

1 Heteroclinic orbits indicate overexploitation in
2 predator–prey systems with a strong Allee effect.

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Abstract

Successful prey species establishment in a model system can be dependent not only on the parameter setting, but also on the initial conditions of the system. Similarly, successful predator species establishment can be dependent on both these conditions. Predator invasion can fail and lead to system collapse, an event referred to as overexploitation. This phenomenon is especially important in models with bistability properties, such as strong Allee effects. The prey extinction threshold then prevents easy re-establishment of the prey species. In this paper we deal with the bifurcation analyses of two previously published predator–prey models with strong Allee effects. We expand the analyses to include not only local, but also global bifurcations. We show the existence of a point-to-point heteroclinic cycle in these models, and discuss numerical techniques for continuation in parameter space. The continuation of such a cycle in two-parameter space forms the boundary of a region in parameter space where the system collapses after predator invasion, i.e. where overexploitation occurs. We argue that the detection and continuation of global bifurcations in these models are of vital importance for the understanding of the model dynamics.

Keywords: Bistability, depensation, extinction threshold, global bifurcation, heteroclinic point-to-point connection, separatrix

1 Introduction

Since the pioneering work by Lotka and Volterra [2,3] two-dimensional models of predator–prey interactions have been studied thoroughly. One recurring aspect of many models is that in absence of the predator the prey species grows to a carrying capacity. An example of that is the logistic growth. Also, if the predator invades, there is always a region in parameter space where the model has a positive equilibrium, implying successful invasion of the predator followed by coexistence of the prey and the predator. One issue is whether it is always possible for a prey species to establish a viable population in a habitat in absence of a predator species. Another matter is, that even when such a prey species can successfully invade or exist in a habitat under certain conditions, it is not always the case that after the invasion of a predator species stable coexistence of prey and predator will result.

In regard of the first issue we recall that in some cases the initial numbers of a species determine the long-term behavior of the system. Population models with an incorporated Allee effect have this property. This effect is named after Allee [4], who described the phenomenon that under natural circumstances populations can benefit from the presence of conspecifics (e.g. [5]). Such benefits, as mentioned by [6], could, among others, be predator dilution, reduction of inbreeding, genetic drift and predator swamping. In addition, the species can at low density suffer from inverse density dependent effects, when the individuals have problems to find food or a mate. Allee effects, benefits for the population at high densities of individuals or costs at low densities, have been shown in all major taxonomic

groups of animals [7, 8], and even in plants [9], for instance in the case where reduced density or quality of compatible mates or scarcity of pollinators can give rise to an Allee effect [10].

Two types of Allee effects are recognized [7]: so-called *weak* Allee effects, also named non-critical depensation, and *strong* Allee effects, also referred to as critical depensation in fisheries literature [11]. With weak Allee effects the net population growth rate at low population densities is still positive, though not at its maximum value. However, the long-term behavior of the system is not expected to differ depending on the initial conditions of the system. With strong Allee effects the population growth rate is negative at low population densities. Thus there is bistability: a critical threshold exists, above which the species profits but below which the species suffers from negative effects. This is then often referred to as an extinction threshold [10], a minimal viable population density or number of individuals below which the population inevitably goes extinct under deterministic dynamics. The same system may exhibit both effects for different settings, for instance in semi-arid systems where plants may facilitate their own growth by decreasing water run-off, leading to a weak Allee effect if water run-off causes light soil degradation or a strong Allee effect when it leads to severe soil degradation [12].

Not only local populations can suffer from Allee effects. In the current age of degrading landscapes by humans, the fragmentation of habitats is of major importance to species' meta-population dynamics. A meta-population model with an Allee effect directly active at the meta-population level was analyzed in [13]. A thorough analysis of incorporating an Allee effect at the local population level in discrete and continuous time deterministic

or stochastic models of meta-populations and its effect on the meta-population is given in [14].

Now, what happens when predators are introduced into the system when the prey population is in equilibrium? The first scenario is that the predator species is not able to establish itself, and it will go extinct while the prey maintains itself in the system. It is also possible that the predator species can successfully invade the system. Coexistence then occurs between the predator and prey species. A third, dramatic option is that predator invasion causes the extinction of both species. We refer to this scenario as *overexploitation*.

How does overexploitation occur? For that, one has to realize that system dynamics depends on the parameter settings of the system. Specific parameter values at which system dynamics change qualitatively are bifurcations. The transition from the first scenario (only prey, no predator establishment) to the second scenario (predator–prey coexistence) is associated with a local bifurcation, i.e. the only information required is about the equilibrium involved in the transition. However, the transition from coexistence to overexploitation is associated with periodic solutions that are destroyed. The kind of bifurcation associated with this event is a global bifurcation, i.e. we require more than just local information.

In this paper, we address these issues by studying two models with strong Allee effects. The means to do this is by both local and global bifurcation analysis. In the Bazykin-Berezovskaya (BB)-model [15] there is a strong Allee effect for the prey population, formulated by incorporation of an extra factor in the logistic growth equation such that the population growth rate is negative at zero biomass. The trophic interaction is modeled with a linear Lotka-Volterra functional response, but qualitatively similar results are ob-

tained for the in many cases more realistic Holling type II functional response [16]. In the model by Kent et al. [1] the prey population is still described by a logistic growth term but also by an in- or outflux of prey, effectively modeling prey immigration or emigration. This model is referred to as the prey flux (PF)-model, where the prey outflux is considered an Allee effect which destabilises the prey dynamics.

The paper continues as follows. In section 2 we briefly introduce the two models that we analyze. After that, in section 3, we discuss the theory on heteroclinic cycles in predator–prey models. In section 4 we give the bifurcation analyses of the models. In section 5 we then discuss the different results, which will be summarized in section 5.2. An appendix A is added in which we discuss the required numerical techniques for successful detection and continuation of global bifurcations in two-dimensional systems, which have not been standardized yet.

2 Formulation of the models

In this section we describe the two models from the literature mentioned in the introduction (the BB-model [15] and the PF-model [1]). In both models we denote the size of the scaled prey population by $x_1(t) \geq 0$ and of the scaled predator population by $x_2(t) \geq 0$. Table 1 explains the different parameters used in both models, which are equal if possible.

2.1 The BB-model

The dimensionless equations of the BB-model are written as

$$\frac{dx_1}{dt} = x_1(x_1 - l)(k - x_1) - x_1x_2, \quad (1a)$$

$$\frac{dx_2}{dt} = c(x_1 - m)x_2, \quad (1b)$$

where the parameters l and m serve as bifurcation parameters. The growth of the prey population in absence of the predator is modeled with an adapted logistic growth. Only if $l > 0$ the prey species suffers a strong Allee effect. Predation is modeled as a Lotka–Volterra functional response, so the predator population grows proportionally with the feeding rate, and predator mortality cm is linear.

The system has the trivial equilibrium $E_0 = (0, 0)$, two positive equilibria for the prey population $E_1 = (l, 0)$ and $E_2 = (k, 0)$, and one internal equilibrium $E_3 = (m, (m - l)(k - m))$, where the prey and predator coexist. Equilibrium E_3 is only positive for $l \leq m \leq k$ in the region $0 \leq l \leq k$.

