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1 Modelling, singular perturbation and bifurcation  
2 analyses of bitrophic food chains

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5 **Abstract**

6 Two predator-prey model formulations are studied: for the classical Rosenzweig-  
7 MacArthur (RM) model and the Mass Balance (MB) chemostat model. When the  
8 growth and loss rate of the predator is much smaller than that of the prey these mod-  
9 els are slow-fast systems leading mathematically to singular perturbation problem.  
10 In contradiction to the RM-model, the resource for the prey are modelled explicitly  
11 in the MB-model but this comes with additional parameters. These parameter val-  
12 ues are chosen such that the two models become easy to compare. In both models a  
13 transcritical bifurcation, a threshold above which invasion of predator into prey-only  
14 system occurs, and the Hopf bifurcation where the interior equilibrium becomes un-  
15 stable leading to a stable limit cycle. The fast-slow limit cycles are called relaxation  
16 oscillations which for increasing differences in time scales leads to the well known  
17 degenerated trajectories being concatenations of slow parts of the trajectory and fast  
18 parts of the trajectory. In the fast-slow version of the RM-model a canard explosion  
19 of the stable limit cycles occurs in the oscillatory region of the parameter space.  
20 To our knowledge this type of dynamics has not been observed for the RM-model  
21 and not even for more complex ecosystem models. When a bifurcation parameter  
22 crosses the Hopf bifurcation point the amplitude of the emerging stable limit cycles  
23 increases. However, depending of the perturbation parameter the shape of this limit  
24 cycle changes abruptly from one consisting of two concatenated slow and fast episodes  
25 with small amplitude of the limit cycle, to a shape with large amplitude of which  
26 the shape is similar to the relaxation oscillation, the well known degenerated phase  
27 trajectories consisting of four episodes (concatenation of two slow and two fast).

28 The canard explosion point is accurately predicted by using an extended asymptotic  
29 expansion technique in the perturbation and bifurcation parameter simultaneously  
30 where the small amplitude stable limit cycles exist. The predicted dynamics of the  
31 MB-model is in a large part of the parameter space similar to that of the RM-model.  
32 However, the fast-slow version of MB-model does not predict a canard explosion  
33 phenomenon.

34 *Keywords:*

35 Aggregation methods; Asymptotic series expansion; Canard; Geometrical Singular  
36 Perturbation theory; Predator-prey models

37 *Mathematics Subject Classification:* 34E17 - 37G15 - 92D25 - 92D40

# 1 Introduction

There is already a long tradition in modelling predator–prey systems under various environmental conditions. In some realistic cases there are differences in the order of magnitudes of the ingestion and growth rates of the two populations leading to so called fast-slow dynamical systems. Various mathematical analyses techniques have been used to analyse these models. Here we focus on the application of perturbation techniques when the processes of the two population occur at different time-scales.

The starting point is the Rosenzweig-MacArthur (RM) model [44] where the prey population grows logistically and the predator-prey interaction is described by the Holling type II functional response. This predator-prey system is mathematically described by two ordinary differential equations, (ODE)s, for the prey and the predator population. This model does not obey mass conservation law, however. Therefore we study also a version where additionally the prey population consumes abiotic nutrients. The resulting model is called the Mass Balance (MB) model where mass conservation is obeyed. This type of model is common practice in modeling food chains in a chemostat reactor which have been studied extensively: we refer to [45, 24]. These systems consist minimally of a nutrient, a prey and a predator. Consequently, the description of the dynamics involves three ODEs. The resulting three dimensional model is reduced to a two dimensional model for prey and predator populations when realistic assumptions are made.

For both types of models it is well known that the long-term dynamics is either a stable equilibrium (boundary: prey only, or interior: predator-prey) or a stable predator-prey limit cycle. For the RM-model, in [19] it was proved that the coexistence equilibrium is globally stable and in [4] that the periodic solution is unique thus a globally stable limit cycle and in [31] a detailed bifurcation analysis is performed.

Nutrient enrichment leads to the risk of extinctions when fluctuating densities during the limit cycle reach low values, called the “paradox of enrichment” [43]. Mathematically the first transition occurs at a transcritical bifurcation and the second at a Hopf bifurcation. This holds for both types of model the RM and MB-model.

When the growth and loss rate of the predator is much smaller than that of the prey, the system becomes a so called slow–fast system. These rates for the predator are multiplied by a perturbation parameter. These systems have been studied intensively in the literature, the RM-model with fast-slow dynamics in [35, 42, 41, 5, 11]. Slow-fast systems can naturally be identified, are often encountered in ecology. This is almost a rule when behavioral and population dynamics are considered at the same time. But also interactions between two populations like plankton and fish, plants and insects, herbs and trees are classical examples of systems with two time scales (see [41]). Another example where there are differences in the order of magnitudes of the ingestion and growth rates is a food chain of sewage-bacterium-worms often found in wastewater treatment plants (see [40]). The worm is the water nymph *Nais elinguis*, a oligochaete species. In a previous paper [25] we took advantage of these different time scales to apply aggregation methods in order to simplify the models for the dynamics of the wastewater treatment plant system.

Using a perturbation technique often the slow variables are frozen with the calculation

80 of the equilibria of the fast system but better approximations are obtained by asymptotic  
 81 expansions [18, 16]. When the perturbation parameter becomes small the resulting limit  
 82 cycle is called the *relaxation oscillation*, see [15], where the periodic orbits are phase plane  
 83 curves with both fast and slow parts of the trajectory.

84 When the time-scales differences are very large, that is with small positive perturbation  
 85 parameter, the presence of the Hopf bifurcation indicates the possible occurrence of so  
 86 called *canards*. In physics this has been studied extensively for the van der Pol equations  
 87 [47, 10, 6, 3, 8, 28, 29, 2]. More recently, in [37, 16] geometric singular perturbation  
 88 techniques [12] have been studied for application in biological practice, including these  
 89 slow-fast predator-prey systems. In this theory *invariant manifolds* play an important role  
 90 in the study of structural stability of dynamical systems or, when a degeneracy occurs,  
 91 in understanding the nature of bifurcations. A trajectory is an example of an invariant  
 92 manifold. Using this approach we will find that similar to the van der Pol equations case  
 93 also for the RM-model application of asymptotic expansions [3, 2] for the critical manifolds  
 94 leads to a divergent expansion. Nevertheless we will show that we are still able to compute  
 95 for which bifurcation parameter values a canard explosion occurs.

96 Bifurcation analysis results show that in the MB-model the singularity in the limiting  
 97 time-scale differences is completely different from that in the RM-model where the prey  
 98 grows logistically. Only local bifurcations occur and therefore continuation of equilibrium  
 99 and limit cycles gives a full picture of the long-term dynamics.

## 100 2 The RM bitrophic food chain model

101 A standard two-level food chain model from the field of theoretical biology is the scaled  
 102 Rosenzweig-MacArthur system (1963). The RM-model reads in dimensionless form derived  
 103 in the Appendix A:

$$\frac{dx_1}{dt} = x_1 \left( 1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (1a)$$

$$\frac{dx_2}{dt} = x_2 \left( \frac{c_1 a_1 x_1}{1 + b_1 x_1} - d_1 \right), \quad (1b)$$

104 with  $x_i(t) \in \mathbb{R}_+$ ,  $t \geq 0$ ,  $i = 1, 2$ , respectively the size of the prey and predator population.  
 105 The first part of (1a) models that the prey population grows logistically in absence of the  
 106 predator. The hyperbolic relationship  $a_1 x_1 / (1 + b_1 x_1)$  is called the Holling type II functional  
 107 response. This expression occurs in both equations and models the consumption of the  
 108 prey population by the predator population. Parameter  $a_1 > 0$  is the searching rate for  
 109 the prey and  $b_1 > 0$  the product of the handling time of the prey by the predator and  
 110 the searching rate. The ratio of the first term of (1b) and the last term on the right-hand  
 111 sides of (1a) is the efficiency  $c_1 > 0$ . The last term of (1b) is death rate  $d_1 > 0$  of the  
 112 predator population but it can also model other biological processes of which the loss rate  
 113 is proportional to the population size similar to maintenance.

114 For a description of the state variables and the biological meaning of the parameters of  
the predator-prey model the reader is referred to Table 1.

Table 1: List of parameters and state variables and their reference values. We take the efficiency  $c_1$  and death rate  $d_1$  both proportional to the positive perturbation parameter  $\varepsilon$ . For numerical studies we take that parameter  $a_1$  co-varies with  $b_1$  via  $a_1 = 5/3 b_1$ , hence handling time is  $3/5$  and the values for parameters  $c = d = 1$  for the RM-model and  $D = e_1 = 1$  for the MB-model. This is without loss of generality.

parameter	ref.values	Interpretation
$t$	$[0, \infty)$	Fast time variable
$\tau$	$[0, \infty)$	Slow time variable
$x_0$	$[0, \infty)$	Nutrient density
$x_1$	$[0, \infty)$	Prey biomass density
$x_2$	$[0, \infty)$	Predator biomass density
$x_r$	$(0, \infty)$	Nutrient concentration in reservoir
$a_1$	$a_1 = 5/3 b_1$	Searching rate
$b_1$	3,4 or 8	Handling time $\times$ searching rate
$c_1 = \varepsilon c$	$c = 1$	Conversion efficiency
$d_1 = \varepsilon d$	$d = 1$	Death rate
$e_1$	1	Conversion efficiency
$D_1 = \varepsilon D$	$D = 1$	Dilution rate
$\varepsilon$	$[0, 1]$	Perturbation parameter

115  
116 The set of equations analysed extensively in the literature that form a model with  
117 slow-fast dynamics reads

$$\frac{dx_1}{dt} = f(x_1, x_2, \varepsilon) = x_1 \left( 1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (2a)$$

$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right), \quad (2b)$$

118 with  $x_i \in \mathbb{R}$ ,  $i = 1, 2$ . We introduced  $c_1 = \varepsilon c$  and  $d_1 = \varepsilon d$  and toke for both parameters  
119 their reference value 1. The efficiency is again the ratio of the first term of (2b) and the  
120 last term on the right-hand sides of (2a) and is now equal to  $\varepsilon$ .

121 The functions  $f : \mathbb{R}^3 \rightarrow \mathbb{R}$  and  $g : \mathbb{R}^3 \rightarrow \mathbb{R}$  are of class smooth enough. The time-scale  
122 separation parameter  $\varepsilon$  is introduced in the model to implement trophic time diversification.  
123 For  $\varepsilon \ll 1$  this is called a fast-slow system.

124 In the mathematical literature, factor  $\varepsilon$  is treated as a perturbation parameter, justified  
125 and described by the ratio between the linear death rate of the predator and the linear  
126 growth rate of the prey in [42, 16]. That is, only when the prey reproduce much faster than  
127 the predators and the predator is, in comparison, not so efficient, when the ratio  $\varepsilon$  becomes

128 a small parameter. For, the efficiency  $c_1 = \varepsilon c$ , where  $c$  is of order 1 (with a reference value  
 129 1) is proportional to the perturbation parameter  $\varepsilon$ .

130 The Holling type II hyperbolic relationship is derived by a time scale argument using  
 131 a time budget modelling spend on searching for and handling of prey individuals by a  
 132 predator individual. The ratio of these two terms is called the assimilation efficiency in  
 133 ecology literature and the yield in the microbiology literature. When the units of both  
 134 state variables equal then consequently  $\varepsilon < 1$  means that there is a smaller than 100%  
 135 biomass conversion, as is always the case in nature. We assume that the formed products  
 136 during this conversion process, have no effects on other processes underlying model (2). In  
 137 general, however, a very small conversion efficiency is not supported in the literature.

138 Observe that also the predator loss rate is multiplied by the same factor  $\varepsilon$  in order to  
 139 facilitate coexistence. In other words when predators efficiency is low they also have to  
 140 have a low loss rate in order to survive. Therefore the parameter  $\varepsilon$  affects two processes,  
 141 mass conversion from prey biomass into predator biomass and the predator loss rate.

## 142 2.1 Existence and stability analysis of equilibria and limit cycles

143 In model (2) there are only three free parameters, namely  $a_1$ ,  $b_1$  and  $\varepsilon$  which scales the  
 144 efficiency and predator loss rate. The following stability analysis is classical for  $\varepsilon > 0$  and  
 145 therefore we recall some results regarding the dynamics of (2) and report some interesting  
 146 results when  $\varepsilon \rightarrow 0$  and  $\varepsilon = 0$

147 The one-parameter bifurcation diagram with varying  $b_1$  where  $\varepsilon = 1$  and  $a_1$  co-varies  
 148 with  $b_1$  via  $a_1 = 5/3 b_1$ , is shown in Fig. 1 for parameter  $b_1$  as free parameter. The three  
 149 relevant equilibria zero-  $E_0$ , boundary-  $E_1$  and interior equilibrium  $E_2$  and the limit cycle  
 150  $L_2$  are summarized in Table 2 and the bifurcation curves the transcritical bifurcation  $TC$   
 151 and Hopf bifurcation  $H$  in Table 3. In [19] it was proved that the coexistence equilibrium  
 152  $E_2$  is globally stable and in [4] that the periodic solution is unique thus a globally unique  
 153 stable limit cycle  $L_2$ . The numerical bifurcation results show that the limit cycle for  
 154 parameter values above the supercritical Hopf bifurcation is stable and that the minimum  
 155 values become very small for large  $b_1$ . This phenomenon is related to the ‘‘paradox of  
 156 enrichment’’ [43], because extinction due to stochastic fluctuations is likely.

157 For the stability analysis of equilibria we need the Jacobian matrix evaluated at point  
 158  $(x_1, x_2)$  ([27]), which reads

$$\mathbf{J} = \begin{pmatrix} 1 - x_1 - \frac{a_1 x_2}{1+b_1 x_1} + x_1 \left( \frac{a_1 x_2 b_1}{(1+b_1 x_1)^2} - 1 \right) & -\frac{a_1 x_1}{1+b_1 x_1} \\ \varepsilon x_2 \left( \frac{a_1}{1+b_1 x_1} - \frac{a_1 x_1 b_1}{(1+b_1 x_1)^2} \right) & \varepsilon \left( \frac{a_1 x_1}{1+b_1 x_1} - 1 \right) \end{pmatrix}. \quad (3)$$

159 In  $E_0$  the Jacobian matrix is

$$\mathbf{J}_0 = \begin{pmatrix} 1 & 0 \\ 0 & -\varepsilon \end{pmatrix}. \quad (4)$$

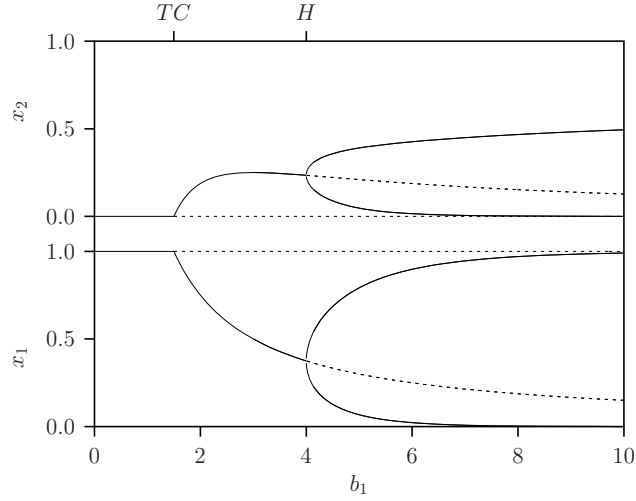


Figure 1: One-parameter bifurcation diagram for  $b_1$  and  $a_1 = 5/3 b_1$  of the RM-system (1) with  $\varepsilon = 1$ . The equilibria  $E_1$  (below  $TC$ ) and  $E_2$  (between  $TC$  and  $H$ ) as well as the maximum and minimum values for the limit cycle  $L_2$  (above  $H$ ) are shown. Note that the critical values where the bifurcations  $TC$  and  $H$  occur in this diagram are independent of  $\varepsilon$  since the expression for the real parts of the eigenvalues of the Jacobian matrix do not depend on  $\varepsilon$ .

