0, \infty) \to [0, \infty)$ one supposes $f(0) = 0$, that there exists a unique solution $x^* > 0$ of $f(x^*) = 1$, which moreover fulfills $f'(x^*) > 0$. Thus, the unique nontrivial equilibrium (x^*, a) of (6) is a center. Indeed, (6) is a separable ODE, whose first integral

$$H(x, y) = y - a\left(1 + \ln \frac{y}{a}\right) - \int_{x^*}^{x} \frac{1 - f(\xi)}{\xi}\, d\xi$$

achieves its unique minimum 0 at (x^*, a). We refer to Fig. 6 for a phase portrait.

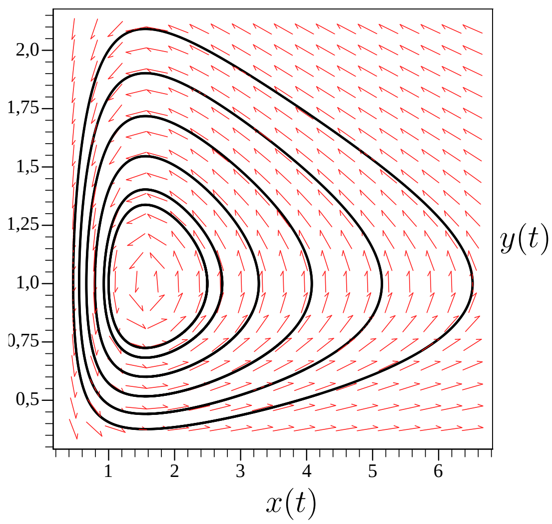

Fig. 6. Phase portrait of (6) for $a = 1$ and $f(x) = \arctan(x)$

In order to understand the effect of the modification from Sec. 2.2 on the dynamics of eqn. (6), we define Δ as in (3) and obtain the difference function

$$\Delta(s) = \epsilon_2(1-s^\delta) - \int_{\epsilon_1}^{s\epsilon_1} \frac{1-f(\xi)}{\xi}\, d\xi + a\delta \ln s.$$

Analogously to the above procedure, one deduces conditions such that the sublevel sets $H^{-1}((-\infty, H(\epsilon_1, \epsilon_2)])$ become (global) attractors resp. repeller for the modified predator-prey system.

3. Lotka-Volterra model

In concrete applications it might be difficult to verify the assumptions of Proposition 2.3 or 2.4, since the critical points of Δ in $(0,1)$ are difficult to compute. In order to illustrate how to handle this problem analytically, we consider a normalized version of the well-known 2-dimensional Lotka-Volterra equations (see for instance [Mur01; p. 80])

$$\begin{cases} \dot{x} = (a-y)x, \\ \dot{y} = (-1+x)y, \end{cases} \tag{7}$$

where x is the size (biomass) of the prey and y is the predator. Here $a > 0$ is the growth rate of the prey in absence of a predator and the decay rate for the predator in absence of a prey is 1. For a further biological or ecological interpretation we refer the interested reader to e.g. [Bra78, Mur01]. The system (7) clearly fits into our more general predator-prey framework of (1) with

$$c = 1, \qquad p(x) = x, \qquad q(x) = 1 \tag{8}$$

and fulfills our hypotheses $(H)_1$–$(H)_3$. As unique nontrivial equilibrium we obtain $(1, a)$, i.e., $x^* = 1$. The corresponding first integral $H : (0,\infty)^2 \to \mathbb{R}$ has the form

$$H(x,y) = x - 1 - \ln x + y - a + a \ln \frac{a}{y}$$

and we obtain the well-known phase portrait from Fig. 7.

In the present situation, the difference function $\Delta : (0,1] \to \mathbb{R}$ defined in (3) simplifies to

$$\Delta(s) = \epsilon_1(s-1) + \epsilon_2(1-s^\delta) + (a\delta - 1)\ln s.$$

We remark that an expression for the period of the solutions to (7) forming the level sets of H can be found in [Hsu83]. Although the methods from Sec. 2 can be applied to (7), we want to discuss and compare it to a further approach.

Finally, note that (7) is also a special case of the general model (6) with $f(x) = x$.