2.2 The PF-model

The dimensionless equations of the PF-model are written as

$$\frac{dx_1}{dt} = (x_1 - a)(1 - x_1) - \frac{x_1x_2}{b + x_1}, \quad (2a)$$

$$\frac{dx_2}{dt} = \frac{cx_2}{b + x_1} (x_1 - d), \quad (2b)$$

where a and d are the primary bifurcation parameters. The prey population increases following a logistic growth adapted by immigration $a < 0$ or emigration $a > 0$. Here we

concentrate on the case with emigration, since it models a strong Allee effect. However, note that we include the weak Allee effect in our bifurcation analysis also for comparison with [1]. Predation is modeled as a Holling type II functional response.

The system does not give rise to the trivial equilibrium $E_0 = (0, 0)$. There exist two positive equilibria with only prey present $E_1 = (a, 0)$ and $E_2 = (1, 0)$, and one internal equilibrium

$$E_3 = \left(d, \frac{(d-a)(1-d)(b+d)}{d} \right).$$

Equilibrium E_3 is only positive for $a \leq d \leq 1$ in the region $0 \leq a \leq 1$.

2.3 Invasion of a predator in a prey-only system

It is particularly interesting to study what will happen when predators are introduced into a system when the prey population density is at carrying capacity (E_2). Basically, three different types of dynamical behavior can occur. The first possibility is that the predators cannot invade, for example because of food shortage, i.e. the prey density in E_2 is too low. Another option is that the predator is able to invade the system, and that this will lead to stable coexistence between the predator and prey populations. This state of coexistence can either be a steady state or a stable limit cycle. The third option that can occur is that predator invasion leads to extinction of both species, an event we refer to as overexploitation. All three possibilities are displayed in Figure 1. Which of these three types of dynamical behavior occurs will depend on the parameter values of the system (see section 4).

3 Heteroclinic cycle formulation

Before discussing the analyses of the BB- and PF-models we need to explain how we can detect global bifurcations. For that, let us define the heteroclinic cycle (or loop) that occurs at the global bifurcation, denoted $G^\neq$ in the results, which consists of two connections between two saddle equilibria. One connection occurs at the boundary of the positive quadrant of the state space (x_1, x_2) , from the equilibrium E_1 to the equilibrium E_2 . This is the trivial branch where the predator is absent ($x_2 = 0$) and the dynamics of the prey population is given by (1a) or (2a), depending on the model. Hence this branch is not discussed further. The other connection is a nontrivial branch from E_2 to E_1 . The space encapsulated by the heteroclinic loop contains equilibrium E_3 .

Mathematically we write this as follows. Let us denote the starting point E_2 of the non-trivial point-to-point connection as $\mathbf{x} \in \mathbb{R}^2$ and the end point E_1 as $\mathbf{y} \in \mathbb{R}^2$. Let us also define the flow $\varphi^t : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ by $\varphi^t(\mathbf{z}_0) = \mathbf{z}(t, \mathbf{z}_0)$, where the function $\mathbf{z}(t)$, considered as a function of t , is the solution of

$$\frac{d\mathbf{z}}{dt} = \mathbf{f}(\mathbf{z}) , \quad (3)$$

starting at $\mathbf{z}_0$. We have a heteroclinic connecting orbit, denoted Γ_0 , to the equilibria $\mathbf{x}$ and $\mathbf{y}$ of system (3) if

$$\varphi^t(\mathbf{z}_0) \rightarrow \mathbf{x} \quad , \quad t \rightarrow -\infty , \quad (4a)$$

$$\varphi^t(\mathbf{z}_0) \rightarrow \mathbf{y} \quad , \quad t \rightarrow \infty , \quad (4b)$$

(see [17, page 195]).

155 Let us now define the stable and unstable manifolds $W^u(\mathbf{x})$ and $W^s(\mathbf{y})$ as

$$W^u(\mathbf{x}) = \{\mathbf{z} \in \mathbb{R}^2 | \varphi^t(\mathbf{z}) \rightarrow \mathbf{x} \text{ as } t \rightarrow -\infty\} , \quad (5a)$$

$$W^s(\mathbf{y}) = \{\mathbf{z} \in \mathbb{R}^2 | \varphi^t(\mathbf{z}) \rightarrow \mathbf{y} \text{ as } t \rightarrow \infty\} . \quad (5b)$$

156 One property of the heteroclinic connection is that the unstable manifold $W^u(\mathbf{x})$ of equi-
157 librium $\mathbf{x}$ overlaps with the stable manifold $W^s(\mathbf{y})$ of equilibrium $\mathbf{y}$, that is

$$\Gamma_0 \subset W^u(\mathbf{x}) \cap W^s(\mathbf{y}) , \quad (6)$$

158 (see [17, page 195]).

159 The numerical schemes used to calculate and continue the heteroclinic cycles are discussed
160 in the appendix. As is demonstrated in the appendix for a fixed value of one parameter
161 a decreasing value of another parameter yields a critical value where the period of the
162 limit cycle goes to infinity while it passes both saddle points E_2 and E_1 closely. The global
163 bifurcation is fixed by the parameter value where the cycle breaks via the heteroclinic cycle
164 defined by (4). This technique can be used to obtain a good first approximation of the
165 heteroclinic cycle.

166 4 Bifurcation analysis

167 In this section we provide the local bifurcation analyses of the two previously mentioned
168 models. Also, we depict and discuss the heteroclinic cycles occurring in these models.
169 Table 1 gives the default values for the different parameters used in both models, when
170 applicable.

4.1 The BB-model

The local bifurcations in the BB-model are analysed in [15, page 85] and in the textbook [18, Chapter 8]. Here we provide a summary of the results.

4.1.1 Local bifurcation analysis

Let us first provide a one-dimensional bifurcation diagram, where $l = 0.5$ is fixed but m is varied. Figure 2 gives the long-term dynamics of the biomasses of the prey and predator population. There are two transcritical bifurcation curves denoted by TC : at $m = 0.5$ (a TC_1 , the 1 indicates it is a bifurcation of equilibrium E_1) and at $m = 1$, where the equilibrium value for the predator population equals zero, $x_2 = 0$ (a TC_2). A Hopf bifurcation point occurs at $m = 0.75$, denoted by H_3 (the subindex 3 is because this is a bifurcation point for equilibrium E_3). At this point we have $Re(\lambda_{1,2}) = 0$, where $\lambda_{1,2} = (\text{tr } \mathbf{J} \pm \sqrt{\text{disc } \mathbf{J}})/2$, for $\text{tr } (\mathbf{J}) = m(k - 2m + l)$ and $\det(\mathbf{J}) = mc(m + l)(k - m)$, so that $\text{disc } \mathbf{J} = \text{tr } \mathbf{J}^2 - 4 \det \mathbf{J}$, where $\mathbf{J}$ is the Jacobian matrix evaluated at the equilibrium E_3 . In mathematical terms the Hopf bifurcation occurs when $\text{tr } (\mathbf{J}) = 0$, while the transcritical bifurcation TC_2 occurs when $\det(\mathbf{J}) = 0$. Below the Hopf bifurcation point the positive equilibrium is unstable and a stable limit cycle around this point exists, which becomes a stable attractor of the system (we recall that the system is two-dimensional and Poincaré–Bendixson theorem applies [18, page 137]).

The two-parameter bifurcation diagram is given below in the section about the global bifurcation analysis. The curve $m = 0$ is a curve where each point is an equilibrium with two zero eigenvalues. Substitution of $m = 0$ in Eqn. (1a) shows that with $x_1 = 0$ all

values for x_2 give an equilibrium, so there is a continuum of solutions. Two transcritical bifurcation curves are associated with the equilibrium E_2 originating at $l = 1$ and $m = 1$, namely the vertical curve $l = 1$ and the horizontal curve $m = 1$. The curve TC_1 on the diagonal $m = l$ is associated with the equilibrium E_1 . The Hopf bifurcation curve H_3 is described by the relationship $m = 0.5l + 0.5k$.