Table 2: Equilibria of RM-model (2) and MB-model (54).

Equilibria	System composition
RM-model	
$E_0 = (0, 0)$	Extinction
$E_1 = (1, 0)$	Prey-only
$E_2 = (x_1^*, x_2^*) = \left(\frac{1}{a_1 - b_1}, \frac{a_1 - b_1 - 1}{(a_1 - b_1)^2}\right)$	Prey-predator
MB-model	
$E_0 = (0, 0)$	Extinction
$E_1 = (1, 0)$	Prey-only
$E_2 = (x_1^*, x_2^*) = \left(\frac{1}{a_1 - b_1}, \frac{a_1 - b_1 - 1}{\varepsilon(a_1 - b_1)^2 + a_1 - b_1}\right)$	Prey-predator



Table 3: Bifurcation curves for RM-model (2) and MB-model (54). Note that for RM-model the expression are independent of  $\varepsilon$ . The arrow indicates the transition of the steady states that occurs when the parameter crosses the bifurcation point.

Bifs.	$a_1(b_1, \varepsilon)$	$b_1$ ( $a_1 = 5/3 b_1$ )	Interpretation
RM-model			
$TC$	$a_1 = b_1 + 1$	1.5	$E_1 \rightarrow E_2$
$H$	$a_1 = \frac{b_1(b_1+1)}{b_1-1}$	4	$E_2 \rightarrow L_2$
MB-model			
$TC$	$a_1 = b_1 + 1$	1.5	$E_1 \rightarrow E_2$
$H$	$a_1 = \frac{2\varepsilon b_1^2 + 1 + \sqrt{4b_1^2\varepsilon(\varepsilon+1)+1}}{2\varepsilon(b_1-1)}$	$b_1 = \frac{4\varepsilon + \sqrt{16\varepsilon^2 + 15\varepsilon}}{(2\varepsilon)}$	$E_2 \rightarrow L_2$

160 The eigenvalues are the diagonal elements and the  $E_0$  is always unstable. At the boundary  
 161 equilibrium  $E_1$  the Jacobian matrix reads

$$\mathbf{J}_1 = \begin{pmatrix} -1 & -\frac{a_1 - b_1 - 1}{1 + b_1} \\ 0 & \varepsilon \left( \frac{a_1 - b_1 - 1}{a_1} \right) \end{pmatrix}. \quad (5)$$

162 The eigenvalues are again the diagonal elements and  $E_1$  is stable when  $a_1 - b_1 - 1 < 0$  and  
 163 unstable when  $a_1 - b_1 - 1 > 0$ . The equality gives the transcritical bifurcation  $TC$  where  
 164  $b_1 = a_1 - 1$  or for the reference value  $a_1 = 5/3 b_1$  we have  $b_1 = 3/2$ .

165 At the equilibrium  $E_2$  the Jacobian matrix reduces to

$$\mathbf{J}_2 = \begin{pmatrix} \frac{a_1(b_1-1) - b_1(1+b_1)}{a_1((a_1-b_1))} & -1 \\ \varepsilon \left( \frac{a_1 - b_1 - 1}{a_1} \right) & 0 \end{pmatrix}. \quad (6)$$

The complex pair of eigenvalues  $\lambda_{1,2}$  of the Jacobian matrix evaluated at the equilibrium  
 $E_2$  read

$$\lambda_{1,2}(b_1, \varepsilon) = \mu(b_1) \pm i\omega(b_1, \varepsilon). \quad (7)$$

166 We calculated the following real  $\mu \in \mathbb{R}$  and imaginary  $\omega \in \mathbb{R}$  parts as functions of parameter  
 167  $\varepsilon$  and  $b_1$  where  $a_1 = 5/3 b_1$

$$\Delta(b_1, \varepsilon) = (\text{Tr } \mathbf{J}_2)^2 - 4 \det \mathbf{J}_2 = \frac{-144 + 72b_1 - 9b_1^2 - 60b_1\varepsilon + 40\varepsilon b_1^2}{25b_1^2}, \quad (8)$$

$$\mu(b_1, \varepsilon) = \frac{3(b_1 - 4)}{10b_1} \pm \frac{1 - \text{sgn } \Delta(b_1, \varepsilon)}{2} \sqrt{|\Delta(b_1, \varepsilon)|}, \quad (9)$$

$$\omega(b_1, \varepsilon) = \pm \frac{1 + \text{sgn } \Delta(b_1, \varepsilon)}{2} \sqrt{|\Delta(b_1, \varepsilon)|}. \quad (10)$$

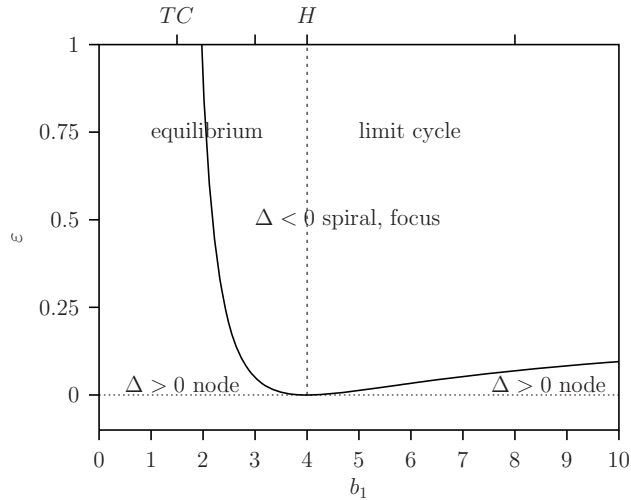


Figure 2: Focus bifurcation where  $\Delta = 0$  curve for  $\varepsilon$  vs  $b_1$ .

168 In Fig. 2 the curve where  $\Delta(b_1, \varepsilon) = 0$  is plotted in the  $(b_1, \varepsilon)$  parameter space. This  
 169 curve separates regions where the equilibrium is a node  $\Delta > 0$  (two real eigenvalues) or  
 170 a spiral or focus  $\Delta < 0$  (two conjugated complex eigenvalues). At  $\Delta = 0$  there are two  
 171 equal real eigenvalues. From this figure we conclude that for  $\varepsilon = 1$  and  $b_1 = 3$  or  $b_1 = 8$   
 172 the equilibria are foci while for  $\varepsilon = 0.01$  the equilibria are nodes, stable and unstable,  
 173 respectively.

174 The positions of the bifurcations  $TC$  and  $H$  are independent of the parameter  $\varepsilon$ . This  
 175 is not true for the so called first Lyapunov coefficient  $\ell^1$  which determines whether the  
 176 Hopf bifurcation is supercritical or subcritical, that is whether the emerging limit cycles  
 177 are stable or unstable, respectively.

178 At the Hopf bifurcation with  $b_1 = 4$  we have for  $\varepsilon > 0$  a zero real part  $\mu(4) = 0$   
 179 and the positive imaginary part equal to the determinant of the Jacobian matrix  $\mathbf{J}_2$ :  
 180  $\omega(4) = \sqrt{\det \mathbf{J}_2} = 1/2 \sqrt{\varepsilon}$ , for the two conjugated complex eigenvalues. The square root of  
 181 the ratio  $\mu(b_1)/\omega(b_1)$  measures the amplitude of the limit cycle that emerge for the Hopf  
 182 bifurcation for  $b_1 > 4$ . Evaluation of this ratio just above  $b_1 = 4$  gives that the oscillatory  
 183 dynamics for values is as with the Hopf bifurcation till the canard explosion occurs.

184 The derivative  $d\mu/db_1(b_1)|_{b_1=4} = 3/40 > 0$  at the Hopf bifurcation equilibrium is posi-  
 185 tive and therefore the transversality condition for applying the normal form theorem [31,  
 186 Theorem (3.3)] is satisfied. Using a similar procedure in Maple, [32] described in [31], the  
 187 first Lyapunov coefficient  $\ell^1$  is evaluated as

$$\ell^1 = -\frac{16}{75} \frac{14\varepsilon + 1}{\varepsilon^{3/2}}. \quad (11)$$

188 Since  $\ell^1$  is negative for  $\varepsilon > 0$ , the Hopf bifurcation is supercritical. Note that for  $\lim \varepsilon \rightarrow$   
 189  $0$  we have  $\ell^1 \rightarrow -\infty$ . That is, the first Lyapunov coefficient  $\ell^1$  becomes unbounded.

190 Furthermore, in the limiting case  $\varepsilon = 0$  at the Hopf bifurcation where  $b_1 = 4$  with  $\mu(4) = 0$   
 191 we get together with  $\omega(4) = 1/2 \sqrt{\varepsilon} = 0$  that this point becomes a degenerated bifurcation  
 192 where both eigenvalues are zero as in a Bogdanov-Takens bifurcation point. Exploration  
 193 of these facts can be done with a blow-up technique [8, 9] which is beyond the scope of  
 194 this paper.

## 195 2.2 Phase-space analysis

196 In this section we discuss results in the phase-space of simulation in time. These results  
 197 where in all simulations the same initial conditions are used, are shown in Fig. 3 and Fig. 4:

- 198 • Left panels of Fig. 3: for  $b_1 = 3$ , in the region between the transcritical  $TC$  and Hopf  
 199  $H$  bifurcation in Fig. 1 where equilibrium  $E_2$  is stable,
- 200 • Fig. 4: for  $b_1 = 4$  at the Hopf bifurcation,
- 201 • Right panels of Fig. 3: for  $b_1 = 8$  above the Hopf bifurcation in Fig. 1 where equilib-  
 202 rium  $E_2$  is unstable.

203 In the top panels of Fig. 3 and Fig. 4 the f-nullcline where  $f(x_1, x_2, \varepsilon) = 0$ :  $x_2 =$   
 204  $(1 - x_1)(1 + b_1 x_1)/a_1$  and the g-nullcline where  $g(x_1, x_2, \varepsilon) = 0$ :  $x_1 = 1/(a_1 - b_1)$ , are  
 205 shown. Both are independent of  $\varepsilon$ . The graph of the f-nullcline is part of a parabola where  
 206 it intersects the horizontal axis  $x_2 = 0$  at  $x_1 = 1$  and of the g-nullcline is just a vertical  
 207 line through the equilibrium point  $E_2$ .

### 208 2.2.1 Stable interior equilibrium

209 With  $b_1 = 3$ , see Fig. 3a with  $\varepsilon = 1$  and Fig. 3c with  $\varepsilon = 0.01$ , the equilibrium  $E_2$  is stable  
 210 and there is convergence to the stable point.

211 For low  $\varepsilon = 0.01$  value shown in Fig. 3c, initially after starting above the nullcline the  
 212 solution goes rapidly to the vertical axis. There is almost no prey population and hence  
 213 the predator population diminishes approximately exponential with rate  $d_1 = 1$ :

$$\frac{dx_2}{d\tau} = -x_2, \quad (12)$$

214 where differentiation is with respect to the slow time variable  $\tau = \varepsilon t$ . The solution crosses  
 215 the critical point  $x_2 = 1/a_1$  the intersection with the nullcline and leaves the vertical  
 216 axis moving fast toward the stable part of the nullcline. Because this happens below  
 217 the critical point (intersection of parabola and vertical axis) this phenomenon is called  
 218 a *delayed bifurcation* which is explained in [42]. Eventually the system converges to the  
 219 stable equilibrium  $E_2$  given in Table 2.

### 220 2.2.2 Hopf interior equilibrium

221 The equilibrium  $E_2$ , see Table 2, at the Hopf bifurcation  $H$  coincides with the top of the  
 222 f-nullcline parabola

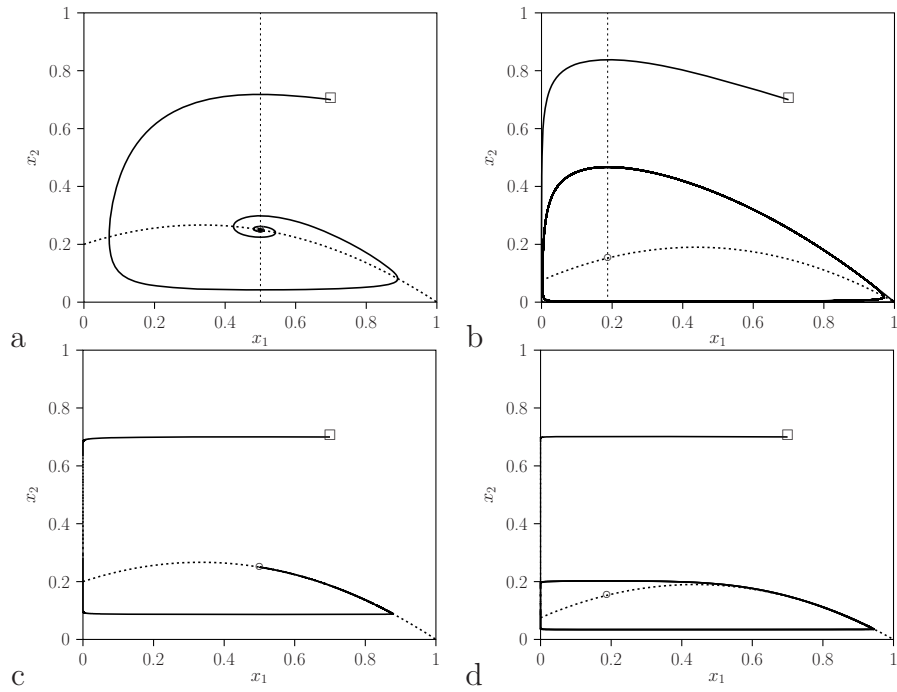


Figure 3: Phase-space analysis for system (2) describing the RM-model with  $b_1 = 3$  (left panels) and  $b_1 = 8$  (right panels) while  $a_1 = 5/3 b_1$ . Top panels (a,b):  $\varepsilon = 1$  and bottom panels (c,d):  $\varepsilon = 0.01$ . (a): Spiral stable equilibrium  $E_2$ , (b): stable limit cycle  $L_2$ , (c): node stable equilibrium  $E_2$  and (d): stable limit cycle  $L_2$ .

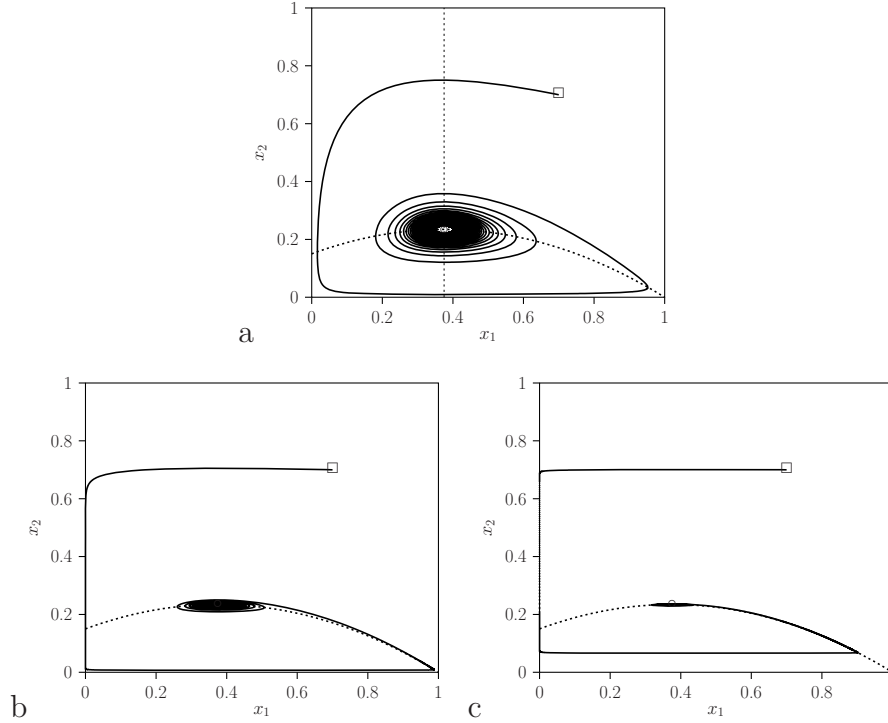


Figure 4: Phase-space analysis for system (2) describing the RM-model,  $b_1 = 4$  and  $a_1 = 5/3 b_1$ , that is at the Hopf bifurcation point for three different values of  $\varepsilon$ :  $\varepsilon = 1$  (a),  $\varepsilon = 0.1$  (b) and  $\varepsilon = 0.01$  (c).

$$(\bar{x}_1, \bar{x}_2)_T = \left( \frac{b_1 - 1}{2b_1}, \frac{(b_1 + 1)^2}{4a_1 b_1} \right). \quad (13)$$

223 At the Hopf point we have the equilibrium  $E_2$

$$(x_1^*, x_2^*)_H = (\bar{x}_1, \bar{x}_2)_T = \left( \frac{3}{8}, \frac{15}{64} \right). \quad (14)$$

224 The simulation results for system (2) are shown in Fig. 4. These results show that the solu-  
 225 tion finally converges very slowly to this, sometimes called a weakly attracting, equilibrium  
 226 (14) at the top of the f-nullcline denoted by (13).