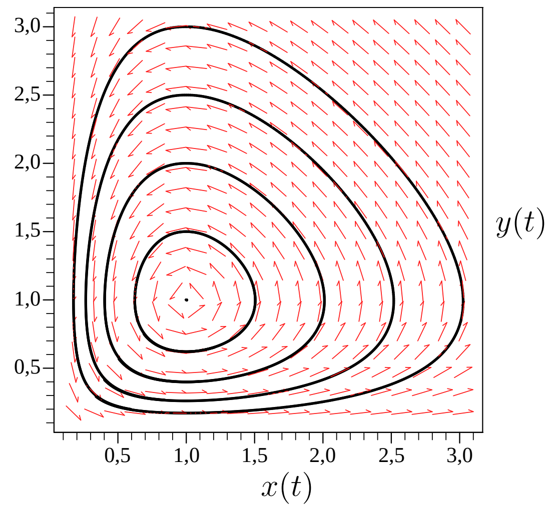

Fig. 7. Phase portrait of (7) for $a = 1$

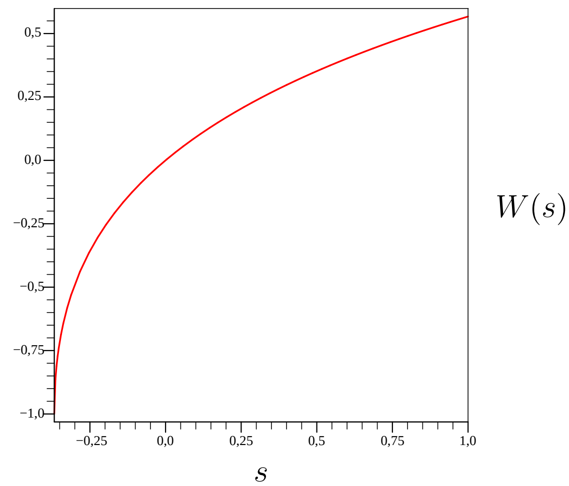

Fig. 8. The Lambert W-function

3.1. Poincaré sections

For a detailed understanding of the dynamics for linearly modified Lotka-Volterra equations, we now make use of a Poincaré section. Given $s_k \in (0,1)$, $k \in \mathbb{N}_0$, we start in a point $(s_k \epsilon_1, \epsilon_2)$ and leave the rectangle B at $\left(\epsilon_1, \epsilon_2 s_k^\delta\right)$ (cf. Sec. 2.2). Then the corresponding trajectory of the unmodified system takes us to the point $(\epsilon_1 s_{k+1}, \epsilon_2)$ on the upper side of the box B. In order to determine the point s_{k+1}, we have to solve the equation

$$H(\epsilon_1 s_{k+1}, \epsilon_2) = H(\epsilon_1, \epsilon_2 s_k^\delta). \qquad (9)$$

This requires to introduce a non-elementary function, namely the *Lambert W-function* $W : [-e^{-1}, \infty) \to [-1, \infty)$, which is the inverse of $x \mapsto xe^x$ (see Fig. 8). It is strictly increasing and for further properties, as well as applications of W, we refer to [CG$^+$96]. In particular, W is differentiable on $(-e^{-1}, \infty)$ with derivative

$$W'(x) = \frac{W(x)}{(1 + W(x))x}$$

and it is not hard to see that W fulfills the limit relation $\lim_{x \to 0} \frac{W(x)}{x} = 1$.

Thanks to the identity

$$\exp(a \ln y - y - x + \ln x) = -y^a e^{-y} W^{-1}(-x)$$

we take (9) into the exponential in order to obtain the recursion

$$s_{k+1} = \Pi(s_k)$$

with right-hand side (*Poincaré map*)

$$\Pi(s) := -\frac{1}{\epsilon_1} W\left(-\epsilon_1 e^{\epsilon_2 - \epsilon_1} s^{a\delta} e^{-\epsilon_2 s^\delta}\right).$$

As a consequence, the trajectory of the modified system starting in $(\epsilon_1 s_0, \epsilon_2)$ enters the box B successively at the points $(\epsilon_1 s_k, \epsilon_2)$ with $s_k = \Pi^k(s_0)$, $k \in \mathbb{N}_0$, as long as one has the inclusion $s_k \in (0, 1]$.

Lemma 3.1. *The Poincaré map* Π *leaves the interval* $[0,1]$ *invariant, is strictly increasing and has the fixed points* 0, 1.