4.1.2 Global bifurcation analysis

Considering the one-dimensional bifurcation diagram again (Figure 2) we see that lowering m gives an increasing period of the limit cycle that exists after the Hopf bifurcation. The period goes to infinity at a global bifurcation point, denoted by $G^\neq$. At that point the peak value of the prey equals $k = 1$ (the carrying capacity) and the minimal value of the prey equals l , while the minimum value of the predator during the cycle goes to zero. Figure 3 provides a three-dimensional picture of predator and prey densities and the bifurcation parameter m , and clarifies the occurrence of the heteroclinic cycle in the system.

In order to get more insight into the dynamics around the global bifurcation point $G^\neq$ we study the dynamics in the phase plane in three consecutive panels of Figure 4 with fixed $l = 0.5$ while we vary m . The manifolds in the figures were calculated using DSTOOL [19]. Fig. 4, upper panel, shows the unstable manifold W_2^u for the saddle E_2 and the stable manifold W_1^s for the saddle E_1 . All orbits above this manifold converge to the zero equilibrium E_0 , i.e. the manifold W_1^s acts as a separatrix for the stable limit cycle and the stable equilibrium E_0 . The unstable manifold W_2^u converges towards the stable limit cycle enclosed by W_1^s . Fig. 4, middle panel, displays the heteroclinic cycle for $m = 0.73544234950$ which is broken

213 into two heteroclinic connections between the two saddle points $(0.5, 0)$ and $(1, 0)$. Outside
 214 the heteroclinic cycle the solution goes asymptotically to the stable zero state E_0 , while
 215 inside the heteroclinic cycle there is convergence towards the heteroclinic cycle. Fig. 4,
 216 lower panel, then shows the stable and unstable manifolds for $m = 0.735$. Now W_2^u is
 217 connected to E_0 while W_1^s is connected to the positive equilibrium E_3 which is a spiral
 218 source since the m -value is close to, but below the Hopf bifurcation value. Orbits above
 219 the curve W_2^u converge to the zero equilibrium E_0 , while below the curve, bounded by
 220 the stable manifold of the saddle E_1 , orbits will oscillate but finally also converge to E_0 .
 221 This is because at the global bifurcation the separatrix has disappeared. Observe that
 222 orbits below the curve W_2^u cannot leave this region by crossing the stable manifold W_1^s
 223 because it is invariant, and due to uniqueness of the solution. The orbit can leave the
 224 region only via the narrow tunnel between the lowest part of the first turn of the stable
 225 manifold belonging to E_1 and the unstable manifold of E_2 . This means that the stable limit
 226 cycle breaks open when the heteroclinic cycle occurs in the neighbourhood of the saddle
 227 E_2 where the stable manifold of E_1 and the unstable manifold of E_2 mismatch. Even when
 228 starting close to the spiral source the system makes a final oscillatory movement around
 229 the positive equilibrium before it eventually converges to E_0 . Starting close to E_1 on the
 230 right-hand side of the stable manifold the system makes one single turn around the spiral
 231 source before extinction occurs.

232 The global bifurcation can be continued in two-parameter space also, and the result-
 233 ing curve is also given in Fig. 5, upper panel. The diagram furthermore displays two
 234 codimension-two points, namely Z^+ (point $(1, 1)$) and Z^- (point $(0, 0)$). The point Z^+ is

on the intersection of the two transcritical bifurcation curves TC_2 , the Hopf bifurcation curve H_3 and the global bifurcation curve $G^\neq$. In Z^+ we have $E_1 = E_2 = E_3$, because $m = l = 1$. At the other point Z^- the TC_1 coincides with the global bifurcation. At this point we have $E_0 = E_1 = E_3$, since $m = l = 0$. Also in this point there is a continuum of solutions $x_1 = 0$ and $x_2 \in \mathbb{R}$, so the predator biomass is not determined. In appendix A, numerical procedures are discussed to calculate the global bifurcation curve $G^\neq$.

4.2 The PF-model

Kent et al. [1] gave a stability analysis of their model in terms of isocline analyses. We connect to their analysis by providing a local bifurcation diagram for the parameters a (equal to $-D$ in [1]) and d (equal to σ in [1]). Recall the strong Allee effect exists only for $a > 0$, but we add the local bifurcation diagram for $-1 < a < 0$ for easier comparison with the results published by Kent et al. [1].

4.2.1 Local bifurcation analysis

We directly provide a two-dimensional bifurcation diagram in Figure 6, upper figure, which resembles [1, Figure 3], but note that it is a mirror image of that figure. Observe that there is an extra transcritical bifurcation TC_1 for $d = a$ in the relevant interval $a \in [0, 1]$.

For $d > 1$ E_2 is the only biologically relevant equilibrium. All positive initial values for x_1, x_2 go to this stable equilibrium E_2 . For $d = 1$ there is a transcritical bifurcation TC_2 occurring. Note that Kent et al. refer to this bifurcation as "an extinction threshold for predators". For $d < 1$ equilibrium E_3 is biologically relevant also, and E_2 and E_3 have exchanged their stability. Equilibrium E_3 now is a stable node or a stable focus, while E_2

is a saddle. Thus, there is coexistence of the predator–prey system.

Crossing the axis $x_1 = 0$ leads to convergence to minus infinity $x_1 \rightarrow \infty$, a biologically relevant situation. In reality when the prey population density becomes zero in a finite time, it remains zero while the predator population goes extinct as well. So, this asymptotic behavior takes over the role of the equilibrium E_0 in the BB-model.

For positive values of a equilibrium E_1 also applies, and this solution is always a saddle in that parameter regime. The line $a = 0$ is not a bifurcation curve, but indicates where equilibrium E_1 is exactly 0. In the region $a > 0$ the stable manifold W_1^s is a separatrix. That means that initial values of x_1, x_2 on the "wrong" side of the manifold will lead to extinction. Initial values of x_1, x_2 starting within the space enclosed by this stable manifold and the axis $x_2 = 0$ will lead to coexistence.

Also shown is a Hopf bifurcation curve H_3^- . To the right of this curve limit cycles occur, while the equilibrium E_3 is unstable.

4.2.2 Global bifurcation analysis

If a limit cycle is continued in two parameters a and T , where T is the cycle period, this results in T tending to infinity at, for example, $a \approx 0.01077219$, $d = 0.4$. At this point the non-trivial orbit in this cycle connects the saddle E_2 to the saddle E_1 , going over the non-trivial equilibrium E_3 .

In Figure 6, upper panel, the continuation curve of the heteroclinic connecting orbit in the parameter space a, d is depicted as $G^\neq$. It can readily be seen that this curve is almost exactly on the Hopf bifurcation curve for a large parameter region ($a \gg 0$, $1 > d \gtrsim 0.5$).

Limit cycles are therefore almost immediately destroyed. For values of a a little greater than zero and $d \approx 0.45$ there is still a significant parameter region where limit cycles do exist, however, within this region there exists also the mentioned separatrix W_1^s , which means that starting at certain values in state space leads to extinction. At the other side of the curve $G^\neq$, beyond the point where the heteroclinic point-to-point connection occurs, the system goes extinct for all positive initial values of x_2 . The prey population can persist, but only when $x_1(0) > a$, $x_2(0) = 0$.