### 227 2.2.3 Unstable interior equilibrium

228 With  $b_1 = 8$ , see Fig. 3b,d equilibrium  $E_2$  is unstable and there is no convergence to  $E_2$   
 229 but to a stable limit cycle  $L_2$ .

230 For positive  $\varepsilon = 0.01$  in Fig. 3d initially the dynamics is similar to that for the stable  
 231 case shown in Fig. 3c. The dynamics on the unique stable limit cycle  $L_2$  consists of four

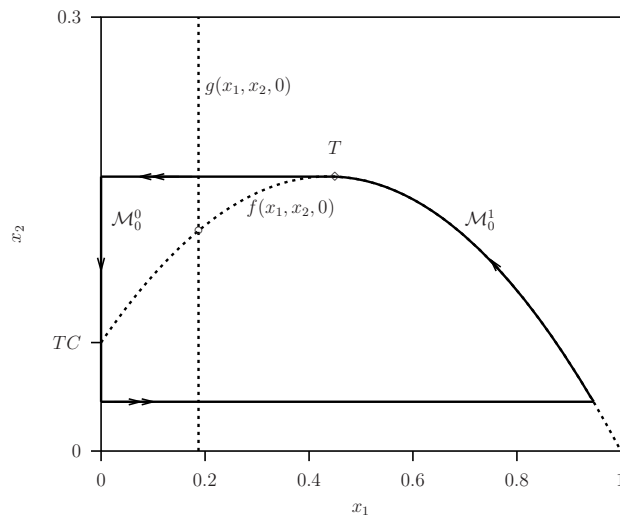


Figure 5: Fast (double arrow) and slow (single arrow) dynamics for system (2) describing the RM-model with  $b_1 = 8$  where for  $\lim \varepsilon \rightarrow 0$  the concatenated trajectories are the degenerated phase curves. The f-nullcline (parabola) and g-nullcline (vertical line through equilibrium) are shown. Point  $T$  is top of parabola given in (13) and  $TC$  is intersection point of f-nullcline and vertical axis.

232 concatenated episodes. Two parts of the trajectory where the predator population changes  
 233 slowly and two parts of the trajectory where the predator population is almost constant  
 234 and the prey population changes fast (the almost horizontal parts of the solution orbit).

#### 235 2.2.4 Degenerate phase curves

236 With  $b_1 > 4$  the limits of the limit cycles  $L_2$ , the periodic *relaxation oscillations*, for  
 237  $\lim \varepsilon \rightarrow 0$  are called *degenerated phase curves* shown in Fig. 5, see [14] It consists of  
 238 four concatenated episodes (families of periodic sets). On two parts of the trajectory the  
 239 dynamics is slow (single arrow): one along the vertical axis where the predator population  
 240 decreases slowly and the other are along parts of the parabolic f-nullcline where the prey  
 241 population decreases while the predator population increases slowly.  
 242 On the other two parts of the trajectory the prey changes fast (double arrows) and the  
 243 predator is constant: one from point  $T$  toward the vertical axis and one from this vertical  
 244 axis to the point on the parabolic f-nullcline. This type of dynamics is discussed intensively  
 245 in the ecological literature, we mention [42, 11] and references therein. These two episodes  
 246 are connected by two fast episodes along the horizontal lines where the prey population  
 247 size increases or decreases fast while the predator population is constant.

248 Starting slowly on the vertical axis above the f-nullcline, during the first episode, the  
 249 solution orbit crosses the critical point  $TC$  and leaves this axis fast horizontally toward  
 250 the parabola. Then it continues, during the second episode, slowly and during the third  
 251 episode again along the parabola passing the top of the parabola point  $T$  given in (13).

252 Note that since  $b_1 > 4$  the equilibrium  $E_2$  indicated by the open circle in Fig. 5 on the  
 253 f-nullcline, does not coincide with this non-hyperbolic point  $T$ . After crossing this point  
 254 the solution orbit, during the forth episode, moves vastly horizontally toward the vertical  
 255 axis again above the f-nullcline, and so on.

256 Note that the dynamics of the degenerate phase curves shown in Fig. 5 are indeed close  
 257 to this for the RM-model in Fig. 3d where  $b_1 = 8$  in both cases. However for the Hopf  
 258 bifurcation  $b_1 = 4$  case the resulting dynamics for small  $\varepsilon \ll 1$  does not look like that of  
 259 Fig. 5 and more importantly also not for  $b_1$  slightly above the Hopf bifurcation. Therefore  
 260 we focus in the next sections on the dynamics for parameter values where the unstable  
 261 equilibrium  $E_2$  is just above the Hopf bifurcation value.

### 262 3 Singular perturbation problem

263 In this section the singular perturbation technique is used to analyse the singular pertur-  
 264 bation problem where  $\varepsilon = 0$  in the RM-model (2). We will also analyse the quasi-steady  
 265 state solution or the relaxation oscillation in detail. The reader is referred to [18, 21, 22]  
 266 for introductions into perturbation analysis.

#### 267 3.1 Heuristic introduction

268 We start with a short overview of singular perturbation techniques. Singular perturbation  
 269 theory deals with systems of the *original* form (2) where  $\varepsilon > 0$ . When  $\varepsilon \ll 1$  the system  
 270 is a fast-slow system.

271 With  $\varepsilon = 0$  we have the *fast system* also called called the *layer system*:

$$\frac{dx_1}{dt} = f(x_1, x_2(0), 0) = x_1 \left( 1 - x_1 - \frac{a_1 x_2(0)}{1 + b_1 x_1} \right), \quad (15a)$$

$$\frac{dx_2}{dt} = 0. \quad (15b)$$

272 The predator populations remains constant hence the trajectories are the horizontal lines  
 273 in Fig. 5.

274 With a change of time-scale, where  $\tau = \varepsilon t$ , we call the resulting system the *slow system*:

$$\varepsilon \frac{dx_1}{d\tau} = f(x_1, x_2, \varepsilon), \quad (16a)$$

$$\varepsilon \frac{dx_2}{d\tau} = \varepsilon g(x_1, x_2, \varepsilon). \quad (16b)$$

275 After substitution of  $\varepsilon = 0$  we get

$$0 = f(x_1, x_2, 0), \quad (17a)$$

$$\frac{dx_2}{d\tau} = g(x_1, x_2, 0) = x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right). \quad (17b)$$

276 This differential algebraic equation (DAE) is called the *reduced system*. The trajectory is  
 277 either part of the vertical axis where  $x_2 = 0$  or part on the parabola, the other f-nullcline  
 278 of the original system (2) in Fig. 5. However, in the fast-slow context these are the sets of  
 279 equilibria of the fast layer-system (15) and then they are called *critical manifolds* where  
 280  $x_1$  is acting as a parameter.

281 These heuristic results suggest the following approach for dealing with the two different  
 282 time scales. The first step consists in setting  $\varepsilon = 0$  which gives the set of fast equilibria  
 283 of the fast system (15) yielding the algebraic equation (17a). This is the critical manifold  
 284 which is the set of equilibria either at the vertical axis or the parabola where  $f(x_1, x_2, 0) =$   
 285 0.

286 From the results presented below in this section the parabolic critical manifold has two  
 287 branches, one stable on the right-hand side (solid curve) and one unstable on the left-hand  
 288 side (dashed curve) of point  $T$  in Fig. 5.

289 With good hypothesis (see below for the details), on the part of the parabola,  $f(x_1, x_2, 0) =$   
 290 0 is equivalent to  $x_1 = p(x_2)$  and we can substitute  $x_1$  by  $p(x_2)$  in equation (17b). The  
 291 result is the slow or reduced system

$$0 = f(p(x_2), x_2, 0), \quad \frac{dx_2}{d\tau} = g(p(x_2), x_2). \quad (18)$$

292 The differentiation is with respect to  $\tau$  and the smooth functions  $f$  and  $g$  are defined in  
 293 (2). Then the slow system becomes

$$\frac{dx_2}{d\tau} = x_2 \left( \frac{(a_1 - b_1)p(x_2) - 1}{b_1 p(x_2) + 1} \right), \quad x_1 = p(x_2) = \frac{1}{2b_1} (b_1 - 1 \pm \sqrt{(b_1 + 1)^2 - 4a_1 b_1 x_2}). \quad (19)$$

294 An alternative method is to use instead of  $x_1 = p(x_2)$  of which the dynamics is described  
 295 by the solution of (19), the inverse function  $x_2 = q(x_1)$  also derived from (17a). This gives  
 296 the relationship

$$x_2 = q(x_1) = \frac{1}{a_1} (1 - x_1)(1 + b_1 x_1), \quad (20)$$

297 and using (17b) the differential equation

$$\frac{dx_2}{d\tau} = g(x_1, q(x_1)) = \frac{dq}{dx_1} \frac{dx_1}{d\tau},$$



298 and we get formally

$$\frac{dx_1}{d\tau} = \frac{q(x_1)(a_1x_1 - (1 + b_1x_1))}{(1 + b_1x_1) dq/dx_1}, \quad \frac{dq}{dx_1} = \frac{1}{a_1} (b_1(1 - 2x_1) - 1). \quad (21)$$

299 Note that this expression is zero at point  $T$  given in (13). Hence the denominator of model  
 300 (21) at that point  $T$  is zero. When the numerator is unequal zero, this means that the rate  
 301 of change becomes unbounded at  $T$  which is a singular point of model (21). Only when in  
 302 the special case  $b_1$  is the Hopf bifurcation parameter value, point  $T$  is a limit point where  
 303 the numerator is also zero. This is studied in the Appendix B.

### 304 3.2 Geometric singular perturbation techniques

305 We discuss the singular perturbation problem outlined in the previous section for the case  
 306 where  $\varepsilon$  is not zero but small and positive:  $0 < \varepsilon \ll 1$ . Here we follow the geometric  
 307 singular perturbation techniques.

308 Let us consider system (2) again. For  $\varepsilon = 0$  the f-nullclines, the set  $\{(x_1, x_2) | f(x_1, x_2, 0) =$   
 309  $0, x_1 \geq 0, x_2 \geq 0\}$  consist of two types of critical manifolds, see Fig. 5

$$\mathcal{M}_0^0 = \{(x_1, x_2) | x_1 = 0, x_2 \geq 0\} \quad (22a)$$

$$\mathcal{M}_1^0 = \{(x_1, x_2) | x_2 = \frac{1}{a_1}(1 - x_1)(1 + b_1x_1), x_1, x_2 \geq 0\}. \quad (22b)$$

310 They form a set of equilibria of the fast system system (15). In the previous section we  
 311 studied the dynamics for  $\varepsilon = 0$  and now we will consider  $0 < \varepsilon \ll 1$ .

312 To that end, let us remind the statement of Fenichel's theorem. We consider differential  
 313 system of the form:

$$\frac{dX}{dt} = F(X, Y, \varepsilon), \quad (23a)$$

$$\frac{dY}{dt} = \varepsilon G(X, Y, \varepsilon), \quad (23b)$$

$$\frac{d\varepsilon}{dt} = 0, \quad (23c)$$

314 where  $F$  and  $G$  are sufficiently smooth. We assume that the set  $F(X, Y, 0) = 0$  can locally  
 315 be written as  $X = H(Y)$ , which defines a critical manifold. If, for all  $Y$  in a given compact  
 316 set  $\mathcal{D}$ , all the eigenvalues of  $\frac{DF}{DX}(H(Y), Y, 0)$  have a non-vanishing real part, then the critical  
 317 manifold is said *normally hyperbolic*. In this case, there exists  $\varepsilon_0$  and a map  $p$  defined on  
 318  $\mathcal{D} \times [0, \varepsilon_0[$  such that:

319 i)  $H(Y) = p(Y, 0);$

320 ii) the graph of  $p$  is invariant under the flow associated to the original differential system  
 321 (23);

322 iii) the graph of  $p$  is tangent to the central space associated to the linearisation of the  
 323 system at  $(H(Y), Y, 0)$ .

324 As a consequence, both critical manifolds  $\mathcal{M}_0^0$  and  $\mathcal{M}_0^1$  are normally hyperbolic and  
 325 there exists  $\varepsilon_0$  such that for  $0 < \varepsilon < \varepsilon_0$ , there are locally invariant manifolds  $\mathcal{M}_\varepsilon^0$  and  
 326  $\mathcal{M}_\varepsilon^1$  except in the neighborhood of point  $T$   $(x_1, x_2) = (\bar{x}_1, \bar{x}_2)$  and in the neighborhood  
 327 of the intersection between  $\mathcal{M}_0^0$  and  $\mathcal{M}_0^1$  on the vertical axis. Indeed, at those points,  
 328 the derivative of the fast part vanishes, which contradicts the assumptions of the theorem  
 329 statement.

330 Using its invariance, the perturbed manifold  $\mathcal{M}_\varepsilon^1$  can be approximated by asymptotic  
 331 expansions in  $\varepsilon$ . It can be described as a graph

$$\{(x_1, x_2) | x_2 = q(x_1, \varepsilon), x_1 \geq 0, x_2 \geq 0\}. \quad (24)$$

332 This manifold is invariant when the following equality holds

$$\frac{dx_2}{dt} = \frac{dx_2}{dx_1} \frac{dx_1}{dt} = \frac{dq(x_1, \varepsilon)}{dx_1} \frac{dx_1}{dt}, \quad (25)$$

333 yields with equation (23) and  $x_2 = q(x_1, \varepsilon)$ :

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} \frac{dx_1}{dt} = \varepsilon q(x_1, \varepsilon) \left( \frac{x_1(a_1 - b_1) - 1}{1 + b_1 x_1} \right). \quad (26)$$

334 Then (23) gives with  $x_2 = q(x_1, \varepsilon)$  the invariance condition

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} x_1 \left( 1 - x_1 - \frac{a_1 q(x_1, \varepsilon)}{1 + b_1 x_1} \right) = \varepsilon q(x_1, \varepsilon) \left( \frac{x_1(a_1 - b_1) - 1}{1 + b_1 x_1} \right), \quad (27)$$

335 or using  $1 + b_1 x_1 > 0$

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} x_1 \left( (1 - x_1)(1 + b_1 x_1) - a_1 q(x_1, \varepsilon) \right) = \varepsilon q(x_1, \varepsilon) (x_1(a_1 - b_1) - 1). \quad (28)$$

### 336 3.2.1 Asymptotic expansion

337 The following asymptotic expansion in  $\varepsilon$  is introduced:

$$q(x_1, \varepsilon) = q_0(x_1) + \varepsilon q_1(x_1) + \varepsilon^2 q_2(x_1) + \dots, \quad (29)$$

338 hence

$$\frac{\partial q}{\partial x_1} = \frac{dq_0}{dx_1} + \varepsilon \frac{dq_1}{dx_1} + \varepsilon^2 \frac{dq_2}{dx_1} + \dots . \quad (30)$$

339 Substitution into (28) gives

$$\begin{aligned} & \left( \frac{dq_0}{dx_1} + \varepsilon \frac{dq_1}{dx_1} + \varepsilon^2 \frac{dq_2}{dx_1} + \dots \right) x_1 \left( (1-x_1)(1+b_1x_1) - a_1(q_0(x_1) + \varepsilon q_1(x_1) + \varepsilon^2 q_2(x_1) + \dots) \right) \\ & = \left( \varepsilon(q_0(x_1) + \varepsilon q_1(x_1) + \dots) \right) (x_1(a_1 - b_1) - 1) . \end{aligned} \quad (31)$$

340 Gathering orders of  $\varepsilon$  results for  $\mathcal{O}(1)$  and assuming  $x_1 > 0$  in:

$$q_0(x_1) = \frac{(1-x_1)(1+b_1x_1)}{a_1} , \quad \frac{dq_0}{dx_1} = \frac{b_1 - 1 - 2x_1b_1}{a_1} . \quad (32)$$

341 At  $b_1 = 4$  we have  $x_1 = (b_1 - 1)/(2b_1)$  and hence  $dq_0/dx_1 = 0$ .

342 For  $\mathcal{O}(\varepsilon)$  and using an updated form of (28)

$$\frac{\partial q(x_1, \varepsilon)}{\partial x_1} x_1 a_1 (q_0 - q(x_1, \varepsilon)) = \varepsilon q(x_1, \varepsilon) (x_1(a_1 - b_1) - 1) , \quad (33)$$

343 gives

$$q_1(x_1) = q_0(x_1) \frac{(x_1(a_1 - b_1) - 1)}{-a_1 x_1 \frac{dq_0}{dx_1}} . \quad (34)$$

344 At  $b_1 = 4$  the numerator and denominator are both zero. we have  $x_1 = (b_1 - 1)/(2b_1)$  and  
345  $dq_0/dx_1 = 0$  but also since it is a equilibrium  $x_1(a_1 - b_1) - 1 = 0$ .