Proof. For the argument of the function W in the definition of Π we abbreviate

$$\psi(s) := -\epsilon_1 e^{\epsilon_2-\epsilon_1} s^{a\delta} e^{-\epsilon_2 s^\delta}$$

and obtain $\psi(0) = 0$,

$$\psi(1) = -\epsilon_1 e^{-\epsilon_1} = W^{-1}(-\epsilon_1) < 0.$$

Thus, the fixed point relations $\Pi(0) = 0$ and $\Pi(1) = 1$ hold. Next we compute the derivative

$$\psi'(s) = -\epsilon_1 e^{\epsilon_2-\epsilon_1} \delta s^{a\delta-1}(a - \epsilon_2 s^\delta) e^{-\epsilon_2 s^\delta}$$

and due to $\epsilon_2 s^\delta \leq \epsilon_2 < a$ we have $\psi'(s) < 0$ for all $s \in (0,1]$. Consequently, ψ is strictly decaying from 0 to $W^{-1}(-\epsilon_1)$. Since W is a strictly increasing function, also the composition $\Pi = -\frac{1}{\epsilon_1} W \circ \psi$ must be strictly increasing from 0 to 1 on the interval $[0,1]$. ∎

Next we prepare some relations in order to investigate the stability properties of the fixed points 0 and 1 for Π. Under the notation from the above proof, one has

$$\lim_{s \searrow 0} \psi'(s) = \begin{cases} 0, & a\delta > 1 \\ -\epsilon_1 e^{\epsilon_2-\epsilon_1}, & a\delta = 1, \\ -\infty, & a\delta < 1 \end{cases}$$

and $\psi'(1) = -\epsilon_1 e^{-\epsilon_1} \delta(a - \epsilon_2) < 0$. Using the relation

$$\begin{aligned} \Pi'(s) &= -\frac{1}{\epsilon_1} W'(\psi(s))\psi'(s) \\ &= -\frac{1}{\epsilon_1} \frac{W(\psi(s))\psi'(s)}{[1 + W(\psi(s))]\psi(s)} \end{aligned}$$

this yields

$$\lim_{s \searrow 0} \Pi'(s) = \begin{cases} 0, & a\delta > 1 \\ e^{\epsilon_2-\epsilon_1}, & a\delta = 1, \\ \infty, & a\delta < 1 \end{cases} \tag{10}$$

and

$$\Pi'(1) = \frac{\delta(a - \epsilon_2)}{1 - \epsilon_1}. \tag{11}$$

Stability properties of the trivial fixed point 0 determine wether our modification prevents the atto-fox problem or not. In case $a\delta < 1$ the equilibrium 0 is unstable and trajectories of the modified Lotka-Volterra equations are driven away from the coordinate axis; the same holds in the critical case $a\delta = 1$ and $\epsilon_2 > \epsilon_1$. Conversely, the atto-fox problem gets worsened when 0 is asymptotically stable, which holds for parameters $a\delta > 1$ or, $\epsilon_2 < \epsilon_1$ and $a\delta = 1$.

The monotonicity properties of the Poincaré map have striking consequences for the global dynamics of our modified Lotka-Volterra system. Indeed, the only possible limit sets are trajectories corresponding to periodic solutions. A more detailed analysis is given in the following.

3.1(A). Stabilizing case

We begin by considering the case

$$\delta_1 > \delta_2 a, \tag{12}$$

$$\delta_1(1 - \epsilon_1) > \delta_2(a - \epsilon_2) \tag{13}$$

and start to argue on basis of the difference function Δ alone. Above all, it is clear that for small values of $\epsilon_1, \epsilon_2 > 0$ the condition in (13) simplifies to (12). Moreover, in our Lotka-Volterra setting relation (13) is equivalent to the first inequality in condition (4).

On the one hand, assumption (12) yields

$$\lim_{s \searrow 0} \Delta(s) = \infty, \qquad \Delta(1) = 0$$

and on the other hand we have $\Delta'(1) < 0$, where

$$\Delta'(s) = \epsilon_1 - \frac{1}{s}\left(1 - a\delta + \epsilon_2 \delta s^{\delta}\right)$$

gives us

$$\lim_{s \searrow 0} \Delta'(s) = -\infty.$$

Thus, under the additional assumption

$$\delta_1 \geq \delta_2 \tag{14}$$

we deduce

$$\begin{aligned}\Delta''(s) =& \frac{1}{s^2} \underbrace{(1 - a\delta)}_{>0} \\ &+ \epsilon_2 \delta \underbrace{(1 - \delta)}_{\geq 0} s^{\delta - 2} > 0\end{aligned}$$

for all $s \in (0,1)$, which means Δ has no turning point — i.e. Δ decreases monotonically from ∞ to 0.