4.3 Implications of global bifurcations

The occurrence of a heteroclinic cycle in the discussed models has serious implications for the system dynamics. Overall we can distinguish three regions both in Fig. 5, lower panel, and Fig 6, lower panel. In the middle grey region, denoted by region **1** and bounded by a local bifurcation curve TC_2 , any predator invasion is unsuccessful. The prey population is then either at carrying capacity (E_2) or absent (E_0), depending on the initial state of the system.

On the other side of the same TC_2 curve there is a positive equilibrium E_3 , which implies coexistence of the predator–prey system. In this dark grey region, denoted **2**, lies the Hopf bifurcation, where a stable limit cycle is born. This local bifurcation curve changes the system’s attractor from an equilibrium to a periodic solution.

Region **2** then is bounded on the other side by the global bifurcation curve $G^\neq$, also the boundary of the lightest grey region denoted by **0**. The trivial solution E_0 is the global attractor in that region and the system collapses for all $x_2(0) > 0$. The prey population

can settle at saddle point E_2 , provided we have $x_1(0) > x^*$, $x_2(0) = 0$, where x^* is the x_1 -value of E_1 . However, any predator invasion knocks the prey population out of the saddle equilibrium and leads to system extinction.

5 Discussion

Global bifurcations can be found in the two models discussed in this paper. They are heteroclinic cycles that consist of two heteroclinic connections between two saddle equilibria in the zero biomass plane of the predator. Previously the global bifurcation curve for the Bazykin–Berezovskaya model was only sketched in [15, page 86], while for the model by Kent et al. [1] this type of bifurcation was not considered. However, we argue that detection and continuation of global bifurcations is vital for understanding mathematically the dynamics of models with Allee effects. Referring again to figure 6, lower panel, we remark the boundary between regions **0** and **1** cannot be calculated easily without a successful technique for the detection and continuation of a global bifurcation.

We can elaborate even further on the importance of global bifurcation analyses especially in the case of the model by Kent et al. [1]. They indicated that limit cycles are not sustained by the Allee effect. Indeed, limit cycles in the PF-model that occur through a Hopf bifurcation are almost immediately destroyed again through a heteroclinic cycle. Thus, we have complemented their local bifurcation diagram by showing the existence of two coupled heteroclinic point-to-point connections in their model. The disappearance of the limit cycles is associated with the occurrence of these heteroclinic connections. No doubt such phenomena occur in other models where the prey population shows an

extinction threshold as well, and the application of our continuation technique likely leads to improved model analyses in general.

5.1 Allee effects and global bifurcations: biological implications

From a mathematical point of view a strong Allee effect is generated by the existence of an unstable equilibrium x^* in a prey model, where $x^* > 0$. This point functions as a threshold, such that for initial values $x_1(0) < x^*$ the prey population goes extinct while for $x_1(0) > x^*$ the prey population will be attracted to another, stable equilibrium, which most likely is the carrying capacity for the prey.

With the invasion of a predator species x_2 three scenarios can occur. Figures 1, 5, lower panel and 6, lower panel, recapitulate these three scenarios. The first option is that invasion of the predator is impossible (region **1**). The system's attractor E_2 is equal to the attractor for the systems with only prey. At a transcritical bifurcation curve (TC_2 , but also simultaneously TC_3) the equilibrium E_2 becomes a saddle equilibrium. This bifurcation curve bounds region **2**, in which invasion of the predator is successful. The new attractor is then equilibrium E_3 , and there is coexistence between the predator and prey species. The equilibrium E_2 is still an attractor on the x -axis, but any predator invasion can establish coexistence. The equilibrium E_3 undergoes a Hopf bifurcation further on.

At the boundary of region **0** something different happens. At this boundary, a heteroclinic cycle, the only positive attractor of the system is destroyed. Without predators, initial values of $x_1(0) > x^*$ still establish a prey population at the equilibrium E_2 , but any predator invasion knocks the system out of this equilibrium causing overexploitation and

340 system collapse.
 341 Cycle destruction and overexploitation do not occur in the default Lotka–Volterra or
 342 Rosenzweig–MacArthur [20] models. Instead there is only a transcritical bifurcation curve
 343 that is the boundary for predator existence, depending on the mortality rate of the preda-
 344 tor, i.e. predators can "die too quickly" and mortality is not compensated by birth. In the
 345 models discussed in our paper, the predator species apparently can also "die too slowly",
 346 i.e. the mortality rate is low such that overexploitation, or "ecological suicide", occurs.
 347 In a system without bistability properties overexploitation leads to system collapse, but
 348 any re-invasion of the prey species can lead to system recovery. However, the potential
 349 devastating result of overexploitation in a system with strong Allee effect should not be
 350 underestimated. In a system with a strong Allee effect the prey species needs to overcome
 351 the Allee threshold, a highly unlikely event. Such a collapse can be caused by two math-
 352 ematically distinct processes: either by stochastic variation of one of the state variables,
 353 or a trend in one of the parameters that governs the behaviour of the system. In the case
 354 of harvested fish populations as reported in [21] it was suggested that a surreptitiously
 355 changing parameter was the cause of collapse in 1 out of 5 observed population collapses.
 356 Both in conservation biology and in biological control programs Allee effects could have
 357 serious implications. Indeed, reintroductions of species are suspected to be hampered by
 358 Allee effects, where it can impact the viability of the populations and metapopulations of
 359 such species [6,14]. If it is known that a particular species suffers from an Allee effect, this
 360 knowledge can help preventing the collapse of a population [22]. For biological control the
 361 occurrence of an Allee effect in a pest population can prevent its establishment (e.g. [7]). It

would be even better if overexploitation could be invoked on purpose, such that predator invasion would lead to extinction of the pest, which can then hopefully not re-establish itself again due to an Allee effect. On the other side, if the pest has established an Allee effect in the population of its natural enemy by some means, this can cause a failure of a biological control program. In that case natural enemies should be introduced in large enough numbers to overcome any Allee effect.

In the fisheries literature both Allee effects and the effects of (over)harvesting are discussed heavily also, since fish populations in the oceans are constantly exploited by humans. In [23] the catch history for a large number of fish species was reported, accompanied by a warning that traditional management techniques might need serious revision. In [6] it was suggested that, in order to get a sustainable harvest, fish populations should overcompensate the harvest pressure.

A fundamental difference between the above predator–prey systems and human-exploited systems is in the feedback mechanism, which is not assumed in fishing models. However, a dramatic phenomenon as overharvesting can also occur in these models. In [21] continuous-time models of a prey population under harvesting with various renewal functions (logistic, Ricker, Beverton–Holt) were studied. These models all showed ‘crashes’ after a plateau-shaped yield under surreptitiously increasing catch levels (i.e. a varied bifurcation parameter) if the renewal function was negative for stock sizes lower than a given threshold. The collapse of many fish populations of strong schoolers subject to harvesting by maximal sustainable yield is reported to be due to an Allee effect in [24].