346 For  $\mathcal{O}(\varepsilon^2)$  in (33) gives

$$q_2(x_1) = q_1(x_1) \frac{\frac{dq_1}{dx_1} x_1 a_1 + x_1(a_1 - b_1) - 1}{-a_1 x_1 \frac{dq_0}{dx_1}} . \quad (35)$$

347 At point  $T$  we have  $x_1 = \bar{x}_1 = (b_1 - 1)/(2b_1)$  where  $dq_0/dx_1 = 0$ . Consequently, at  
348 that point the denominator in the expression for  $q_i(\bar{x}_1), i > 0$  is zero. Therefore the  
349 coefficients  $q_i(\bar{x}_1), i > 0$  are unbounded when the numerator is not equal zero. Only when  
350 the parameter  $b_1 = 4$  is at the Hopf bifurcation the numerator is zero and the coefficients  
351  $q_i(\bar{x}_1)$  remain finite.

352 **3.2.2 Asymptotic expansion in phase space**

353 The expression for  $q_0$  describes the critical manifold  $\mathcal{M}_0^1$ . This expression is the inverse  
 354 (when it exists) of  $p(x_2)$  in (19). The voluminous expressions for the higher order  $q_i$ ,  $i > 1$   
 355 coefficients obtained by equating the  $\mathcal{O}(\varepsilon^i)$  terms on the left- and right-hand side of the  
 356 invariance condition (28), are not given here but are available using Maple, [32]. This  
 357 yields the approximation of the perturbed slow manifold  $\mathcal{M}_\varepsilon^1$

358 For  $\varepsilon = 0$  the limit (16b) prescribes the singular slow flow on  $\mathcal{M}_0^1$  with  $\tilde{x}_2 = q_0(\tilde{x}_1)$   
 359 given by (32)

$$\frac{d\tilde{x}_1}{dt} = \tilde{x}_1 \left( 1 - x_1 - \frac{a_1 q_0(\tilde{x}_1)}{1 + b_1 \tilde{x}_1} \right). \quad (36)$$

360 For sufficiently small non-zero  $\varepsilon \ll 1$  the flow on the perturbed slow manifold  $\mathcal{M}_\varepsilon^1$  can be  
 361 approximated by inserting  $\tilde{x}_2 = q(\tilde{x}_1, \varepsilon)$  with  $q(\tilde{x}_1, \varepsilon)$  given by (29). In order to simulate  
 362 the model we solve

$$\frac{d\tilde{x}_1}{dt} = \tilde{x}_1 \left( 1 - \tilde{x}_1 - \frac{a_1 q(\tilde{x}_1, \varepsilon)}{1 + b_1 \tilde{x}_1} \right), \quad (37)$$

363 with properly chosen the initial values.

364 The results are shown in Fig. 6 for  $b_1 = 3$ , where the equilibrium  $E_2$  is stable. They  
 365 show that in this case the solution of the original model on  $\mathcal{M}_\varepsilon^1$  is already well approximated  
 by the second order approximation when  $\varepsilon = 0.1$ .

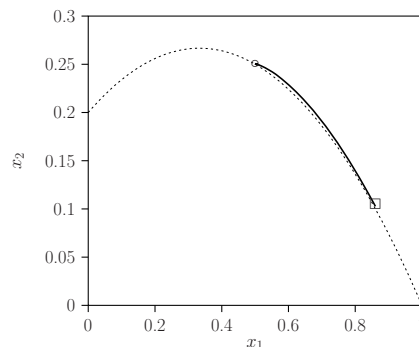


Figure 6: Results for the original system (2) (solid) describing the RM-model (29) with  $b_1 = 3$  where  $a_1 = 5/3 b_1$  and initial conditions  $x_1 = 0.86038$  and  $x_2(0) = 0.102646$ .

366

367 In Fig. 7a and Fig. 7b the graph of the function  $q(x_1, \varepsilon)$  is shown for  $b_1 = 3$  and  $b_1 = 8$ ,  
 368 respectively. These results show that the asymptotic expansion for  $\varepsilon > 0$  is only locally a  
 369 good approximation for  $\mathcal{M}_\varepsilon^1$  but fails at the top of the parabola point  $T$ .

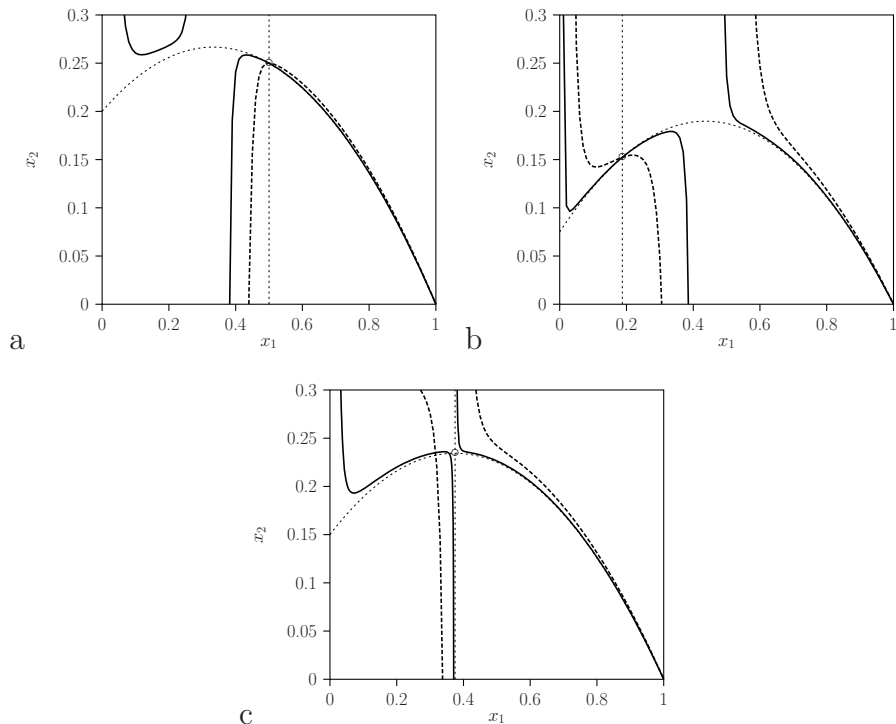


Figure 7: Second-order approximation of  $\mathcal{M}_\varepsilon^1$  results with (a):  $b_1 = 3$  (b):  $b_1 = 8$  and (c):  $b_1 = 4$  where  $a_1 = 5/3 b_1$  for the RM-model (29). Solid: with  $\varepsilon = 0.01$ . Dotted with  $\varepsilon = 0.1$ .

370 **At the Hopf bifurcation** In Fig. 7c the graph of the function  $q(x_1, \varepsilon)$  is shown for  
 371  $b_1 = 4$ . While the solution converges to the neutral stable equilibrium  $E_2$  where the  
 372 rate of convergence becomes slower when approaching the non-hyperbolic point (see also  
 373 Fig. 4b,c) the asymptotic expansion approximation explodes and there is discontinuity at  
 374  $x_1 = x_1^* = \bar{x}_1$ :

$$\lim_{x_1 \downarrow \bar{x}_1} q(x_1, \varepsilon) = \infty \quad \text{and} \quad \lim_{x_1 \uparrow \bar{x}_1} q(x_1, \varepsilon) = -\infty. \quad (38)$$

375 In the next section we extend the asymptotic expansion in  $\varepsilon$  by varying parameter  $b_1$   
 376 in addition to  $\varepsilon$  in order to repair this unwanted property.

### 377 3.3 Canard explosion

378 In this section we analyse the Canard dynamics that occurs for  $b_1$  values just above the  
 379 Hopf bifurcation at  $b_1 = 4$  similar to the analysis performed in [2]. Other papers on canards  
 380 are [10, 6, 8, 11, 2]. We will expand the asymptotic expansion discussed in the previous  
 381 section where the equilibrium point is unstable and the system itself shows oscillatory  
 382 behaviour, a stable limit cycle.

383 We start with an exploration of this oscillatory behaviour for  $b_1$  values just above the  
 384 Hopf bifurcation by simulation of the full model in time for small  $\varepsilon$  values. In order to  
 385 study the dynamics for small  $\varepsilon$  in more detail we re-analyse the continuation as in Fig. 1  
 386 where  $\varepsilon = 1$  in the region close to the Hopf bifurcation at  $b_1 = 4$ . The results are shown  
 387 for  $\varepsilon = 0.01$  in Fig. 8.

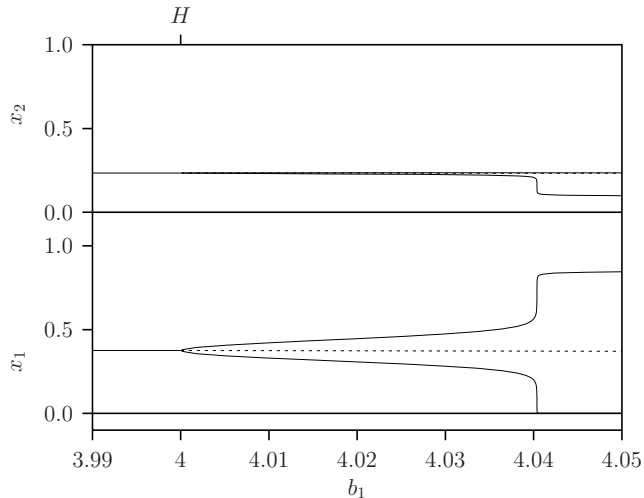


Figure 8: One-parameter bifurcation diagram for  $b_1$  and  $a_1 = 5/3 b_1$  of the RM-system (1) with  $\varepsilon = 0.01$ .

388 Unexpectedly the amplitude of the limit cycle increases sharply when  $b_1$  passes a value  
 389 just above  $b_1 = 4.04$ . In Fig. 9 parameter  $\varepsilon$  is varied continuously for a number values of  
 390  $b_1$  just above the Hopf bifurcation point. Using (8) these results support the analytical  
 391 expression for the amplitude of the unique stable limit cycles emerging from the Hopf  
 392 bifurcation for small  $\varepsilon$  values being:  $\sqrt{\mu(b_1)/\omega(b_1)}$ .

393 The continuation of the curves calculated with AUTO [7] failed for small  $\varepsilon$ . This is due  
 394 to the part of the cycle close to the vertical axis where  $x_1$  is small, see Fig. 3bd. In order  
 395 to avoid this dynamics we study now an augmented system

$$\frac{dx_1}{dt} = \delta + f(x_1, x_2, \varepsilon) = \delta + x_1 \left( 1 - x_1 - \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (39a)$$

$$\frac{dx_2}{dt} = \varepsilon g(x_1, x_2, \varepsilon) = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right), \quad (39b)$$

396 where  $\delta$  is a small allochthonous input rate of the prey population. Addition of this extra  
 397 term removes the transcritical bifurcation at  $x_2 = 1/a_1$  because it is structurally unstable  
 398 with respect to such a perturbation. Fig. 10 is a similar diagram as Fig. 9 where  $\delta = 0.0001$   
 399 instead of  $\delta = 0$ . Note that the Hopf bifurcation occurs at values slightly different from  
 400  $b_1 = 4$ , namely at  $b_1 = 4.000711364$  and this is taken into account in what follows. The

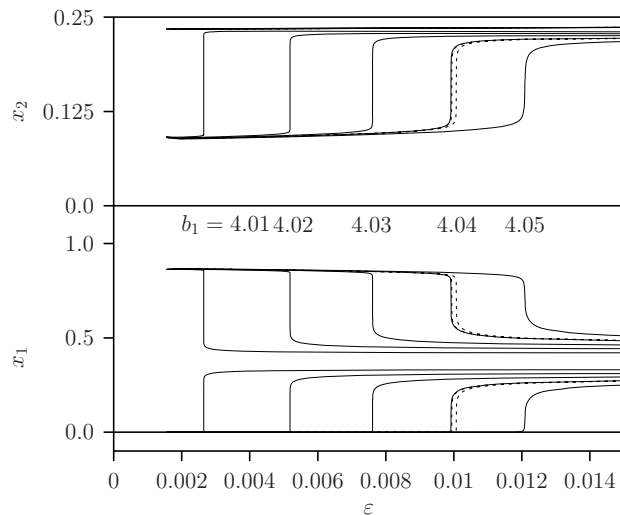


Figure 9: One-parameter bifurcation diagram for  $\varepsilon$  with various  $b_1 = 4.01, 4.02, 4.03, 4.04, 4.0401, 4.0407, 4.05$  values where  $a_1 = 5/3 b_1$  of the RM-system (1). For  $b_1 > 4$  the minimum and maximum populations values during the stable limit cycle are shown. Also the two dashed curves are shown for  $b_1 = 4.0409$  and  $4.04061$ . Between these two values the explosion occurs at  $\varepsilon = 0.01$  see also Fig. 8. The curves terminate for low  $\varepsilon$  values. This is due to numerical problems of the parameter continuation for these low values. Theory predicts that these curves of maximums and minimums are continuing almost horizontally.

401 results in Fig. 10 imply that continuation is possible toward very low  $\varepsilon$  values. The results  
 402 show that the canard is a robust and smooth phenomenon that occurs for stable limit  
 403 cycles. When  $\varepsilon \downarrow 0$  the canard explosion point converges to the point  $T$ .

404 In Fig. 11 the shape of the limit cycles is shown for two values of  $b_1$  just below and above  
 405 the sudden changes:  $b_1 = 4.04019$  and  $b_1 = 4.04061$  where  $\varepsilon = 0.01$ . These results show  
 406 how the unique stable limit cycle changes shape very abruptly at  $b_1 \approx 4.0403$  where  $b_1$   
 407 is varied keeping  $\varepsilon$  fixed: the canard explosion. In Fig. 12 the shape of the limit cycles is shown  
 408 for four values:  $\varepsilon = 0.008, 0.009$ , big stable limit cycles and  $\varepsilon = 0.01, 0.011$ , small stable  
 409 limit cycles with fixed  $b_1 = 4.0403$ , the value calculated with the extended asymptotic  
 410 expansion technique. These results show the dynamics with  $\varepsilon$  values above the canard  
 411 explosion at approximately  $\varepsilon = 0.01$ , are limit cycles with small amplitudes consisting of  
 412 two concatenated slow (close to the critical manifold and just above the parabola) and fast  
 413 (almost horizontal part of the trajectory below the parabola). Below the canard explosion  
 414 the limit cycles with large amplitudes consist of four episodes, two slow (close to the  
 415 critical manifold, one just above the parabola and one close to the vertical axis) and two  
 416 fast (almost horizontal, one leaving close from point  $T$  and one leaving the vertical axis  
 417 and landing close to the parabola).