In particular, Δ has no critical point in the interval $(0,1)$, i.e., $\Gamma = \emptyset$. Hence, we are in the situation of Proposition 2.3 yielding a global attractor of the linearly modified Lotka-Volterra equations.

Using the Poincaré map Π and the above we can show:

Proposition 3.2. *Under the assumptions* (12)–(14) *the Poincaré map* Π *has exactly the fixed points* $0, 1$*. Here, the point* 0 *is unstable, while* 1 *is asymptotically stable.*

Proof. Due to (10) and (12) the trivial fixed point 0 is unstable, whereas 1 is asymptotically stable by (13).

Proceeding indirectly, the existence of a fixed point s^* of Π in $(0,1)$ implies that $\Delta(s^*) = 0$. This contradicts our above considerations guaranteeing $\Delta(s) > 0$. ∎

Geometrically, the above Proposition 3.2 in conjunction with Lemma 3.1 yield that the sequence $(s_k)_{k \in \mathbb{N}_0}$ generated by the Poincaré map Π is monotonously increasing. More precisely, the forward iterates converge towards 1, while backward iterates tend to 0 (see Fig. 9). For every initial point

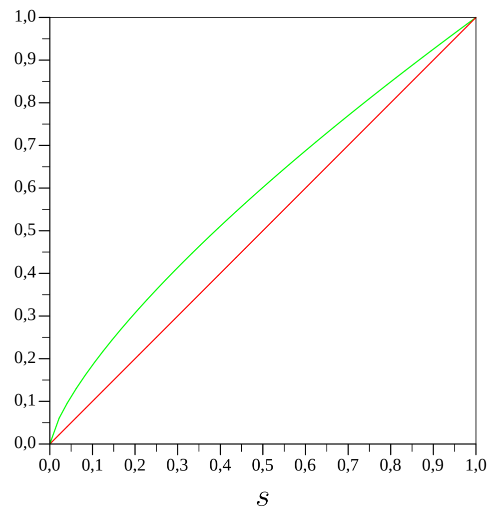

Fig. 9. Stabilizing case: Poincaré map for $a = 1$, $\epsilon_1 = \epsilon_2 = 0.5$, $\delta_1 = 1.5$, $\delta_2 = 1.1$

$s_0 \in (0,1)$ the complete orbit $(\Pi^k(s_0))_{k \in \mathbb{Z}}$ exists uniquely and connects the two fixed points of Π.

3.1(B). Destabilizing case

The dual assumptions to (12), (13) and (14) are

$$\begin{cases} \delta_1 < \delta_2 a, \\ \delta_1(1 - \epsilon_1) < \delta_2(a - \epsilon_2), \end{cases} \tag{15}$$

respectively

$$\delta_1 \leq \delta_2. \tag{16}$$

For the classical Lotka-Volterra equations the first inequality in (5) is equivalent to the second relation in (15).

An analogous analysis as given in the previous Sec. 3.1(A) tells us that the difference function Δ increases monotonically from $-\infty$ to 0. Again, Δ has no critical points in $(0,1)$ and we obtain a global repeller from Proposition 2.4.

In the following we investigate the dynamical behaviour using the Poincaré map Π alone. Here, in order to replace hypothesis (16) we define the 2nd order polynomial $\phi : (0,1) \to \mathbb{R}$,

$$\phi(t) := \epsilon_2^2 \delta t^2 + \epsilon_2(1-\delta-2a\delta)t + a(\delta a - 1)$$

and assume:

$$\begin{cases} \text{The polynomial } \phi \text{ possesses} \\ \text{no zero in the interval } (0,1). \end{cases} \tag{17}$$

Proposition 3.3. *Under the assumptions* (15) *and* (17) *the Poincaré map* Π *has exactly the fixed points* 0, 1. *Here, the point* 0 *is asymptotically stable, while* 1 *is unstable.*

