Heteroclinic orbits indicate overexploitation in 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. Simi-
larly, successful predator species establishment can be dependent on both these con-
ditions. 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 oc-
curs. 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, het-
eroclinic 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 were 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

\[
\begin{align*}
\frac{dx_1}{dt} &= x_1(x_1 - l)(k - x_1) - x_1x_2, \quad (1a) \\
\frac{dx_2}{dt} &= c(x_1 - m)x_2, \quad (1b)
\end{align*}
\]

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

\[
\begin{align*}
\frac{dx_1}{dt} &= (x_1 - a)(1 - x_1) - \frac{x_1x_2}{b + x_1}, \quad (2a) \\
\frac{dx_2}{dt} &= \frac{cx_2}{b + x_1}(x_1 - d), \quad (2b)
\end{align*}
\]

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 nontrivial point-to-point connection as $x \in \mathbb{R}^2$ and the end point $E_1$ as $y \in \mathbb{R}^2$. Let us also define the flow $\varphi^t : \mathbb{R}_+^2 \to \mathbb{R}_+^2$ by $\varphi^t(z_0) = z(t, z_0)$, where the function $z(t)$, considered as a function of $t$, is the solution of

$$\frac{dz}{dt} = f(z),$$

starting at $z_0$. We have a heteroclinic connecting orbit, denoted $\Gamma_0$, to the equilibria $x$ and $y$ of system (3) if

$$\varphi^t(z_0) \to x, \quad t \to -\infty,$$

$$\varphi^t(z_0) \to y, \quad t \to \infty,$$

(see [17, page 195]).
Let us now define the stable and unstable manifolds $W^u(x)$ and $W^s(y)$ as

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

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

One property of the heteroclinic connection is that the unstable manifold $W^u(x)$ of equilibrium $x$ overlaps with the stable manifold $W^s(y)$ of equilibrium $y$, that is

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

(see [17, page 195]).

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

4 Bifurcation analysis

In this section we provide the local bifurcation analyses of the two previously mentioned models. Also, we depict and discuss the heteroclinic cycles occurring in these models.

Table 1 gives the default values for the different parameters used in both models, when 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

\[
\lambda_{1,2} = \frac{(\text{tr}\ J \pm \sqrt{\text{disc}\ J})}{2},
\]

for \( \text{tr}\ (J) = m(k - 2m + l) \) and \( \text{det}(J) = mc(m + l)(k - m) \), so that

\[
\text{disc}\ J = \text{tr}\ J^2 - 4 \text{det}\ J,
\]

where \( J \) is the Jacobian matrix evaluated at the equilibrium \( E_3 \).

In mathematical terms the Hopf bifurcation occurs when \( \text{tr}\ (J) = 0 \), while the transcritical bifurcation \( TC_2 \) occurs when \( \text{det}(J) = 0 \). 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 $G^\#$. 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 $G^\#$ 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 $W^u_2$ for the saddle $E_2$ and the stable manifold $W^s_1$ for the saddle $E_1$. All orbits above this manifold converge to the zero equilibrium $E_0$, i.e. the manifold $W^s_1$ acts as a separatrix for the stable limit cycle and the stable equilibrium $E_0$. The unstable manifold $W^u_2$ converges towards the stable limit cycle enclosed by $W^s_1$. Fig. 4, middle panel, displays the heteroclinic cycle for $m = 0.73544234950$ which is broken.
into two heteroclinic connections between the two saddle points $(0.5, 0)$ and $(1, 0)$. Outside
the heteroclinic cycle the solution goes asymptotically to the stable zero state $E_0$, while
inside the heteroclinic cycle there is convergence towards the heteroclinic cycle. Fig. 4,
lower panel, then shows the stable and unstable manifolds for $m = 0.735$. Now $W^u_2$ is
connected to $E_0$ while $W^s_1$ is connected to the positive equilibrium $E_3$ which is a spiral
source since the $m$-value is close to, but below the Hopf bifurcation value. Orbits above
the curve $W^u_2$ converge to the zero equilibrium $E_0$, while below the curve, bounded by
the stable manifold of the saddle $E_1$, orbits will oscillate but finally also converge to $E_0$.
This is because at the global bifurcation the separatrix has disappeared. Observe that
orbits below the curve $W^u_2$ cannot leave this region by crossing the stable manifold $W^s_1$
because it is invariant, and due to uniqueness of the solution. The orbit can leave the
region only via the narrow tunnel between the lowest part of the first turn of the stable
manifold belonging to $E_1$ and the unstable manifold of $E_2$. This means that the stable limit
cycle breaks open when the heteroclinic cycle occurs in the neighbourhood of the saddle
$E_2$ where the stable manifold of $E_1$ and the unstable manifold of $E_2$ mismatch. Even when
starting close to the spiral source the system makes a final oscillatory movement around
the positive equilibrium before it eventually converges to $E_0$. Starting close to $E_1$ on the
right-hand side of the stable manifold the system makes one single turn around the spiral
source before extinction occurs.