418 Carefully examination indicates that there is one point where the trajectories for the  
 419 four  $\varepsilon$  values intersect. Starting at that point and changing  $\varepsilon$  gives the unique stable limit

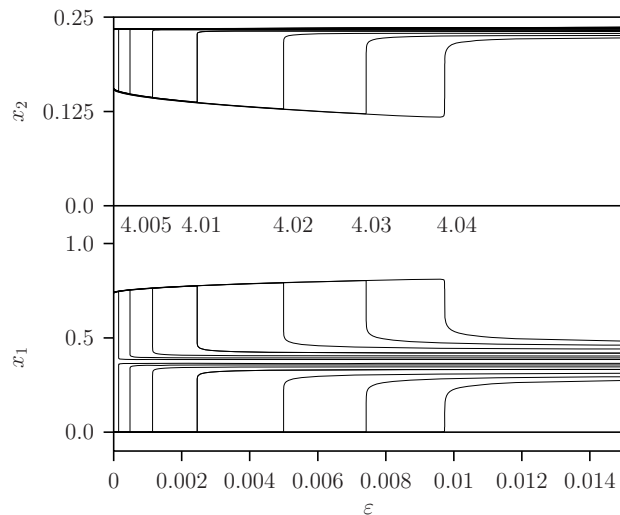


Figure 10: One-parameter bifurcation diagram for  $\varepsilon$  with various  $b_1 = 4.00125, 4.0025, 4.005, 4.01, 4.02, 4.03, 4.04$  values where  $a_1 = 5/3 b_1$  of system (39) with prey input rate  $\delta = 0.0001$ . The parameter continuation is here successful to very small values of  $\varepsilon$ .

420 cycles calculated and this shows that these curves change smoothly, only the sensitivity of  
 421 the shape of the cycles is very large at the explosion point.

### 422 3.3.1 Asymptotic expansion and canard explosion

423 Following [13] we repeat the extended asymptotic expansion in  $\varepsilon$  technique introduced in  
 424 (29) now near the Hopf bifurcation point. To that end the expansion is not only taken  
 425 for the function  $x_2 = q(x_1, \varepsilon)$  evaluated at  $q_0(x_1)$  (see (32)) but also in the bifurcation  
 426 parameter  $b_1 = b_1(\varepsilon)$  and consequently  $a_1(\varepsilon) = 5/3 b_1(\varepsilon)$  evaluated at the Hopf bifurcation  
 427 point  $b_{10} = 4$  with  $a_{01} = 20/3$ . This comes with more freedom which leads to an extra  
 428 criterion: the singularity of the approximation at point  $T$  is removed. This function is now  
 429 denoted as  $r(x_1, \varepsilon)$  and the expansion is evaluated at  $r(x_1 = \bar{x}_1, \varepsilon = 0)$ . When  $b_1 = b_{10}$  we  
 430 have  $r(\bar{x}_1, \varepsilon) = q(\bar{x}_1, \varepsilon)$ .

431 Similar to the invariance condition of the perturbed slow manifold  $\mathcal{M}_\varepsilon^1$  we derive now  
 432 the adapted equation that replaces (28) where we substitute  $a_1(\varepsilon) = 5/3 b_1(\varepsilon)$ :

$$\frac{\partial r}{\partial x_1} x_1 \left( (1 - x_1)(1 + b_1(\varepsilon)x_1) - 5/3 b_1(\varepsilon)r(x_1, \varepsilon) \right) = \varepsilon r(x_1, \varepsilon) (2/3 x_1 b_1(\varepsilon) - 1). \quad (40)$$

433 The following extended asymptotic expansion in  $\varepsilon$  for  $r(x_1, \varepsilon)$  is introduced as follows:

$$x_2 = r(x_1, \varepsilon) = r_0(x_1) + \varepsilon r_1(x_1) + \varepsilon^2 r_2(x_1) + \dots, \quad (41)$$



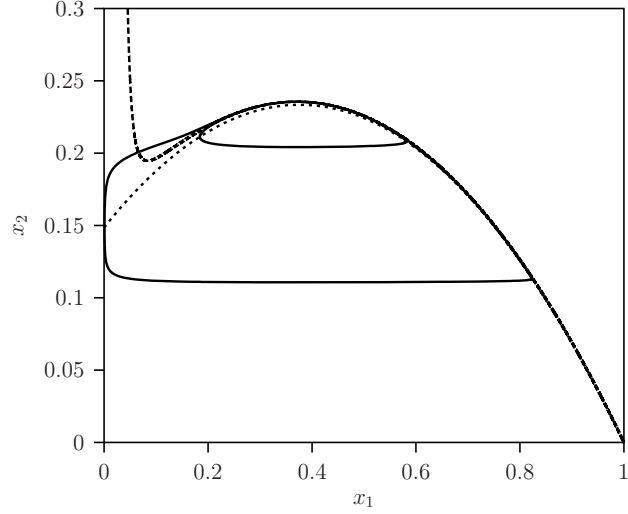


Figure 11: Phase-space diagram with  $\varepsilon = 0.01$ . Solid lines: stable limit cycle for two values of  $b_1 = 4.04019$  (small cycle) and  $b_1 = 4.04061$  (big cycle) while  $a_1 = 5/3 b_1$  of the RM-system (1). Dashed line: extended asymptotic expansion  $r(x_1, \varepsilon)$  of  $\mathcal{M}_\varepsilon^1$  (41) where  $b_1 = 4.0403$ .

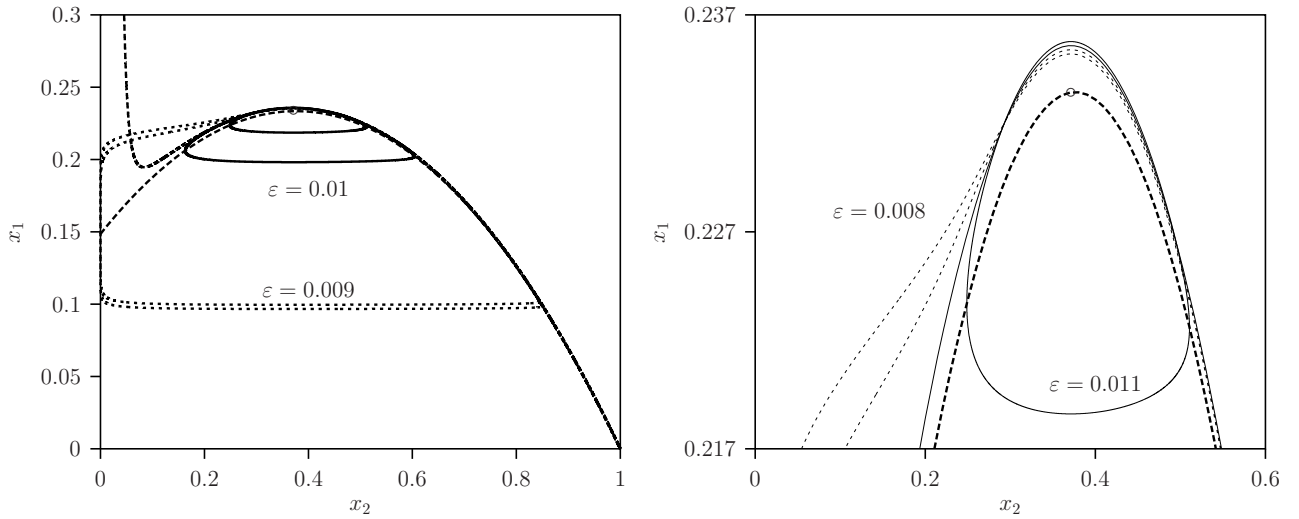


Figure 12: Phase-space diagram with  $\varepsilon = 0.008, 0.009, 0.01, 0.011$ . Solid lines: stable limit cycle for two values  $\varepsilon = 0.008, 0.009$  (big cycle) and two values  $\varepsilon = 0.01, 0.011$  (small cycle) of the RM-system (1). Dashed line: extended asymptotic expansion  $r(x_1, \varepsilon)$  of  $\mathcal{M}_\varepsilon^1$  (41) where  $b_1 = 4.0403$ .

434 and

$$\frac{\partial r}{\partial x_1} = \frac{dr_0}{dx_1} + \varepsilon \frac{dr_1}{dx_1} + \varepsilon^2 \frac{dr_2}{dx_1} + \dots, \quad (42)$$

435 whereby  $b_1(\varepsilon)$  is given by

$$b_1(\varepsilon) = b_{10} + \varepsilon b_{11} + \varepsilon^2 b_{12} + \varepsilon^3 b_{13} + \varepsilon^4 b_{14} \dots, \quad (43)$$

436 where  $r_j$  and  $b_{1j}$ ,  $j = 1 \dots$  are independent of  $\varepsilon$  and are described by the invariance  
437 condition (40) by equality order by order of powers of  $\varepsilon$  of this condition. Equating  $\mathcal{O}(1)$   
438 terms yields:

$$r_0 = \frac{(1 - x_1)(1 + b_{10}x_1)}{5/3 b_{10}}. \quad (44)$$

439 With  $b_{10} = 4$  this gives the zero order approximation of  $\mathcal{M}_\varepsilon^1$  equal to  $\mathcal{M}_0^1$ . Using (44)  
440 and substitution of (41), (42) and (43) in (40) and equating the resulting first order  $\mathcal{O}(\varepsilon)$   
441 terms, yields:

$$r_1(x_1) = \frac{3(1 - x_1)(1 - b_{10} + 2x_1 b_{10})b_{11}x_1 b_{10} - x_1 b_{10}^2 - 3b_{10} + 2x_1^2 b_{10}^3}{5b_{10}^2(1 + 2x_1 b_{10} - b_{10})x_1}. \quad (45)$$

442 It appears that the terms with  $b_{11}$ , namely  $3x_1 b_{11}(b_{10} - 1 - 2x_1 b_{10}) = 0$ , are already  
443 eliminated when they are evaluated at the Hopf bifurcation support point with  $b_{10} = 4$  and  
444  $a_{10} = 20/3$  at the equilibrium  $E_2$  with  $x_1 = \bar{x}_1 = x_1^* = 1/(a_{10} - b_{10})$ . At that point both  
445 the numerator and the denominator are zero but  $\lim_{x_1 \downarrow \bar{x}_1} r_1(x_1) = \lim_{x_1 \uparrow \bar{x}_1} r_1(x_1)$  and this  
446 shows that function  $r_1(x_1)$  is continuous for all  $b_{11}$ .

447 From this point a recursive procedure can be followed. One by one,  $r_i$ ,  $i \geq 2$  is  
448 determined by taking the  $i^{\text{th}}$  order term in the invariance condition (40) equal to zero and  
449 thereafter the term  $b_{1(i-1)}^{\text{th}}$  by the condition that this term is continuous at  $x_1 = \bar{x}_1 =$   
450  $(b_{10} - 1)/(2b_{10})$ . This means that the free parameter is chosen such that the singularity is  
451 removed. The requirement that the sum of second order terms is zero gives

$$r_2 = (1 - x_1) \frac{(-288x_1^4 + 108x_1^3)b_{12} + (72x_1^4 - 27x_1^3)b_{11}^2 + (96x_1^3 + 84x_1^2)b_{11} + 256x_1^3 - 128x_1^2 - 112x_1 - 16}{960x_1^3(8x_1 - 3)}. \quad (46)$$

452 At the support point  $T$  being the Hopf bifurcation point with  $b_{10} = 4$  and  $x_1 = \bar{x}_1$  given by  
453 (14) we have  $(-288x_1^4 + 108x_1^3)b_{12} = 0$ . Furthermore the denominator is zero  $b_{10} = 4$ . The

454 expression for  $b_{11}$  is then obtained by setting also the numerator equal to zero in order to  
 455 remove the singularity at that support point.

456 This is related to the case analysed in the previous section for the asymptotic expansion  
 457  $x_2 = q(x_1, \varepsilon)$  at  $q(\bar{x}_1, \varepsilon)$  for coefficient  $q_1$  given in (34) where this expression was also  
 458 unbounded. Now, because we have more freedom we can take  $b_{11}$  so that the expression  
 459 stays bounded at this point. The expression  $b_{11} = 100/27$  is obtained by substitution of  
 460 the equilibrium value for  $x_1 = \bar{x}_1 = 3/8$  given by (14) into (45).

461 Further recursion gives higher order approximations, again first  $r_n$  with  $b_{n-1}$  then  $r_{n+1}$   
 462 with  $b_n$  and so on. We calculated the following fourth order approximation

$$\begin{aligned}
 b_1(\varepsilon) &= b_{10} + \varepsilon b_{11} + \varepsilon^2 b_{12} + \dots, \\
 b_1(\varepsilon) &= 4 + \varepsilon \frac{100}{27} + \varepsilon^2 \frac{58700}{2187} + \varepsilon^3 \frac{80536900}{177147} + \varepsilon^4 \frac{171270040300}{14348907}.
 \end{aligned}
 \tag{47}$$

463 In Fig. 11 besides the shape of the limit cycles for two values  $b_1 = 4.04019$  (small  
 464 limit cycle) and  $b_1 = 4.04061$  (big limit cycle) also the result of the extended asymptotic  
 465 expansion  $r(x_1, \varepsilon)$ , where  $\varepsilon = 0.01$ , (41) with  $b_1 = 4.0403$  is shown. The approximation  
 466 for  $\mathcal{M}_\varepsilon^1$  follows the limit cycle closely up-to a separation point where the small limit cycle  
 467 bends toward the nullcline which is crossed where the rate of  $x_1$  changes sign and the rate  
 468 becomes fast. This occurs for the smallest  $b_1 = 4.04019$ -value. For the big limit cycle at  
 469  $b_1 = 4.04061$ , from the separation point the trajectory along the cycle continuous to move  
 470 toward the vertical axis. The asymptotic expansion for  $\mathcal{M}_\varepsilon^1$  with  $b_1 \approx 4.0403$  continuous  
 471 after the separation point between the two limit cycles before the approximation becomes  
 472 unbounded.

473 These results show how the unique stable limit cycle changes its shape very abruptly  
 474 when  $b_1 \approx 4.0403$  is varied keeping  $\varepsilon$  fixed, here in our example 0.01: the canard explo-  
 475 sion. That the iteration process converges to this bifurcation parameter value where the  
 476 approximation of the asymptotic expansion  $r(x_1, \varepsilon)$  works for the limit cycle with the small  
 477 amplitude that intersect with the parabolic f-nullcline vertically at the minimum predator  
 478 size during the limit cycle. This makes in plausible that the iteration procedure yields  
 479 indeed the canard point.

480 However, the extended asymptotic expansion  $r(x_1, \varepsilon)$  (41) is divergent as shown in  
 481 Fig. 13 where the coefficients  $b_{1i}$  as function of  $i$  is depicted.

482 It was shown in [39, 38] and reference therein, that the summation up to the smallest  
 483 term gives an optimal (and very accurate) approximation in the case of the van der Pol  
 484 system. In Fig. 14, again with allochthonous prey input where  $\delta = 0.0001$ , the parameter  
 485 value where the explosion occurs is plotted. This  $b_1$  parameter value is taken from Fig. 10.  
 486 Fortunately, the result presented are in agreement.