383 Despite these results there seems to be much debate about the impact of an Allee effect on
 384 the level of population dynamics. In [25] four types of compensatory mechanisms in several
 385 models were reviewed, and it was concluded that many studies support the existence of
 386 these mechanisms, but that they are not strong enough to be of importance. However, they
 387 warn this should not be interpreted as evidence that the Allee effect is rare or not important.
 388 In [26] it was argued that empirical support for compensation from population-level data is
 389 "hard to obtain and inconclusive". Nevertheless, it is recognised that apparently depleted
 390 fish stock populations display a reduced capacity for recovery [27].
 391 Although in this paper we have analyzed two systems with incorporated Allee effects,
 392 these systems are not the only type of system that display bistability. The occurrence
 393 of alternative steady states for a certain range of a parameter (a phenomenon known as
 394 'hysteresis') is extensively reviewed in [28]. In aquatic systems the vegetation versus algal
 395 bloom is a famous example. For terrestrial systems, in a spatially explicit model in [12] the
 396 occurrence of bistability is shown where the system can alternate between a vegetation-
 397 dominated system with low soil degradation and a state with almost no vegetation and
 398 high soil degradation. Another example are systems with symbiosis [29], where two con-
 399 sumer populations feed on separate resources but also need each other's products. There
 400 the resource and the excretion product of one consumer species form two separate, non-
 401 interchangeable resources for the second consumer species, which results in the creation of
 402 a deadlock system and thus leads to bistability.

5.2 Conclusions

In this paper we have discussed the existence of global bifurcation curves in two-parameter space in two-dimensional systems. We have also shown that some model results can be better understood with a global bifurcation analysis, as in the prey-flux model for instance. A very general and practical notion is that global bifurcations are associated with boundaries of regions in parameter space where catastrophic events occur. Of particular interest in this respect is system destruction after a global bifurcation, for instance in the case of overexploitation, which can be the ironical result of a predator population that has a mortality rate that is too low. The ecological impact of overexploitation (or overharvesting for that matter) should not be underestimated, especially in models that display bistability, like models with strong Allee effects. In systems that have no bistability re-establishment of a species after overexploitation might be possible. However, in systems with strong Allee effects it is very likely that once overexploitation has occurred the Allee effect prevents any easy system recovery.

6 Acknowledgments

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Table 1: Explanation of the parameters used in the BB-model and the PF-model. Parameters without a default value but a parameter range are considered bifurcation parameters.

symbol	description	value (BB)	value (PF)
a	in-/outflux of prey	-	$[-1, 1]$
b	ratio of searching to handling per predator	-	0.1
c	conversion ratio of consumed prey per biomass	1	0.1
d	predator extinction threshold	-	$[0, 1]$
k	carrying capacity	1	-
l	extinction threshold	$[0, 1]$	-
m	mortality rate of predator	$[0, 1]$	-

Figure legends

Fig. 1 Three possible scenarios for invasion of a small predator population in a system with a prey population subject to a strong Allee effect in equilibrium (E_2). With option 1 there is only persistence of the prey population, given that the predator initial population size is on the right side of the stable manifold of E_1 , which is the system's separatrix. With option 2 there exists some positive system attractor with both prey and predator present. With option 0 any predator invasion knocks the system out of the saddle equilibrium and lead to extinction of both predator and prey (the separatrix has disappeared).

Fig. 2 One-parameter bifurcation diagram with free parameter m for BB-model ($l = 0.5$). Points TC_1 and TC_2 are transcritical bifurcation points. Point H_3 is the Hopf bifurcation point and $G^\neq$ indicates the heteroclinic orbit. Between these two points the solution is a stable limit cycle of which the extrema are plotted. At the heteroclinic orbit the prey biomass ranges from 0.5 to 1 while the predator biomass becomes very small during one cycle of which the period is infinitely large.

Fig. 3 A three-dimensional bifurcation diagram with one free parameter and two state variables: x_1, m, x_2 . A solid line indicates a stable solution and a dashed line an unstable one. The projection on the left face is Fig 2 again. The projection on the ground face gives a x_1, m diagram. It is obvious how an increasing limit cycle leads to the destruction of the system attractor at the heteroclinic cycle.

Fig. 4 Upper panel: Stable and unstable manifold where $m = 0.74837$ and $l = 0.5$. For the saddle E_2 point $(1, 0)$ the unstable manifold W_2^u (dashed line) and for the saddle E_1 point $(0.5, 0)$ the stable manifold W_1^s (solid line) are shown. Since the m -value is between the Hopf bifurcation H_3 and the heteroclinic orbit $G^\neq$ values, there is a stable limit cycle. All orbits above the stable manifold W_1^s converge to the stable zero equilibrium E_0 point $(0, 0)$. All orbits below the stable manifold W_1^s converge to the stable limit cycle.

Middle panel: The heteroclinic connection plotted in the x_1, x_2 phase space for $l = 0.5$. The unstable manifold W_2^u and the stable manifold W_1^s intersect. For starting values inside the heteroclinic cycle the orbit converges outward to the heteroclinic cycle. With starting values outside the heteroclinic cycle the system converges to the stable zero equilibrium E_0 point $(0, 0)$.

Lower panel: Stable and unstable manifold where $m = 0.735$ and $l = 0.5$, thus below $G^\neq$. For the saddle E_2 point $(1, 0)$ the unstable manifold W_2^u (dashed line) and for the saddle E_1 point $(0.5, 0)$ the stable manifold W^s (solid line) are shown. Since the m -value is below the heteroclinic orbit $G^\neq$ and hence below the Hopf bifurcation, there is an unstable positive equilibrium (spiral source). All orbits above the unstable manifold of E_2 converge directly towards the stable zero equilibrium E_0 . Inside the curve bounded by the stable manifold of the saddle E_1 , the orbit oscillates before finally converging slowly to the stable zero equilibrium E_0 as well.

Fig. 5 Upper panel: Two-parameter bifurcation diagram for the BB-model with l and m as bifurcation parameters. The TC_2 curve $m = 1$ indicates a predator invasion boundary. Curve H_3 is the supercritical Hopf bifurcation curve and $G^\neq$ the heteroclinic cycle curve. The points Z^+ $(1, 1)$ and Z^- $(0, 0)$ are different types of codim 2 points. For more information see text.

Lower panel: The same two-dimensional diagram of the BB-model, but now the regions are indicated where there are qualitatively different outcomes. Region **1** indicates that only the prey can exist. In region **2** both the prey and predator can coexist after predator invasion. In region **0** the prey can exist at carrying capacity. However, any predator invasion leads to system extinction, a situation referred to as overexploitation.

560

Fig. 6 Upper panel: Two-parameter diagram of the PF model with a and d as bifurcation parameters. The TC_2 curve $d = 1$ indicates a predator invasion boundary. The curve H_3 indicates the Hopf bifurcation and the curve $G^\neq$ is the heteroclinic cycle curve. Points Z^+ $(1, 1)$ and Z^- $(0, 0)$ are different types of codim 2 points. For more information see text.

Lower panel: The same two-dimensional diagram of the PF model, but now with the indication of regions with qualitatively different behavior. Notation and meaning are equal to Fig. 5, lower panel.