Proof. Thanks to assumptions (15) the fixed point 0 is asymptotically stable. Next we show that Π has no fixed point in $(0,1)$. Thereto, using (15) we observe

$$\phi(0) = a(\delta a - 1) > 0$$

and consequently $\phi(t) > 0$ for all $t \in (0,1)$ by (17). Using the notation from the proof of Lemma 3.1 we notice

$$\psi(s) < 0,$$

$$\psi'(s) = \frac{\delta}{s} \underbrace{\psi(s)}_{<0} \underbrace{(a - \epsilon_2 s^\delta)}_{>0} < 0,$$

$$\psi''(s) = \frac{\delta}{s^2} \underbrace{\psi(s)}_{<0} \underbrace{\phi(s^\delta)}_{>0} < 0$$

for all $s \in (0,1)$. Hence, $W(\psi(s)) \in (-1,0)$ and for the 2nd derivative we compute

$$\begin{aligned} \Pi''(s) = &-\frac{1}{\epsilon_1} \frac{W(\psi(s))}{\underbrace{[1+W(\psi(s))]}_{>0}{}^3 \psi(s)^2} \\ &\cdot \Big(- \underbrace{W(\psi(s))}_{<0} \underbrace{[2+W(\psi(s))]}_{>0} \psi'(s)^2 \\ &+ [1+W(\psi(s))]^2 \underbrace{\psi(s)}_{<0} \underbrace{\psi''(s)}_{<0} \Big) > 0 \end{aligned}$$

for all $s \in (0,1)$. Therefore, Π is a strictly convex function, has no turning point and no fixed point in $(0,1)$. ∎

The sequence $(s_k)_{k \in \mathbb{N}_0}$ obtained via the forward iterates of the Poincaré map Π is strictly decreasing towards the asymptotically stable fixed point 0 (see Fig. 10) and the uniquely determined complete orbit $(\Pi^k(s_0))_{k \in \mathbb{Z}}$, $s_0 \in (0,1)$, connects the two fixed points of Π.

3.1(C). Critical case

Now we consider the critical and nongeneric case

$$\delta_1 = a\delta_2,$$

which in particular holds for $\delta_1 = a$, $\delta_2 = 1$, i.e. if we simply discard the nonlinear terms in the box B, leave the linear part and turn off the nonlinearities. As a result,

$$\Delta(s) = \epsilon_1(s-1) + \epsilon_2(1 - s^\delta),$$

$$\Pi(s) = -\frac{1}{\epsilon_1} W\left(-\epsilon_1 e^{\epsilon_2 - \epsilon_1} s e^{-\epsilon_2 s^\delta}\right).$$

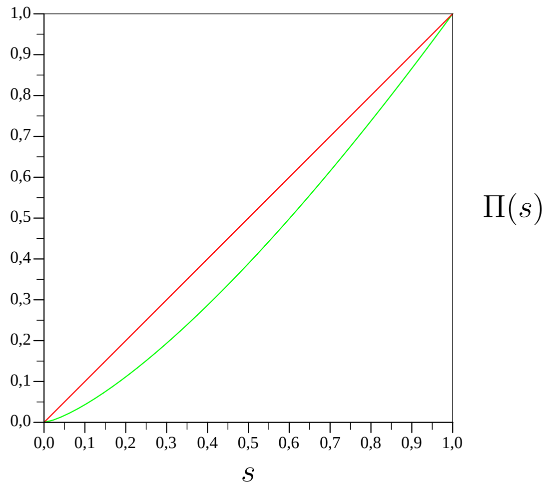

Fig. 10. Destabilizing case: Strictly convex Poincaré map for $a = 1$, $\epsilon_1 = \epsilon_2 = 0.5$ and $\delta_1 = 1.1$, $\delta_2 = 1.5$

Proposition 3.4. *The fixed point* 0 *of* Π *is asymptotically stable for* $\epsilon_2 < \epsilon_1$ *and unstable for* $\epsilon_2 > \epsilon_1$. *Moreover, the fixed point* 1 *of* Π *is asymptotically stable for* $\epsilon_1 < \delta\epsilon_2$ *and unstable for* $\epsilon_1 > \delta\epsilon_2$.