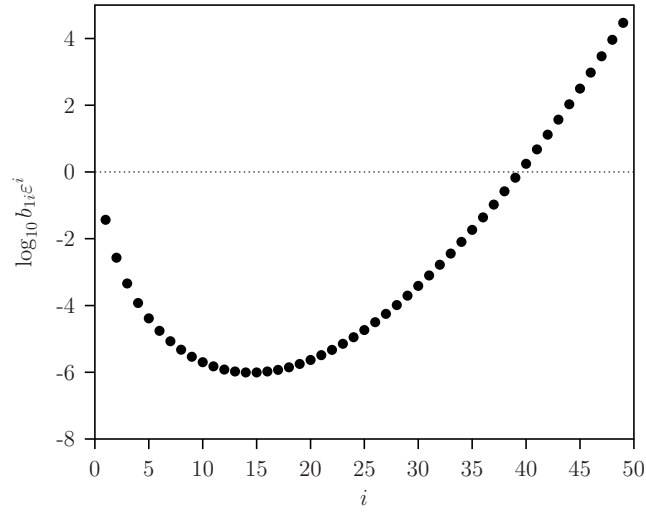


Figure 13: Coefficients  $b_{1i}$  as function of  $i$  given by (47) with  $\varepsilon = 0.01$ .

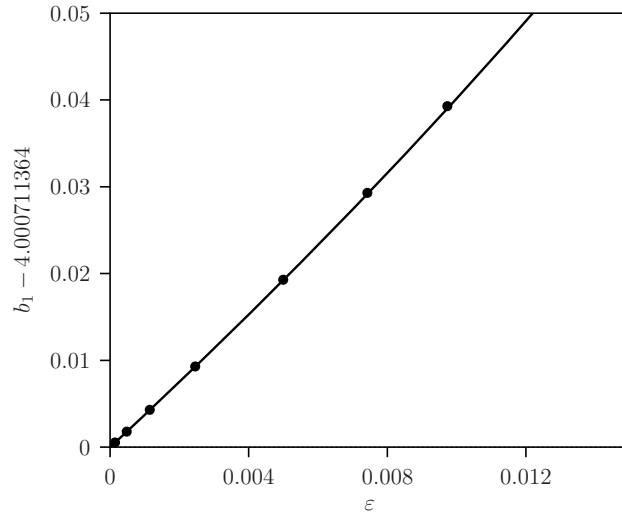


Figure 14: Distance from parameter value  $b_1$  where canard explosion occurs from  $b_1 = 4.000711364$  where the Hopf bifurcation occurs with allochthonous prey input  $\delta = 0.0001$  as function of  $\varepsilon$ . Solid line is graph of the truncated expression (43) and the dots taken from Fig. 10.

## 4 The MB bitrophic food chain model

This section presents the Monod chemostat model [34, 45, 24, 26]. In this model the nutrients consumed by the prey are modelled explicitly instead of using a logistic growth model for the growth of the prey in absence of the predator. Let  $x_0(t)$  denote the density of the nutrient, and  $x_i(t) \in \mathbb{R}_+$ ,  $t \geq 0$ ,  $i = 1, 2$  the biomass densities of prey and predator, respectively. The scaled version of the Monod model reads

$$\frac{dx_0}{dt} = (x_r - x_0)D_1 - a_0x_0x_1, \quad (48a)$$

$$\frac{dx_1}{dt} = a_0x_0x_1 - D_1x_1 - \frac{a_1x_1x_2}{1 + b_1x_1}, \quad (48b)$$

$$\frac{dx_2}{dt} = e_1 \frac{a_1x_1x_2}{1 + b_1x_1} - D_1x_2. \quad (48c)$$

where  $x_r$  is the concentration of nutrient in the reservoir and  $D_1$  the dilution rate, the rate at which the nutrient enters and all trophic levels are exported from the chemostat reactor. The second term of (48a) and the first term of (48b) model the Lotka-Volterra functional response at the prey-nutrient level. The first term of (48c) and the last term on the right-hand sides of (48b) represent the Holling type II functional response. The efficiency  $e_1$  is the ratio of these two terms. For simplicity we assume  $e_1 = 1$  and  $a_0 = 1$ .

It can be shown that all solutions system (48) starting in the non-negative cone eventually lie in the set

$$\Omega = \{x = (x_0, x_1, x_2) \in \mathbb{R}_+^3 : x_0 + x_1 + x_2 \leq x_r\}. \quad (49)$$

So, the asymptotic behavior of system (48) is bounded by  $x_r$ . It is possible to decouple this system by the introduction of the function

$$H(t) = x_0(t) + x_1(t) + x_2(t) - x_r, \quad t \geq 0. \quad (50)$$

This gives

$$\frac{dH}{dt} = -D_1H, \quad (51a)$$

$$\frac{dx_1}{dt} = (H + x_r - x_1 - x_2)x_1 - D_1x_1 + D_1\left(\frac{a_1x_1x_2}{1 + b_1x_1}\right), \quad (51b)$$

$$\frac{dx_2}{dt} = D_1x_2\left(\frac{a_1x_1}{1 + b_1x_1} - 1\right). \quad (51c)$$

When furthermore  $H = 0$  for the asymptotic dynamics we can study the two dimensional predator-prey system

$$\frac{dx_1}{dt} = x_1 \left( x_r - x_1 - x_2 - D_1 - D_1 \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (52)$$

$$\frac{dx_2}{dt} = D_1 x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right). \quad (53)$$

506 In order to be able to make a clear comparison with the RM-model formulations possible  
 507 we use  $x_r = 1 + D_1$ . This gives with  $D_1 = \varepsilon$

$$\frac{dx_1}{dt} = x_1 \left( 1 - x_1 - x_2 - \varepsilon \frac{a_1 x_2}{1 + b_1 x_1} \right), \quad (54a)$$

$$\frac{dx_2}{dt} = \varepsilon x_2 \left( \frac{a_1 x_1}{1 + b_1 x_1} - 1 \right). \quad (54b)$$

508 We call this the MB-model. One main difference with the RM-model is that the last term  
 509 of (54a) is proportional to  $\varepsilon$  and consequently the efficiency, is constant. Another difference  
 510 with the RM-model is that the logistic prey growth equation  $x_1(1 - x_1)$  is replaced by the  
 511 expression  $x_1(1 - x_1 - x_2)$  with one extra term namely that of the predator biomass,  $x_2$ .  
 512 In absence of the predator,  $x_2 = 0$ , both expressions for the prey growth are the same.  
 513 For the three trophic system including the nutrients, which is used with the derivation of  
 514 the MB-model, the biomass allocated in the predator gives a feed-back mechanism so that  
 515 there is less nutrient available for the prey. In the food chain the predator has two adverse  
 516 effects on the growth of prey population. Firstly the prey is consumed by the predator and  
 517 they consume building-block material not only for themselves but also for their predators  
 518 population that can only exists when the prey exists in the absence of inter-guild predation.

519 The biological interpretation of the  $-D_1 H = -\varepsilon H$  term in (51a) is the difference  
 520 between the influx rate and the out-flux rate of the total biomass expressed in the biomass  
 521 of the predator. In [45] (50) is used to show that Monod's model is dissipative and that the  
 522 system converges asymptotically to the manifold  $H = 0$  where the influx rate and out-flux  
 523 rate of the total biomass are the same. Observe that where  $H = 0$  there is with respect to  
 524 the RM-model a new  $x_2$  term in the expression for the prey growth rate.

## 525 4.1 Existence and stability analysis of equilibria and limit cycles

526 For the analysis of model in the chemostat environment we refer to [45]. The three relevant  
 527 equilibria are summarized in Table 2. In Table 3 the bifurcation analysis results are given.  
 528 Important difference of these results with those for the RM-model is that while the expres-  
 529 sions for the  $TC$  bifurcation are the same those for the Hopf  $H$  bifurcation still depends  
 530 on  $\varepsilon$ .

531 Firstly we calculate by continuation of the parameter  $b_1$  the bifurcation diagram shown  
 532 in Fig. 15. This diagram looks very much the same as Fig. 1 for the RM model. The main  
 533 difference is that the Hopf bifurcation occurs at a somewhat higher  $b_1$  value.

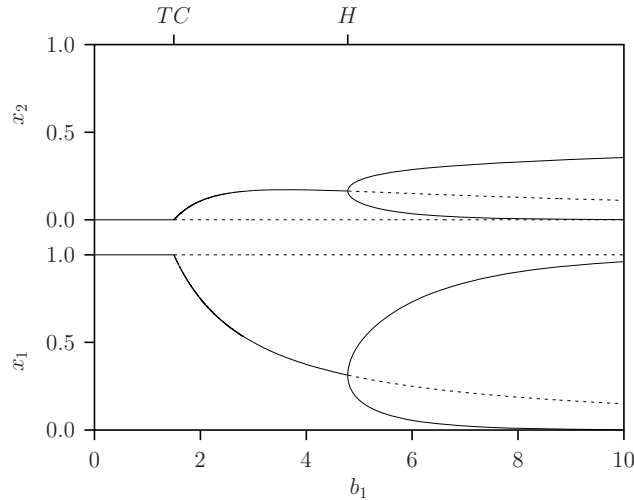


Figure 15: One-parameter bifurcation diagram for  $b_1$  and  $a_1 = 5/3 b_1$  of the MB-system (54) with  $\varepsilon = 1$ .

## 534 4.2 Phase-space analysis

535 Figure 16 displays the simulation results for the MB-model for three values of  $\varepsilon$  where  
 536  $b_1 = 3$ . There is convergence to a stable equilibrium, similar as we found for the RM-  
 537 model in Fig. 3a,c.

538 For  $b_1 = 8$  the results are shown in Fig. 17. These results differ much from the RM-  
 539 model in Fig. 3b,d case where the equilibrium  $E_2$  was unstable. Here this holds true for  
 540  $\varepsilon = 1$  (Fig. 17a) but for smaller values the equilibrium becomes stable (Fig. 17b,c).

## 541 4.3 The degenerate phase point

542 With  $\varepsilon = 0$  substituted in the MB-model (54) there is no input of nutrients (54a) and also  
 543 no export of the abiotic and biotic elements from the reactor environment. The prey grows  
 544 logistically to the equilibrium  $x_0(0) + x_1(0)$  and the predator population remains constant  
 545  $x_2(0)$ . Hence, the equilibrium  $E_2$  is neutral stable. The degenerate phase curve is just this  
 546 point which is an equilibrium point  $x_1$  together with the initial predator size  $x_2(0)$ .

547 This degenerate phase curve differs completely from that of the RM-model. This is a  
 548 consequence of the fact that in the MB-model the second term of (54a) is proportional to  
 549  $\varepsilon$  and therefore the ratio of this and the first term of (54b), the efficiency, is constant.

## 550 4.4 Bifurcation analysis of MB-model

551 In order to find-out why this happens we calculated a two-parameter bifurcation diagram  
 552 shown in Fig. 18 where besides  $b_1$  (whereby  $a_1 = 5/3 b_1$ ), parameter  $\varepsilon$  is the second variable.

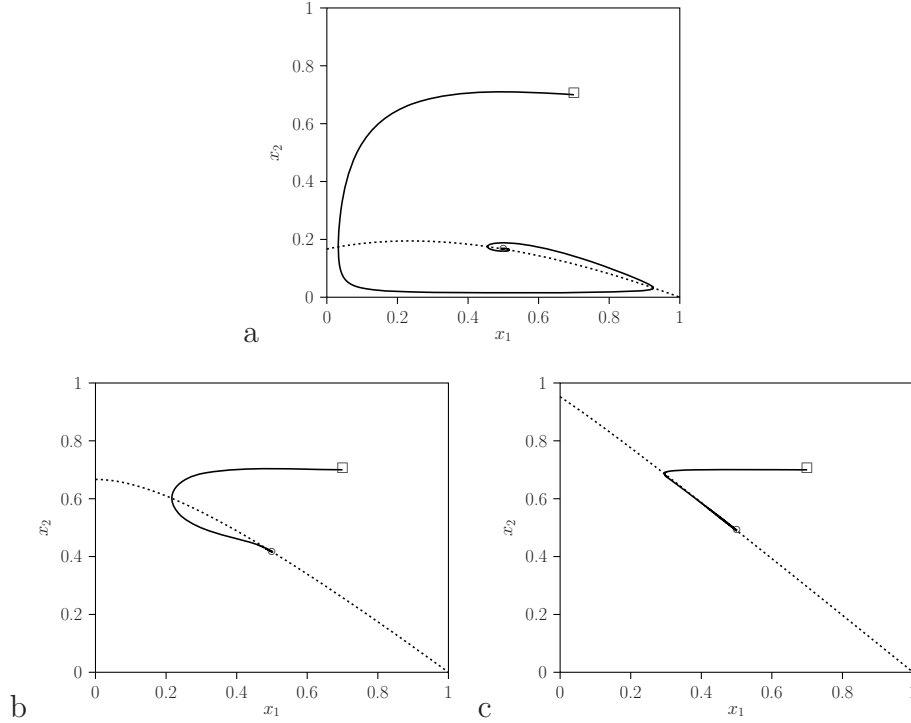


Figure 16: Phase-space analysis for system (54) describing the MB-model with  $a_1 = 5/3 b_1$ ,  $b_1 = 3$ , for three different values of  $\varepsilon$ :  $\varepsilon = 1$ ,  $\varepsilon = 0.1$  and  $\varepsilon = 0.01$ .

553 In this diagram the transcritical bifurcation  $TC$ , and the Hopf bifurcation  $H$ , curves are  
 554 drawn (see Table 3 for the expressions that describe the curves).

555 The transcritical bifurcation  $TC$ , is the same for all models. This is obviously due to  
 556 the fact that the model for the dynamics of the predator is the same for all models and  
 557 furthermore that for the prey-only ( $x_2 = 0$ ) equilibrium  $E_1$  is also the same. For the MB-  
 558 model the Hopf bifurcation  $H$  terminates at the origin where  $b_1 \rightarrow \infty$  and  $\varepsilon \rightarrow 0$ . There  
 559 is a stable equilibrium  $E_2$  in almost the whole  $b_1 > 4$  range up to  $\lim b_1 \uparrow \infty$  while in the  
 560 RM-model there is a stable limit cycle  $L_2$ .

561 From this we conclude that in the case of the MB-model the parameter  $\varepsilon$  can not to  
 562 be used as a single perturbation parameter. We conclude that the complete model has  
 563 to be analysed using a straight-forward phase-space and bifurcation analysis of the local  
 564 bifurcations  $H$  and  $TC$ .

## 565 5 Discussion and conclusions

566 The use of time-scale separation technique has a long tradition in ecology and biochemistry,  
 567 starting with the quasi-steady-state approximation (QSSA) used to derive the Holling types  
 568 functional response [17] and Michaelis-Menten kinetics.

569 In this paper we compared two fast-slow versions of predator-prey models: the RM-



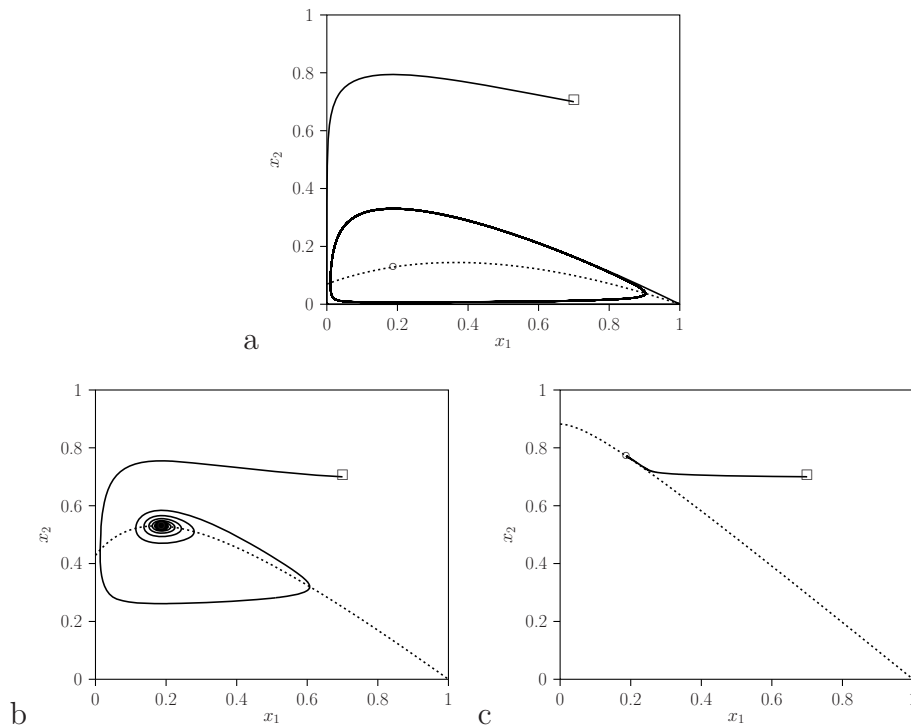


Figure 17: Phase-space analysis for system (54) describing the MB-model with  $a_1 = 5/3 b_1$ , and  $b_1 = 8$ , that is at the Hopf bifurcation point for three different values of  $\varepsilon$ :  $\varepsilon = 1$ ,  $\varepsilon = 0.1$  and  $\varepsilon = 0.01$ .