The global bifurcation can be continued in two-parameter space also, and the result-
ing curve is also given in Fig. 5, upper panel. The diagram furthermore displays two
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 $\sigma$ 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 \( x_1 \to \infty \), 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 \( W^s_1 \) 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 \( G^\# \). It can readily be seen that this curve is almost exactly on the Hopf bifurcation curve for a large parameter region (\( a \gg 0, \ 1 > d \gg 0.5 \)).
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
system collapse.

Cycle destruction and overexploitation do not occur in the default Lotka–Volterra or Rosenzweig–MacArthur [20] models. Instead there is only a transcritical bifurcation curve that is the boundary for predator existence, depending on the mortality rate of the predator, i.e. predators can "die too quickly" and mortality is not compensated by birth. In the models discussed in our paper, the predator species apparently can also "die too slowly", i.e. the mortality rate is low such that overexploitation, or "ecological suicide", occurs.

In a system without bistability properties overexploitation leads to system collapse, but any re-invasion of the prey species can lead to system recovery. However, the potential devastating result of overexploitation in a system with strong Allee effect should not be underestimated. In a system with a strong Allee effect the prey species needs to overcome the Allee threshold, a highly unlikely event. Such a collapse can be caused by two mathematically distinct processes: either by stochastic variation of one of the state variables, or a trend in one of the parameters that governs the behaviour of the system. In the case of harvested fish populations as reported in [21] it was suggested that a surreptitiously changing parameter was the cause of collapse in 1 out of 5 observed population collapses.

Both in conservation biology and in biological control programs Allee effects could have serious implications. Indeed, reintroductions of species are suspected to be hampered by Allee effects, where it can impact the viability of the populations and metapopulations of such species [6,14]. If it is known that a particular species suffers from an Allee effect, this knowledge can help preventing the collapse of a population [22]. For biological control the 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].
Despite these results there seems to be much debate about the impact of an Allee effect on the level of population dynamics. In [25] four types of depensatory mechanisms in several models were reviewed, and it was concluded that many studies support the existence of these mechanisms, but that they are not strong enough to be of importance. However, they warn this should not be interpreted as evidence that the Allee effect is rare or not important. In [26] it was argued that empirical support for depensation from population-level data is "hard to obtain and inconclusive". Nevertheless, it is recognised that apparently depleted fish stock populations display a reduced capacity for recovery [27].

Although in this paper we have analyzed two systems with incorporated Allee effects, these systems are not the only type of system that display bistability. The occurrence of alternative steady states for a certain range of a parameter (a phenomenon known as 'hysteresis') is extensively reviewed in [28]. In aquatic systems the vegetation versus algal bloom is a famous example. For terrestrial systems, in a spatially explicit model in [12] the occurrence of bistability is shown where the system can alternate between a vegetation-dominated system with low soil degradation and a state with almost no vegetation and high soil degradation. Another example are systems with symbiosis [29], where two consumer populations feed on separate resources but also need each other’s products. There the resource and the excretion product of one consumer species form two separate, non-interchangable resources for the second consumer species, which results in the creation of 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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References


### Tables

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.