Proof. This is an immediate consequence of relation (10) and (11). ∎

For the function Δ we obtain the derivative

$$\Delta'(s) = \epsilon_1 - \delta\epsilon_2 s^{\delta-1},$$

consequently $\Delta'(1) = \epsilon_1 - \delta\epsilon_2$ and the unique point s^* with $\Delta'(s^*) = 0$ is

$$s^* = \left(\tfrac{\epsilon_1}{\epsilon_2\delta}\right)^{\frac{1}{\delta-1}} \quad \text{for } \delta \neq 1.$$

We begin with the case $\delta < 1$ and thus

$$\lim_{s \searrow 0} \Delta'(s) = -\infty.$$

- Provided $\epsilon_1 < \epsilon_2$ and $\epsilon_1 \leq \delta\epsilon_2$ we have $s^* \geq 1$ and Δ decreases strictly from $\Delta(0) = \epsilon_2 - \epsilon_1 > 0$ to $\Delta(1) = 0$. Thus, $\Delta(s) > 0$ in $(0, 1)$ and the system gets stabilized, i.e., the dynamics is as in Sec. 3.1(A).
- For $\epsilon_1 < \epsilon_2$, $\epsilon_1 > \delta\epsilon_2$ it is $s^* \in (0, 1)$. The function Δ decreases strictly from $\Delta(0) = \epsilon_2 - \epsilon_1 > 0$ to its negative minimum at s^*. It is positive on the interval $(0, s_0)$, where $s_0 \in (0, s^*)$ denotes the unique root of $\Delta(s) = 0$, resp. the unique fixed point of Π in $(0, 1)$ (see Fig. 11). In particular, the parameter value s_0 corresponds to a periodic solution of the modified system starting in the box B. The trajectory of this solution is attractive.
- If $\epsilon_2 \leq \epsilon_1$, then $\epsilon_1 > \delta\epsilon_2$ and also $s^* \in (0, 1)$. Here, Δ decreases strictly from $\Delta(0) = \epsilon_2 - \epsilon_1 \leq 0$ to its unique minimum at $s = s^*$ and then increases strictly to $\Delta(1) = 0$. Thus, the difference function Δ is strictly negative on $(0, 1)$ and the system gets destabilized, i.e., its dynamical behaviour is as described in Sec. 3.1(B).

In case $\delta > 1$ we have

$$\Delta'(0) = \epsilon_1 > 0$$

and arrive at:

- If $\epsilon_2 \geq \epsilon_1$, then $\epsilon_1 < \delta\epsilon_2$ and additionally $s^* \in (0, 1)$ holds. Thus, the difference function Δ increases strictly from $\Delta(0) \geq 0$ to its unique positive maximum at s^* and then decreases to $\Delta(1) = 0$. Thanks to $\Delta(s) > 0$ on $(0, 1)$ the system becomes stabilized.

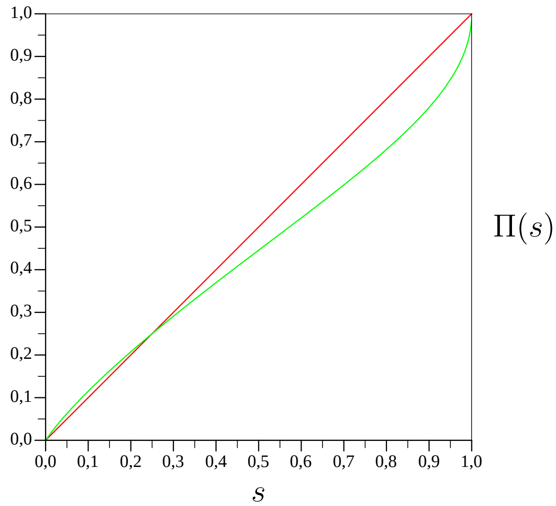

Fig. 11. Critical case: Asymptotically stable fixed point $s_0 = \frac{1}{4}$ of the Poincaré map for $a = 2$, $\epsilon_1 = 1.0$, $\epsilon_2 = 1.5$, $\delta_1 = 2.1$, $\delta_2 = 1.05$

- If $\epsilon_2 < \epsilon_1$ and $\epsilon_1 < \delta\epsilon_2$, then Δ increases strictly from $\Delta(0) < 0$, vanishes at a unique point $s_0 \in (0, s^*)$, reaches its positive maximum at s^* and decreases to $\Delta(1) = 0$. The point s_0 corresponds to the unique fixed point of Π in $(0, 1)$ and there exists a periodic solution of the modified system; its trajectory is repulsive.

- For $\epsilon_2 < \epsilon_1$ and $\epsilon_1 \geq \delta\epsilon_2$ the function Δ increases strictly from $\Delta(0) < 0$ to $\Delta(1) = 0$. Due to $\Delta(s) < 0$ on the interval $(0, 1)$ the system is destabilized.