568

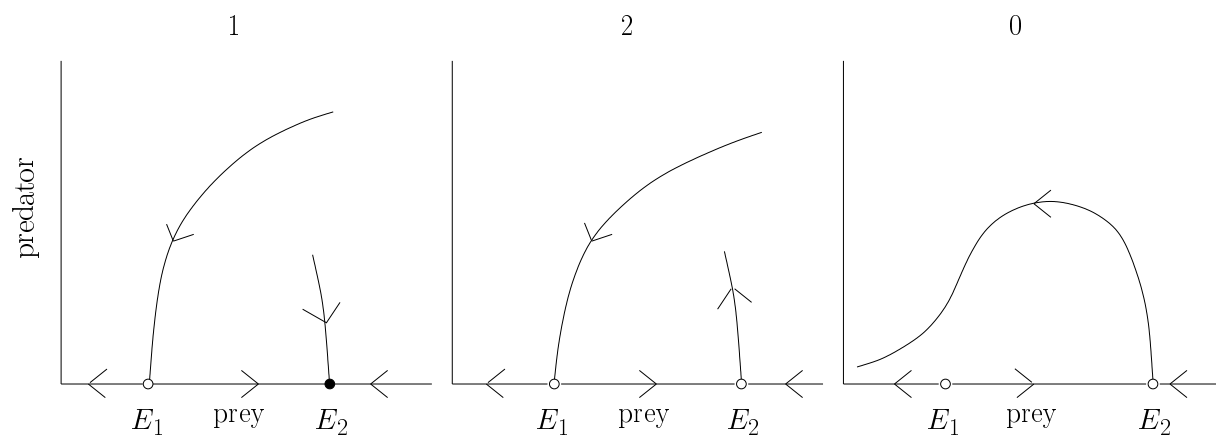


Figure 1:

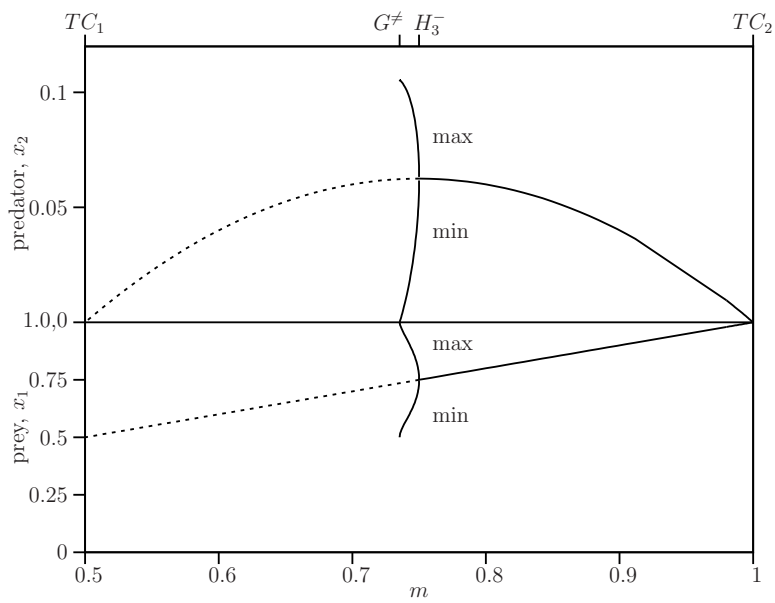


Figure 2:

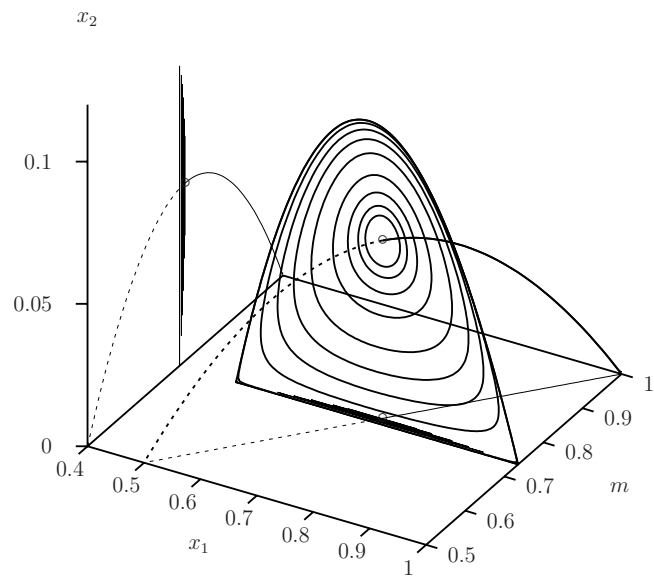


Figure 3:

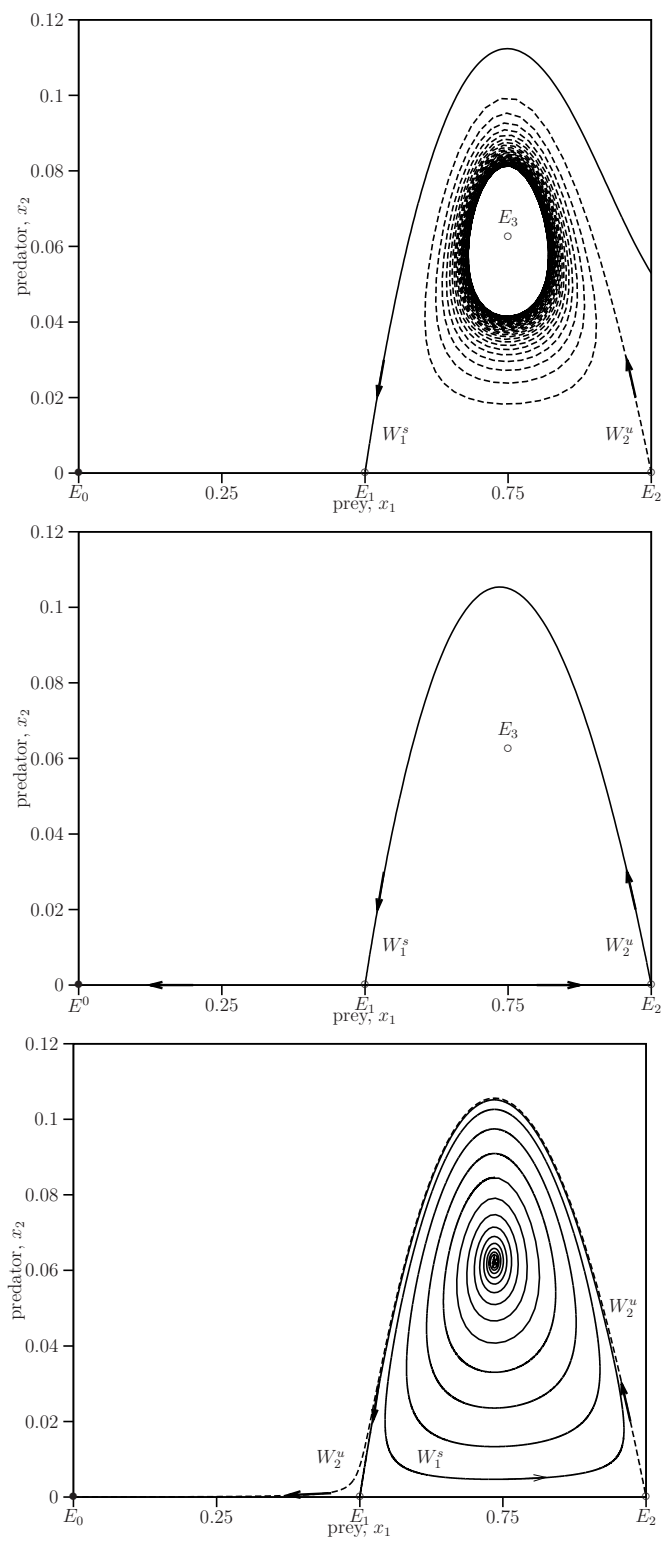


Figure 4:

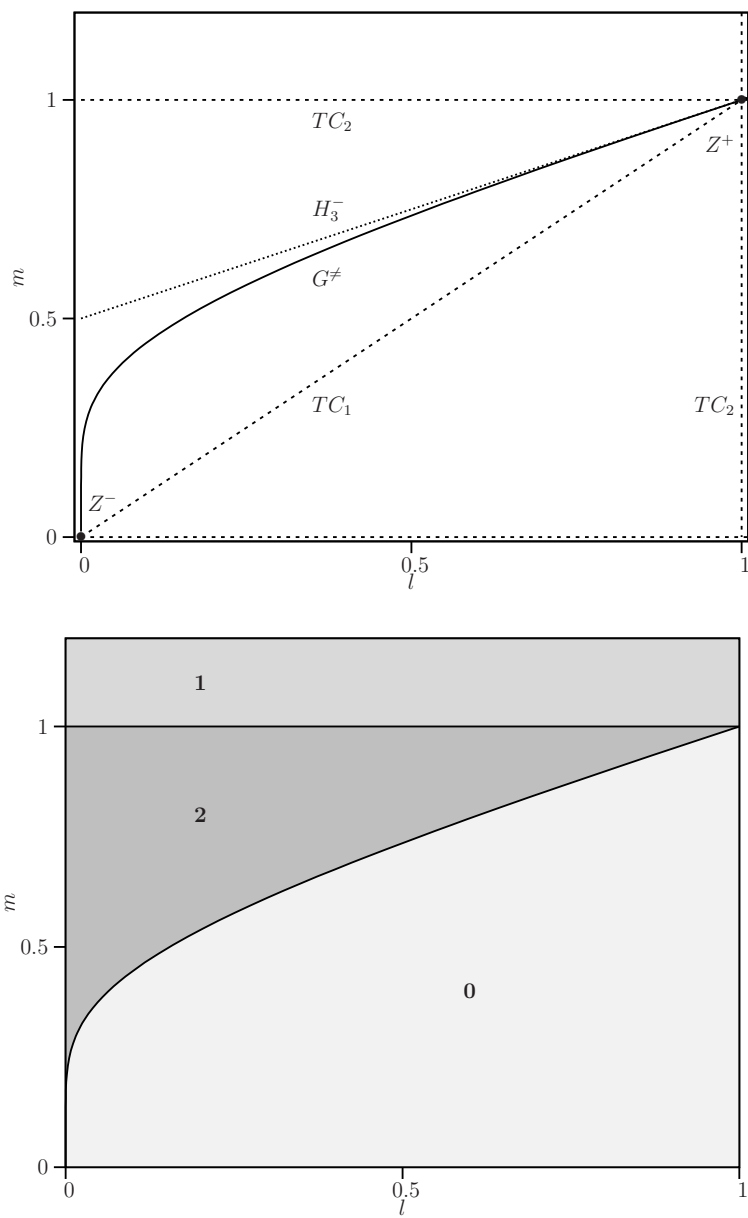


Figure 5:

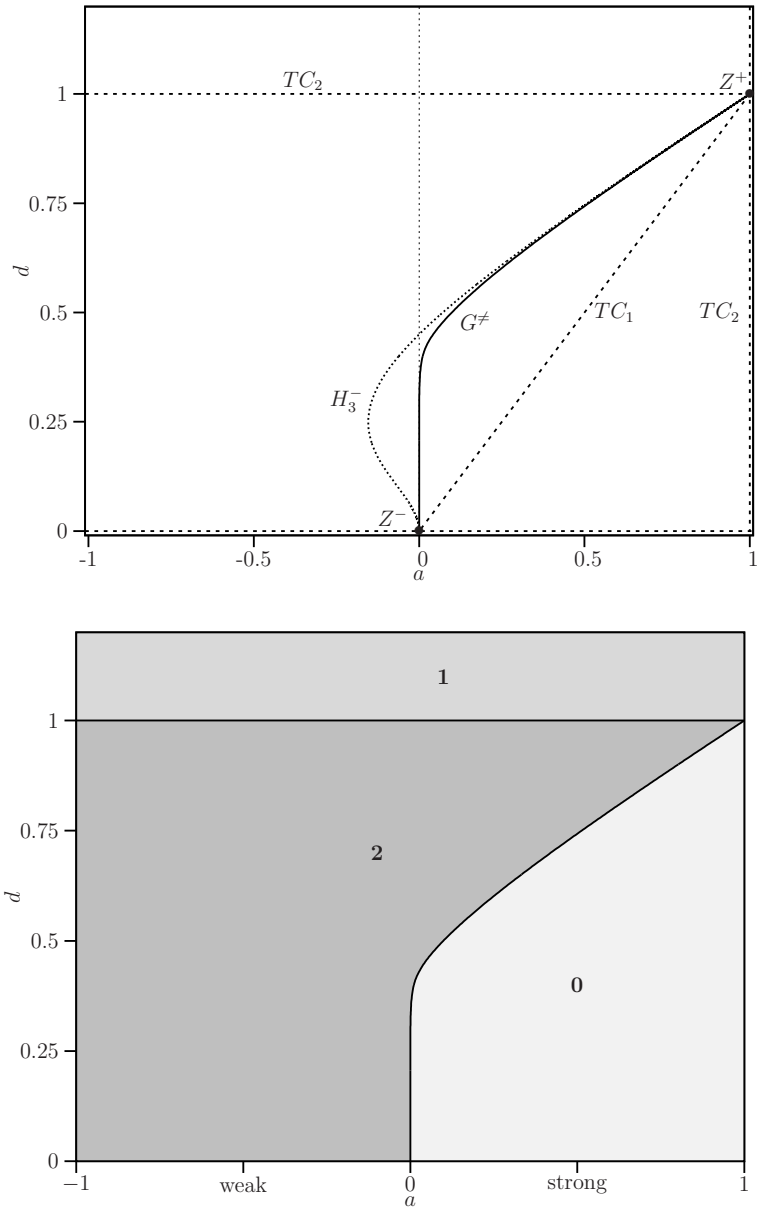


Figure 6:

A Numerical schemes for calculation of heteroclinic cycles

A.1 Formulation of the truncated boundary conditions

Calculating the global bifurcation curve boils down to solving the BVP (4), followed by continuation in two parameters. The BVP is truncated into a finite time interval $(-T, T)$ where T is large enough, and certain boundary conditions (BC's) at the end points of that interval are imposed. An appropriate ODE solver can be used to calculate the orbit. In the following we will discuss two techniques.

First the BC's have to be adapted to this finite time interval. The local linear approximation of the unstable invariant manifold $W^u(\mathbf{x})$ is denoted as $T^u(\mathbf{x})$ and of the stable invariant manifold $W^s(\mathbf{y})$ is denoted as $T^s(\mathbf{y})$. This requires calculation of the Jacobian matrix evaluated at the saddle points, its eigenvalues and eigenvectors.

The saddle equilibria and the eigenvalues and eigenvectors of the Jacobian matrix evaluated in those points are calculated by solving

$$\mathbf{f}(\mathbf{z}) = 0 . \tag{7}$$

where $\mathbf{z}$ ($\mathbf{x}$ or $\mathbf{y}$) is the equilibrium and

$$\mathbf{J} \mathbf{p} = \lambda \mathbf{p} , \tag{8}$$

$$\langle \mathbf{p}, \mathbf{p} \rangle = 1 , \tag{9}$$

585 where λ is the eigenvalue, $\mathbf{p}$ the associated normalized eigenvector and $\langle \mathbf{r}, \mathbf{s} \rangle = \mathbf{r}^T \mathbf{s}$ is the
586 standard scalar product in $\mathbb{R}^2$.