570 model and MB-model. In the classical RM-model the small perturbation parameter is  
 571 proportional to the efficiency of the predator-prey trophic interaction and the predator  
 572 death rate. In a series of papers [35, 42, 41] the dynamics of this bitrophic systems has  
 573 been studied intensively.

574 In [11] this subject was also studied focusing on the dynamics close to the critical  
 575 manifold  $\mathcal{M}_0^0$  (Fig. 5) (part of the vertical axis where the prey is absent) and related to  
 576 a delayed (transcritical) bifurcation phenomenon. Recently in [16] the analysis technique  
 577 based on the geometric singular perturbation theory was applied. This theory can also be  
 578 used where the interior equilibrium is unstable and relaxation dynamics occurs.

579 We used the invariant manifold criterion together with an extended asymptotic expansion  
 580 with respect to both, the perturbation parameter and the free bifurcation parameter.  
 581 This gives an iteration process that approximates the  $\mathcal{M}_\varepsilon^1$  slow manifold close to the  
 582 parabolic critical manifold  $\mathcal{M}_0^1$  in the neighbourhood of its top. In the parameter range  
 583 just above the Hopf bifurcation where stable limit cycles exist, this process converges to  
 584 the point where the canard explosion occurs. In [2] a similar method has been used: here  
 585 the advantage is that all calculations are done in Maple, [32] with rational numbers.

586 Direct application, however, showed that the delayed transcritical bifurcation dynamics  
 587 close to the critical manifold  $\mathcal{M}_0^0$  leads to an disturbing effect because the prey population

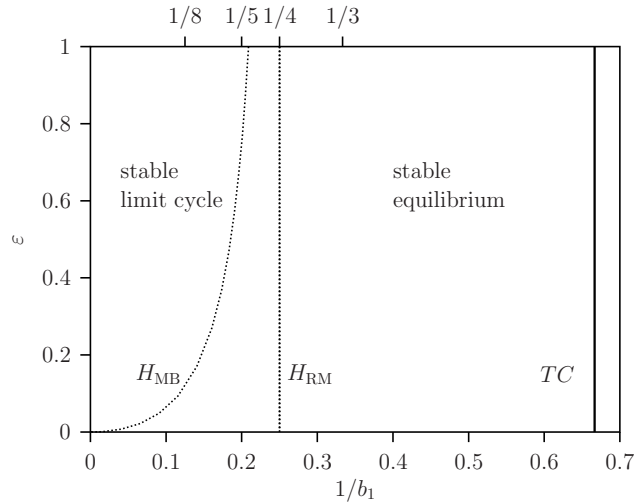


Figure 18: Two-parameter bifurcation diagram with  $\varepsilon$  and  $1/b_1$  as free parameters. The expressions are given in Table 3. The transcritical bifurcation curve  $TC$  is for both models RM-model and MB-model the same. For  $\varepsilon = 1$  the point of the Hopf bifurcations differ slightly but for  $\lim \varepsilon \downarrow 1$  they differ essentially. In the MB-model there is a stable equilibrium  $E_2$  in almost the whole  $b_1 > 4$  range up to  $\lim b_1 \uparrow \infty$  while there is a stable limit cycle  $L_2$  in the RM-model.

588 becomes very low. Therefore we introduced a small allochthonous input of prey in which  
 589 case the non-generic transcritical bifurcation disappears. In [46] the uniqueness of the limit  
 590 cycles in the RM-model with prey immigration is shown that supports the applicability of  
 591 this additionally introduced mechanism.

592 The canard phenomenon found can be described as follows. Also for small perturba-  
 593 tion parameter values the trajectories follow the stable limit cycles like in the case where  
 594 no time scale differences occur  $\varepsilon = 1$ . However, just above the Hopf bifurcation point  
 595 depending also on the perturbation parameter the stable limit cycle with small amplitude  
 596 consists of two concatenated slow and fast episodes. In the phase space, the top part is  
 597 just above the parabolic stable and unstable critical manifold and the bottom just below  
 598 the horizontal line connecting the two points where the limit cycle intersects with the f-  
 599 nullcline vertically. At the canard point of the bifurcation parameter, the dynamics tends  
 600 abruptly toward the relaxation dynamics. This transition point resembles what happens  
 601 due to the delayed bifurcation effect where the trajectory leaves the vertical axis below the  
 602 transcritical bifurcation  $TC$  in Fig. 5. For higher bifurcation parameters values the limit  
 603 cycle with large amplitude changes smoothly and approaches the degenerated phase curves  
 604 consisting of a concatenation of two slow and two fast episodes (Fig. 5).

605 Despite the approximate series expansion diverges, we found accurate approximations  
 606 for small  $\varepsilon$  of the part the limit cycles originating from the Hopf bifurcation point. Further-  
 607 more, the numerical approximate asymptotic iterative scheme, gives very good approxima-  
 608 tions of the bifurcation parameter  $b_1$  and perturbation parameter  $\varepsilon$  values where a canard  
 609 explosion occurs (see Fig. 11).

610 An other mathematical method to analyse a canard explosion is the blow-up technique  
611 [8, 9, 29, 30]. This technique can be used to study the unfolding of the degenerated Hopf  
612 bifurcation where  $\lim \varepsilon \rightarrow 0$ . This will be the subject of a forthcoming paper.

613 In [35, 42, 41, 20, 16, 11] the RM-model predator-prey slow-fast model showed complex  
614 relaxation oscillation dynamics, however, no canard explosion was observed.

615 In [26, 1, 23] food chain systems were already studied where the small parameter, mea-  
616 suring the timescale disparity between the rate of changes in the prey (fast) and predator  
617 (slow), in the MB-model was introduced. Then the fast subsystem converges to a criti-  
618 cal manifold of stable equilibria which yields an algebraic relationship between the state  
619 variable leading to a reduced (aggregated) lower dimensional (DAE) system. Predator prey  
620 systems with fast oscillating migrations were studied in [36] and with slow migrations in  
621 [33] wherein reduction methods were proposed. In those papers, relaxation oscillations  
622 were not discussed.

623 In the MB-model, conservation of mass is obeyed and therefore it is more realistic than  
624 the RM-model where nutrients are not modelled explicitly. An open chemostat environment  
625 is assumed with inflowing nutrients and the outflow of all abiotic and biotic components.  
626 Under specific situations the logistic growth rate of the prey is replaced by a prey growth  
627 model whereby nutrients are not only used for its own growth but also for its predator.  
628 This is a bottom-up effect in addition to the top-down effect of the prey consumption by  
629 the predator. The consumption occurs with a constant efficiency like in the alternative  
630 fast-slow version of the RM-model introduced in [16, Example 2.2]. The introduction of  
631 this constant efficiency in the fast-slow RM-model, however, leads to unrealistic equilibrium  
632 population sizes when  $\varepsilon$  becomes small. In the MB-model (54) these sizes remain realistic.  
633 A constant efficiency, instead of the less realistic variable efficiency, was earlier used in [26]  
634 in the fast-slow version of the RM-model and described by (2) [16, Example 2.1].

635 The dynamics of the MB-model was analysed using a classical phase-space and bifurca-  
636 tion analysis approach where only equilibria and limit cycles occur in the whole parameter  
637 space. Calculations showed that in this more realistically and mechanistically underpinned  
638 model the complex fast-slow canard explosion does not occur.

## 639 References

- 640 [1] P. Auger, R. Bravo de la Parra, J-C. Poggiale, E. Sanchez, and L. Sanz. Aggrega-  
641 tion methods in dynamical systems and applications in population and community  
642 dynamics. *Phys Life Rev*, 5(2):79–105, 2008.
- 643 [2] M. Brons. An iterative method for the canard explosion in general planar systems.  
644 *Discrete and continuous dynamical systems*, 250:77–83, 2013.
- 645 [3] M. Canalis-Durand. Formal expansion of van der pol equation canard solutions are  
646 gevrey. In E. Benoît, editor, *Dynamic Bifurcation*, pages 28–39. Springer, 1990.
- 647 [4] K.-S. Cheng. Uniqueness of a limit cycle for predator-prey system. *SIAM Journal on*  
648 *Mathematical Analysis*, 12:541–548, 1981.

- 649 [5] B. Deng. Food chain chaos with canard explosion. *Chaos*, 14(4):1083–1092, 2004.
- 650 [6] M. Diener. The canard unchained or how fast/slow dynamical problems bifurcate.  
651 *The Mathematical Intelligencer*, 6:38–49, 1984.
- 652 [7] E. J. Doedel and B. Oldeman. Auto 07p: Continuation and bifurcation software  
653 for ordinary differential equations. Technical report, Concordia University, Montreal,  
654 Canada, 2009.
- 655 [8] F. Dumortier and R. Roussarie. *Canard cycles and center manifolds*, volume 121 of  
656 *Memoires of the American Mathematical Society*. American Mathematical Society,  
657 AMS, Providence, RI, USA, 1996.
- 658 [9] F. Dumortier and R. Roussarie. Geometric singular perturbation theory beyond nor-  
659 mal hyperbolicity. In C. K. R. T. Jones and A. I. Khibnik, editors, *Multiple Time*  
660 *Scale Dynamical Systems*, volume 122 of *IMA*, pages 29–64. Springer-Verlag, Berlin,  
661 2000.
- 662 [10] W. Eckhaus. Relaxation oscillations including a standard chase on french ducks. In  
663 *Asymptotic analysis II*, volume 985 of *Lecture Notes in Mathematics*, pages 449–494,  
664 Berlin, 1983. Springer-Verlag.
- 665 [11] C. Lobry F. Campillo. Effect of population size in a predator-prey model. *Ecol Model*,  
666 246:1–10, 2012.
- 667 [12] N. Fenichel. Geometric singular perturbation theory. *JDE*, 31:53–98, 1979.
- 668 [13] J-M. Ginoux and J. Llibre. Flow curvature method applied to canard explosion. *J.*  
669 *Phys. A Math. Theor.*, 44(46):465203, 2016.
- 670 [14] J. Guckenheimer. *Normal Forms, Bifurcations and Finiteness Problems in Differential*  
671 *Equations*, volume 137 of *NATO Sci. Ser. II Math. Phys. Chem.*, chapter Bifurcations  
672 of relaxation oscillations, pages 295–316. Kluwer, Dordrecht, The Netherlands, 2004.
- 673 [15] J. Guckenheimer and P. Holmes. *Nonlinear Oscillations, Dynamical Systems and*  
674 *Bifurcations of Vector Fields*, volume 42 of *Applied Mathematical Sciences*. Springer-  
675 Verlag, New York, 2 edition, 1985.
- 676 [16] G. Hek. Geometric singular perturbation theory in biological practice. *J Math Biol*,  
677 60:347–386, 2010.
- 678 [17] C. S. Holling. Some characteristics of simple types of predation and parasitism. *Can-*  
679 *adian Entomologist*, 91:385–398, 1959.
- 680 [18] F. C. Hoppensteadt. *Analysis and Simulation of Chaotic Systems*. Applied Mathe-  
681 matical Sciences. Springer-Verlag, Berlin, 1993.
- 682 [19] S.-B. Hsu. On global stability of a predator-prey system. *Math Biosci*, 174(1-2):1–10,  
683 1978.
- 684 [20] S.-B. Hsu and J. Shi. Relaxation oscillation profile of limit cycle in perdator-prey  
685 system. *Discrete and continuous dynamical systems series B*, 11(4):893–911, 2009.

- 686 [21] C. K. R. T. Jones. Geometric singular perturbation theory. *Dynamical Systems*,  
687 1609:44–118, 1995.
- 688 [22] J. Kevorkian and J.D. Cole. *Multiple Scale and Singular Perturbation Methods*, volume  
689 114 of *Applied Mathematical Sciences*. Springer-Verlag, Berlin, 1995.
- 690 [23] B. W. Kooi. Modelling the dynamics of traits involved in fighting-predators-prey  
691 system. *J Math Biol*, 71:1575–1605, 2016.
- 692 [24] B. W. Kooi, M. P. Boer, and S. A. L. M. Kooijman. Consequences of population  
693 models on the dynamics of food chains. *Math Biosci*, 153(2):99–124, 1998.
- 694 [25] B. W. Kooi, J. C. Poggiale, and P. Auger. Aggregation methods in food chains. *Math.*  
695 *Comp. Mod.*, 27(4):109–120, 1998.
- 696 [26] B. W. Kooi, J. C. Poggiale, P. Auger, and S. A. L. M. Kooijman. Aggregation methods  
697 in food chains with nutrient recycling. *Ecol Model*, 157(1):69–86, 2002.
- 698 [27] M. Kot. *Elements of Mathematical Ecology*. Cambridge University Press, Cambridge,  
699 2001.
- 700 [28] M. Krupa and P. Szmolyan. Geometric analysis of the singularly perturbed fold.  
701 In J. K. R. T. Christopher and A Khibnik, editors, *Multiple-Time-Scale Dynamical*  
702 *Systems*, volume 122 of *The IMA Volumes in Mathematics and its Applications*, pages  
703 89–116. Springer, 2001.
- 704 [29] M. Krupa and P. Szmolyan. Relaxation oscillation and canard explosion. *Journal of*  
705 *Differential Equations*, 174:312–368, 2001.
- 706 [30] C. Kuehn. *Multiple Time Scale Dynamics*, volume 191 of *Applied Mathematical Sci-*  
707 *ences*. Springer-Verlag, New York, 2015.
- 708 [31] Yu. A. Kuznetsov. *Elements of Applied Bifurcation Theory*, volume 112 of *Applied*  
709 *Mathematical Sciences*. Springer-Verlag, New York, 3 edition, 2004.
- 710 [32] Maple. *Maple software*. Maplesoft, Waterloo, Ontario, Canada, 2008.
- 711 [33] M. Marva, J-C. Poggiale, and R. Bravo de la Parra. Reduction of slow-fast periodic  
712 systems with applications to population dynamics models. *Mathematical Models and*  
713 *Methods in Applied Sciences*, 22(10), 2012.
- 714 [34] J. Monod. *Recherches sur la croissance des cultures bacteriennes*. Hermann, Paris,  
715 1942.
- 716 [35] S. Muratori and S. Rinaldi. Low- and high-frequency oscillations in three-dimensional  
717 food chain systems. *SIAM J Appl Math*, 52:1688–1706, 1992.
- 718 [36] J. C. Poggiale and P. Auger. Fast oscillating migrations in a predator-prey model.  
719 *Mathematical Models & Methods in Applied Sciences (M3AS)*, 6(2):217–226, 1996.
- 720 [37] J. C. Poggiale, P. Auger, F. Cordoleani, and T. Nguyen-Huu. Study of a virus-bacteria  
721 interaction model in a chemostat: application of geometrical singular perturbation the-  
722 ory. *Philos T Roy Soc B*, 367:4685–3428, 2009.