<table>
<thead>
<tr>
<th>symbol</th>
<th>description</th>
<th>value (BB)</th>
<th>value (PF)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a$</td>
<td>in-/outflux of prey</td>
<td>-</td>
<td>$[-1, 1]$</td>
</tr>
<tr>
<td>$b$</td>
<td>ratio of searching to handling per predator</td>
<td>-</td>
<td>0.1</td>
</tr>
<tr>
<td>$c$</td>
<td>conversion ratio of consumed prey per biomass</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>$d$</td>
<td>predator extinction threshold</td>
<td>-</td>
<td>$[0, 1]$</td>
</tr>
<tr>
<td>$k$</td>
<td>carrying capacity</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>$l$</td>
<td>extinction threshold</td>
<td>$[0, 1]$</td>
<td>-</td>
</tr>
<tr>
<td>$m$</td>
<td>mortality rate of predator</td>
<td>$[0, 1]$</td>
<td>-</td>
</tr>
</tbody>
</table>
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 (E₂). 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 E₁, 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 $G$ 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 $W^u_2$ (dashed line) and for the saddle $E_1$ point $(0.5,0)$ the stable manifold $W^s_1$ (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 $W^s_1$ converge to the stable zero equilibrium $E_0$ point $(0,0)$. All orbits below the stable manifold $W^s_1$ 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 $W^u_2$ and the stable manifold $W^s_1$ 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 $W^u_2$ (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.

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.
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 \(W^u(x)\) is denoted as \(T^u(x)\) and of the stable invariant manifold \(W^s(y)\) is denoted as \(T^s(y)\). 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

\[ f(z) = 0 . \]  \hspace{1cm} (7)

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

\[ J \, p = \lambda \, p , \]  \hspace{1cm} (8)

\[ \langle p, p \rangle = 1 , \]  \hspace{1cm} (9)
where $\lambda$ is the eigenvalue, $p$ the associated normalized eigenvector and $\langle r, s \rangle = r^T s$ is the standard scalar product in $\mathbb{R}^2$.

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

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

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

\[ z(-T) = x + \varepsilon p^u_2 , \quad (10a) \]
\[ z(T) = y + \xi p^s_1 , \quad (10b) \]

where $\varepsilon$ and $\xi$ are two fixed sufficiently small parameters. The eigenvector $p^u_2$ belongs to the positive eigenvalue at $E_2$, in Fig. 4 tangent to the unstable manifold $W^u_2$, while $p^s_1$ is the eigenvector belonging to the negative eigenvalue at $E_1$ in Fig. 4, tangent to the stable manifold $W^s_1$.

A.2 Numerical techniques to solve and continue BVP

In order to solve the BVP we can distinguish between two popular numerical techniques, 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 $T_c \to \infty$, 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 $p_2^u$ and the positive eigenvalue of $E_2$ using the Jacobian matrix. Similarly, we calculate the stable eigenvector $p_1^s$ 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 $\xi$ (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 $\varepsilon$ and vary the integration time or we fix the integration time and vary $\varepsilon$. Either way, we are left with one unknown initial variable and one equation. We can solve this by using, for instance, Newtonian equation solvers.
With shooting there is a constant build-up of error with every integration step. To improve the performance of the time-integration one can implement a so-called multiple shooting method for the calculation of the heteroclinic cycle of the system. Multiple shooting has been used before already for the continuation of global bifurcations in both biological and non-biological ODE systems, for instance see [35–38].

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

$$u = \varphi^0(x + \varepsilon p_2^u),$$

$$0 = \langle x - y, u - 0.5(x + y) \rangle. \quad (11a)$$

The initial point at $t = -T$ is given by the identity $\varphi^{-T}(x + \varepsilon p_2^u) = x + \varepsilon p_2^u$ - recall $\varphi^t$ is the flow (see section 3) - and the endpoint at $t = T$ by $\varphi^T(x + \varepsilon p_2^u) = y + \xi p_1^s$. Eqn. (11b) is an inner product that, when solved for 0, gives a projection condition that ensures that point $u$ is orthogonal. The truncated heteroclinic cycle starts at the distance fixed by the scalar $\varepsilon$ from $E_2$ with equilibrium point $x$ on the local linear approximation $T^u(x)$, of the unstable manifold $W_2^u(x)$ fixed by the eigenvector corresponding to the positive eigenvalue of the Jacobian evaluated at $x$.

Starting in this point the system is solved numerically using a Runge-Kutta method for a fixed time period $T$. This point is denoted by $u$. Thereafter integration starts from point $u$ until a point on the stable manifold $W_1^s$ of $E_1$ at distance $\xi$ from the equilibrium point.
y is reached. We used a fixed truncation time interval $T$ and free values for $\xi$ and $\epsilon$. 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 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.