587 Now we can have two kinds of BC formulations. In projection BC formulations [30, 31]
588 instead of the normal Jacobian matrices the adjoint Jacobian matrices in the appropriate
589 saddle points are used. With explicit BC formulations [32] we use the local linearizations
590 of the stable and unstable manifolds at E_2 and E_1 , respectively.

591 Generally no explicit expressions are known for the equilibrium values, the eigenvalues and
592 the eigenvectors and each set of equations for the two saddles E_1 and E_2 leads to the addi-
593 tional scalar equations for additional scalar variables which are solved at each continuation
594 step. Although here analytical expressions are available, these quantities are numerically
595 determined.

596 We mostly used the explicit BC's, which are written as

$$\mathbf{z}(-T) = \mathbf{x} + \varepsilon \mathbf{p}_2^u, \quad (10a)$$

$$\mathbf{z}(T) = \mathbf{y} + \xi \mathbf{p}_1^s, \quad (10b)$$

597 where ε and ξ are two fixed sufficiently small parameters. The eigenvector $\mathbf{p}_2^u$ belongs to
598 the positive eigenvalue at E_2 , in Fig. 4 tangent to the unstable manifold W_2^u , while $\mathbf{p}_1^s$ is
599 the eigenvector belonging to the negative eigenvalue at E_1 in Fig. 4, tangent to the stable
600 manifold W_1^s .

601 **A.2 Numerical techniques to solve and continue BVP**

602 In order to solve the BVP we can distinguish between two popular numerical techniques,
603 namely the (single and multiple) shooting method and the orthogonal collocation method.

The methods are used in combination with either projection and/or explicit boundary condition formulations. To start the calculation of the heteroclinic connection in both approaches, we have to start with an appropriate initial guess for the connection. This can be obtained by continuation of the limit cycle in one bifurcation parameter while monitoring the cycle period T_c . We select the limit cycle for which approximately $T_c \rightarrow \infty$, in practice a value of T_c large enough and where the value of the bifurcation parameter does not change visibly anymore. A part of this limit cycle is then converted to a starting connection. After a connecting orbit was found, the continuation of the connection was done by means of a predictor-corrector continuation method with step-size control [17, 33, 34].

A.2.1 Shooting methods

Shooting methods for solving BVP's of ODE-systems are combinations of an initial value problem (IVP) solver and a solver for a system of non-linear equations. In shooting, first the initial conditions must be formulated. For that we calculate exactly the unstable eigenvector $\mathbf{p}_2^u$ and the positive eigenvalue of E_2 using the Jacobian matrix. Similarly, we calculate the stable eigenvector $\mathbf{p}_1^s$ and negative eigenvalue of E_1 . Next, assuming we use explicit BC's, the end point is determined that should be reached by a time-integrated orbit by setting ξ (according to Equation 10b). Some freedom is required to obtain an orbit that fulfills these conditions. We select one of two choices: either we fix ε and vary the integration time or we fix the integration time and vary ε . Either way, we are left with one unknown initial variable and one equation. We can solve this by using, for instance, Newtonian equation solvers.

625 With shooting there is a constant build-up of error with every integration step. To improve
626 the performance of the time-integration one can implement a so-called multiple shooting
627 method for the calculation of the heteroclinic cycle of the system. Multiple shooting has
628 been used before already for the continuation of global bifurcations in both biological and
629 non-biological ODE systems, for instance see [35–38].

630 In the BB-model (1) single shooting gives spurious results near de codim two points, so
631 multiple shooting is used to improve the results for the whole parameter range close to
632 $l = 1$ and $m = 1$. We introduce a midpoint $\mathbf{u}$, that divides the heteroclinic orbit in two
633 pieces of equal length, in the plane given by

$$\mathbf{u} = \varphi^0(\mathbf{x} + \varepsilon \mathbf{p}_2^u) , \quad (11a)$$

$$0 = \langle \mathbf{x} - \mathbf{y}, \mathbf{u} - 0.5(\mathbf{x} + \mathbf{y}) \rangle . \quad (11b)$$

634 The initial point at $t = -T$ is given by the identity $\varphi^{-T}(\mathbf{x} + \varepsilon \mathbf{p}_2^u) = \mathbf{x} + \varepsilon \mathbf{p}_2^u$ – recall φ^t is
635 the flow (see section 3) – and the endpoint at $t = T$ by $\varphi^T(\mathbf{x} + \varepsilon \mathbf{p}_2^u) = \mathbf{y} + \xi \mathbf{p}_1^s$. Eqn. (11b)
636 is an inner product that, when solved for 0, gives a projection condition that ensures that
637 point $\mathbf{u}$ is orthogonal. The truncated heteroclinic cycle starts at the distance fixed by the
638 scalar ε from E_2 with equilibrium point $\mathbf{x}$ on the local linear approximation $T^u(\mathbf{x})$, of the
639 unstable manifold $W_2^u(\mathbf{x})$ fixed by the eigenvector corresponding to the positive eigenvalue
640 of the Jacobian evaluated at $\mathbf{x}$.

641 Starting in this point the system is solved numerically using a Runge-Kutta method for a
642 fixed time period T . This point is denoted by $\mathbf{u}$. Thereafter integration starts from point
643 $\mathbf{u}$ until a point on the stable manifold W_1^s of E_1 at distance ξ from the equilibrium point

$\mathbf{y}$ is reached. We used a fixed truncation time interval T and free values for ξ and ϵ . Note that the introduction of the mid point generates an extra condition and thus there is an extra free parameter.

A.2.2 Orthogonal collocation methods

With collocation methods the solution is approximated by piecewise polynomials leading to a huge system of non-linear equations which has to be solved numerically using some Newtonian method. In the computer package AUTO [39] this technique is efficiently implemented together with a pseudo-arclength continuation technique. For local bifurcations the code detects higher order codimension bifurcations and also calculates the emanating branches of these bifurcations after detection. The use of an orthogonal collocation method has serious advantages, like a division of error over the mesh points and superconvergence, which leads to a better performance.

We used AUTO in two modes. Firstly, we used the part of AUTO called HOMCONT [39, Chapter 16] and [40], a collection of easy to use subroutines for the continuation of homoclinic and heteroclinic cycles. Secondly, we implemented the BC's in AUTO using facilities described in [39, Chapter 11] to solve the BVP's. The BVP solver implemented in AUTO gives flexibility in the choice of the formulation of the boundary conditions. The cost however is that all boundary and integral conditions need coding and there is no detection of the various higher order bifurcation points as implemented in HOMCONT [39, Chapter 16] and [40].

A.3 Performance

Both collocation and (multiple) shooting methods can be used together with either explicit or projection boundary conditions. In this paper we primarily used the explicit BVP's in combination with orthogonal collocation for the detection and continuation of the heteroclinic cycles. For the BB-model we also used a multiple shooting method with one intermediate step. Both methods give comparable results. A third method employed was the use of the more user-friendly HOMCONT.

One important note is that the accuracy of the continuation of the heteroclinic connection decreases near the codim 2 points. In some cases this leads to spurious results. A pragmatic solution is to stop continuation in two parameters when approaching a codim 2 point, then fix one primary bifurcation parameter and increase the truncation time interval T , which gives a better accuracy, then restart continuation in two parameters with the higher value of T [41]. Starting with a high T does not work, however, since the numerical accuracy then becomes too high and the continuation conditions are not met at all.