In the remaining case $\delta = 1$ the difference function degenerates to a linear mapping and we obtain

$$\Delta(s) = (\epsilon_1 - \epsilon_2)s + \epsilon_2 - \epsilon_1.$$

Finally, this allows us to conclude:

- $\epsilon_1 < \epsilon_2$: Δ decreases from $\epsilon_2 - \epsilon_1$ to 0, i.e., $\Delta(s) > 0$ for $s \in (0, 1)$ and the modification stabilizes our system as in Sec. 3.1(A).

- $\epsilon_1 = \epsilon_2$: Δ vanishes identically and the modification has no effect.

- $\epsilon_2 < \epsilon_1$: Δ increases from $\epsilon_1 - \epsilon_2$ to 0 and $\Delta(s) < 0$ for $s \in (0, 1)$. The dynamical behaviour is as described in Sec. 3.1(B).

4. Perspective and Conclusion

In our analysis of the Lotka-Volterra model we neglected the parameter constellations

$$\begin{aligned} \delta_1 &> \delta_2 a, \\ \delta_1(1 - \epsilon_1) &\leq \delta_2(a - \epsilon_2) \end{aligned} \tag{18}$$

and

$$\begin{aligned} \delta_1 &< \delta_2 a, \\ \delta_1(1 - \epsilon_1) &\geq \delta_2(a - \epsilon_2) \end{aligned} \tag{19}$$

since they are not feasible for small boxes B, i.e. values of $\epsilon_1, \epsilon_2 > 0$ close to 0. Yet, the following remarks might indicate the corresponding dynamical behavior:

- In the situation (18) (with strict inequalities) both the fixed points $0, 1$ of Π are unstable. Since the function $\pi : [0, 1] \to \mathbb{R}$, $\pi(s) := \Pi(s) - s$ has the properties

$$\pi(0) = 0, \qquad \pi(1) = 0,$$
$$\lim_{s \searrow 0} \pi'(s) = \infty, \qquad \pi'(1) > 0,$$

due to continuity reasons, there exists a further fixed point s_0 in $(0, 1)$. The interested reader may try to verify the uniqueness of s_0. For our modified Lotka-Volterra model this means that there exists a global attractor consisting of the periodic motions corresponding to fixed points of Π in $(0,1]$, their connecting orbits and the orbits of (7) not entering the box B.

- In case (19) holds with strict inequalities, the two fixed points $0,1$ of Π are asymptotically stable. Moreover, as above there exists a further fixed point $s_0 \in (0,1)$. Furthermore, for the modified Lotka-Volterra we have a repeller consisting of fixed points for Π in $(0,1]$, their connecting orbits and all trajectories of (7) not entering the box B.
- In the final nongeneric situation

$$\delta_1(1-\epsilon_1) = \delta_2(a-\epsilon_2)$$

the fixed point 1 is nonhyerbolic with $\Pi'(1) = 1$. Its stability properties can be determined using well-known tools involving the second derivative (see [FEP03; Theorem 2.3]). We obtain

$$\Delta''(1) = \frac{\epsilon_1(a-\epsilon_2)^2 - \epsilon_2(1-\epsilon_1)^2}{(a-\epsilon_2)^2(1-\epsilon_1)}$$

and 1 is asymptotically stable for parameters $\epsilon_1(a-\epsilon_2)^2 > \epsilon_2(1-\epsilon_1)^2$, while the fixed point 1 is unstable in case $\epsilon_1(a-\epsilon_2)^2 < \epsilon_2(1-\epsilon_1)^2$.

To draw a conclusion, in generic situations, a modification of predator-prey equations near the origin to linear problems, guarantees the existence of a global attractor or repeller. The latter invariant set consists of closed trajectories for the unperturbed differential equations.

For critical parameter constellations a further phenomenon occurs: The attractor/repeller from the above generic situation is surrounded by a closed trajectory of the linearly modified problem, which is repulsive resp. attractive.

Last but not least, notice that our approach generalizes to structurally unstable predator-prey models, where a first integral H is available (see [Hsu05] for a survey), whose level sets are closed curves in the first quadrant. In addition, the set B can have a possibly more complicated shape then a box, like for instance the sector of a circle centered around the origin. Indeed, the simple linear structure of eqn. (2) enables us to compute the entry and exit times for B.

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