- 723 [38] J. P. Ramis. Les développements asymptotiques après Poincaré : continuité et...  
724 divergences. *La gazette des mathématiciens*, 134:17–36, 2012.
- 725 [39] J. P. Ramis. Poincaré et les développements asymptotiques. *La gazette des*  
726 *mathématiciens*, 133:33–72, 2012.
- 727 [40] C. H. Ratsak, S. A. L. M. Kooijman, and B. W. Kooi. Modelling the growth of an  
728 oligochaete on activated sludge. *Wat. Res.*, 27(5):739–747, 1993.
- 729 [41] S. Rinaldi and A. Gragnani. Destabilizing factors in slow-fast systems. *Ecol Model*,  
730 180:445–460, 2004.
- 731 [42] S. Rinaldi and S. Muratori. Slow fast limit-cycles in predator prey models. *Ecol Model*,  
732 61(3-4):287–308, 1992.
- 733 [43] M. L. Rosenzweig. Paradox of enrichment: destabilization of exploitation ecosystems  
734 in ecological time. *Science*, 171:385–387, 1971.
- 735 [44] M. L. Rosenzweig and R. H. MacArthur. Graphical representation and stability con-  
736 ditions of predator-prey interactions. *Am Nat*, 97:209–223, 1963.
- 737 [45] H. L. Smith and P. Waltman. *The Theory of the Chemostat*. Cambridge University  
738 Press, Cambridge, 1994.
- 739 [46] J. Sugie and Y. Saito. Uniqueness of limit cycles in a Rosenzweig-MacArthur model  
740 with prey immigration. *SIAM J Appl Math*, 72(1):299–316, 2012.
- 741 [47] B. Van der Pol. On relaxation oscillations. *Philosophical Magazine*, 7:978–992, 1926.
- 742 [48] G. A. K. van Voorn and B. W. Kooi. Combining bifurcation and sensitivity analysis  
743 for ecological models. *Eur. Phys. J. Special Topics*, 226:2101–2118, 2017.

## 744 A Derivation of the dimensionless RM-model

From [48] we recall (after some adjustments of the notation), that the classical RM-model is given as

$$\frac{dX_1}{dT} = RX_1(1 - X_1/K) - AF(X_1)X_2, \quad (55a)$$

$$\frac{dX_2}{dT} = (CAF(X_1) - M)X_2, \quad (55b)$$

745 where  $F(X_1) = X_1(1 + AkX_1)^{-1}$  is the well-known Holling type II functional response,  
746 with  $X_j$  the state variables,  $k$  handling time,  $A$  the attack rate,  $C$  a conversion efficiency,  
747  $M$  the predator removal rate (mortality, maintenance, and harvesting), and  $T$  is time. A  
748 list of symbols is given in Table 4.

749 This model can be rescaled by using  $t = TR$ ,  $x_1 = X_1/K$ , and  $x_2 = X_2/K$ . Note that  
750 in the last transformation for the predator biomass differs from [48] to let the efficiency  $C$   
751 not disappear in the dimensionless formulation and to be able to deal with the time-scale  
752 difference in the fast-slow system the subject here.

Table 4: List of symbols used for RM-model with dimension with their meaning. the biomass of both populations have the same dimension.

Symbol	Meaning
$T$	Dimensional time
$t$	Dimensionless time
$X_j$	Dimensional state variable, indicated by $j$
$x_j$	Dimensionless state variable, indicated by $j$
$R$	Intra-specific growth rate
$A$	Attack rate
$F(X_1)$	Functional response, non-dimensional
$C$	Efficiency, conversion yield, non-dimensional
$M$	Mortality rate per unit of time
$k$	Handling time

753 The non-dimensional model then reads

$$\frac{dx_1}{dt} = x_1(1 - x_1) - \frac{a_1 x_1}{1 + b_1 x_1} x_2, \quad (56a)$$

$$\frac{dx_2}{dt} = x_2 \left( \frac{c_1 a_1 x_1}{1 + b_1 x_1} - d_1 \right), \quad (56b)$$

754 where  $a_1 = AK/R$ ,  $b_1 = kAK$ ,  $c_1 = C$  and  $d_1 = M/R$ .

## 755 **B The slow dynamics on the parabola part of the $f$ -** 756 **nullcline**

757 We give the results for the slow dynamics in the degenerated case  $\varepsilon = 0$  where the dynamics  
758 is on a part of the  $f$ -nullclines critical manifolds.

759 The slow dynamics on the vertical axis is described again by the system (12). We will  
760 now focus on the slow dynamics on the parabola shown in Fig. 19 where the dynamics  
761 of the reduced system (21) is solved numerically, yielding the prey population size  $x_1(\tau)$   
762 while (20) is used to get the associated predator population size  $x_2(\tau)$ . Figure 19a gives  
763 the results for the stable equilibrium  $E_2$ ,  $b_1 = 3$  where  $a_1 = 5/3$   $b_1 = 5$  case with initial  
764 condition  $x_2(0) = 0.225$ . This value is below point  $T$ , where  $x_2 = 0.25$ . In this case there  
765 are two valid initial points given by (19). Starting at the largest  $x_1$  prey value on the  
766 right-hand parabolic branch there is convergence toward the equilibrium  $E_2$ . But at the  
767 lowest prey value on the left-hand branch there is convergence to the trivial zero-solution  
768 where  $x_1 = 0$  and  $x_2 = 0$ .



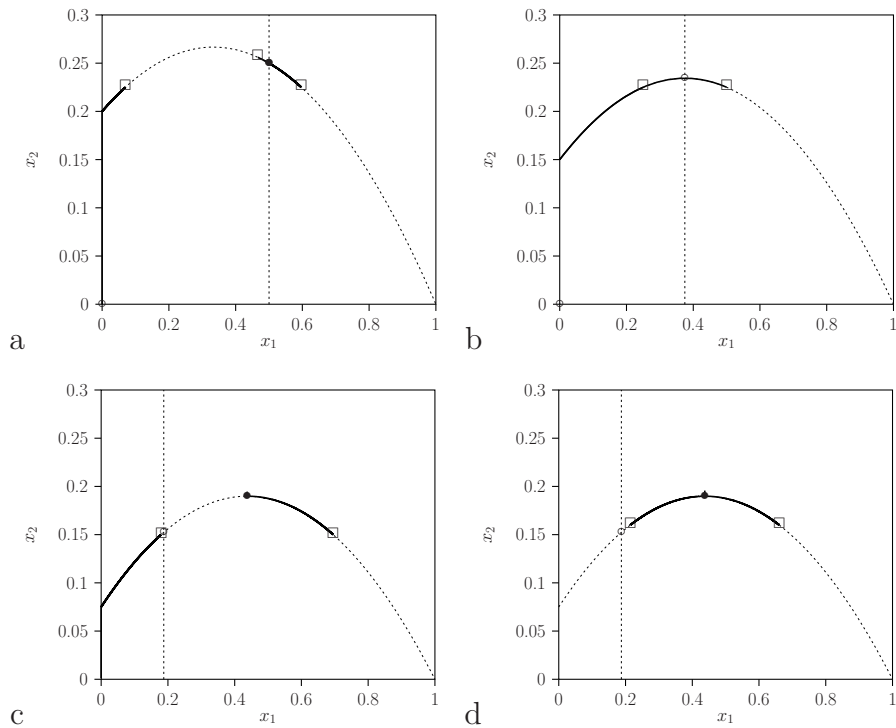


Figure 19: Phase-space analysis for slow system (19) of the RM-model. (a): At the top-panel left  $b_1 = 3$  and  $a_1 = 5/3 b_1$ , with initial values  $x_2 = 0.225$  and  $x_2 = 0.256$ . The equilibrium  $E_2$  is stable and the right-branch of the parabola is the basin of attraction. On the other hand the left-branch of the parabola is in the attraction basin of the zero solution. (b): At the top-panel right  $b_1 = 4$  and  $a_1 = 5/3 b_1$ , with initial values  $x_2 = 0.225$ . The equilibrium  $E_2$  is unstable. (c) and (d): The lower panel with  $b_1 = 8$  and  $a_1 = 5/3 b_1$  the two initial values  $x_2 = 0.15$  and  $x_2 = 0.16$ . The associated initial value of the  $x_1(0)$  is for  $x_2 = 0.15$  below the unstable equilibrium  $E_2$  value. For  $x_2 = 0.16$  the associated initial value of the  $x_1(0)$  is above the unstable equilibrium  $E_2$  value.

769 Hence, the right-hand branch of the parabola is in the basin of attraction of the stable  
770 equilibrium of the reduced system equal to that of the original system  $E_2$ . On the other  
771 hand for the left-hand branch it is in the basin of attraction of the zero solution.

772 Figure 19c,d were calculated with parameter values  $b_1 = 8$  and  $a_1 = 5/3 b_1 = 40/3$  where  
773 the equilibrium  $E_2$  of the original system is unstable. In Fig. 19c starting at the lowest  
774 prey value and  $x_2(0) = 0.15$ , the results are similar to that in the above discussed case.  
775 However, starting with the largest prey value on the critical manifold there is convergence  
776 to the limit point  $T$  for the reduced system, and not to the unstable equilibrium  $E_2$  of the  
777 full model. Note that the vector field is not defined at the top  $T$ . In Fig. 19d the initial  
778 value is  $x_2(0) = 0.16$  where both simulations terminate at a limit point  $T$  of the reduced  
779 system. Hence, the unstable equilibrium  $E_2$  of the full system is a separatrix between the  
780 two equilibrium points of the reduced system, being limit point  $T$  in (13) and the zero  
781 point  $E_0(x_1, x_2) = (0, 0)$ .



782 For the special case  $b_1 = 4$  at the Hopf bifurcation the results are shown in Fig. 19b.  
 783 The equilibrium  $E_2$  of the full system (2) at point  $T$  in (14) is now for the reduced system  
 784 restricted to the critical manifold not an equilibrium of the reduced system and there is no  
 785 convergence to that point. Starting for  $x_2(0) = 0.225$  there is always convergence to the  
 786 trivial zero solution  $E_0$  which is here a global stable equilibrium of the reduced system.

787 In order to study the dynamics at the critical manifold (the parabola) further we plot  
 $dx_1/dt$  versus  $x_1(t)$  in Fig 20 in addition to  $x_2(t)$  versus  $x_1(t)$  in the phase space. For the

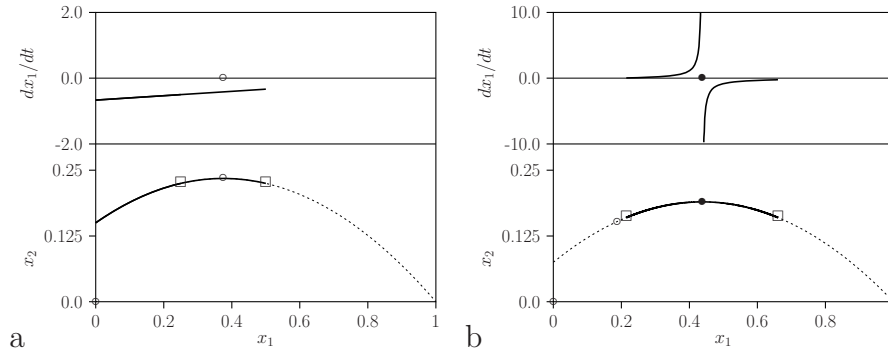


Figure 20: Phase-space analysis for slow system (19) of the RM-model. In the top-subpanels the rate  $dx_1/dt$  versus  $x_1(t)$  while in the bottom-subpanel the dynamics  $x_2(t)$  versus  $x_1(t)$  on the critical manifold (see also Fig 19). (a): The left-panel  $b_1 = 4$  and  $a_1 = 5/3 b_1$ , with initial value  $x_2 = 0.225$  where the equilibrium  $E_2$  is stable. (b): The right-panel with  $b_1 = 8$  and  $a_1 = 5/3 b_1$  the initial value is  $x_2 = 0.16$  whereby the associated initial value of the  $x_1(0)$  is above the unstable equilibrium value.

788  
 789 Hopf bifurcation value  $b_1 = 4$  the rate  $dx_1/dt$  given in (21) is always negative and hence  
 790 there is convergence always to the global stable zero solution. Note that the numerator in  
 791 (21) is zero and this does not hold when  $b_1 \neq 4$ . However, for  $b_1 = 8$  where the equilibrium  
 792 is unstable the situation differs. Now when starting on the left side of point  $T$  the rate  
 793  $dx_1/dt$  is positive and there is convergence toward the limit point  $T$  given in (13). Similarly  
 794 starting on the right-side the rate  $dx_1/dt$  is negative and there is also convergence toward  
 795  $T$ . Now, the plot shows a vertical asymptote. Thus the rate is discontinuous at point  $T$   
 796 and this is due to the fact that  $dq/dx_1$  (20) is zero at  $T$ . Calculations showed that the  
 797 equilibrium point of the reduced system is reached in finite time. This is proved in the  
 798 Appendix B.

799 In summary, the computational results show that point  $T$  is in the case of the reduced  
 800 system not a simple tangent bifurcation. When the parameter equals the Hopf bifurcation  
 801 value it is not even an equilibrium. Otherwise it is a limit point reached in finite time.

802 To support this the dynamics of the RM-model (2) on the parabola, the  $\mathcal{M}_0^1$  part of  
 803 the  $f$ -nullcline (22b) is studied. From equations (20) and (21), one has

$$\frac{dx_1}{d\tau} = \frac{(1-x_1)((a_1-b_1)x_1-1)}{b_1-2b_1x_1-1}. \quad (57)$$

804 Since we have :

$$\frac{-2b_1x_1 + b_1 - 1}{(1 - x_1)((a_1 - b_1)x_1 - 1)} = \frac{b_1 + 1}{b_1 + 1 - a_1} \frac{1}{1 - x_1} + \frac{b_1^2 + b_1 - a_1b_1 + a_1}{b_1 + 1 - a_1} \frac{1}{(a_1 - b_1)x_1 - 1}, \quad (58)$$

805 it follows that equation (57) is equivalent to

$$\frac{b_1 + 1}{1 - x_1} + \frac{b_1^2 + b_1 - a_1b_1 + a_1}{(a_1 - b_1)x_1 - 1} dx_1 = (b_1 + 1 - a_1) d\tau, \quad (59)$$

806 thus

$$\int_{x_1(0)}^{x_1(T)} \left( \frac{b_1 + 1}{1 - x_1} + \frac{b_1^2 + b_1 - a_1b_1 + a_1}{(a_1 - b_1)x_1 - 1} \right) dx_1 = \int_0^T (b_1 + 1 - a_1) d\tau, \quad (60)$$

807 where  $x_1(T)$  is the coordinate of the top of the parabola:  $x_1(T) = \bar{x}_1 = \frac{b_1 - 1}{2b_1}$ .

808 If we consider that the equilibrium point ( $x_1^* = \frac{1}{a_1 - b_1}$ ) is at point  $T$ , that is at the  
809 Hopf bifurcation point when  $b_1 = 4$ , it follows that:  $b_1^2 + b_1 - a_1b_1 + a_1 = 0$ .

810 We can then express the time  $t_T$  needed for starting from  $x_1(0)$  to reach the equilibrium  
811  $E_2$  at point  $T$

$$t_T = \frac{1}{a_1 - b_1 - 1} \left( (1 + b_1) \ln \left( \frac{(1 + b_1)/(2b_1)}{1 - x_1(0)} \right) \right). \quad (61)$$

812 But in this case point  $T$  is not an equilibrium. If one assumes that the equilibrium is on  
813 the right of point  $T$ , that is  $b_1 < 4$ , see Fig. 3a, (60) shows that the equilibrium is not  
814 reach in a finite time.

815 Finally, if we assume that the equilibrium  $x_1^*$  is on the left of point  $T$  that is  $b_1 > 4$   
816 and if we consider an initial condition between  $x_1^*$  and 1, see Fig. 3d, point  $T$  attracts the  
817 trajectory. It is, however, not an equilibrium in the usual sense because equation (57) does  
818 not vanish, it is actually not well defined. Nevertheless this point is reached in a finite  
819 time according to (60), and the time needed to reach this point  $t_T^*$  is

$$t_T^* = \frac{1}{a_1 - b_1 - 1} \left( (1 + b_1) \ln \left( \frac{(1 + b_1)/(2b_1)}{1 - x_1(0)} \right) + \frac{A}{a_1 - b_1} \ln \left( \frac{A/(2b_1)}{(a_1 - b_1)x_1(0) - 1} \right) \right), \quad (62)$$

820 where  $A = a_1b_1 - a_1 - b_1^2 - b_1 > 0$  under the above mentioned conditions.