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Invariant Planes and Periodic Oscillations in the May–Leonard Asymmetric Model

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Abstract

We propose an approach for the qualitative investigation of polynomial systems of ODEs based on algorithms of computational commutative algebra. It can be applied to study various models of chemical reactions derived using the mass action law. Using it we find all families of systems with invariant planes different from $x = 0$, $y = 0$ and $z = 0$ in the May-Leonard asymmetric model, which is a three-dimensional Lotka-Volterra system depending on six parameters. Then we prove existence of periodic solutions for some of these families.

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1 Introduction

The usual deterministic model of the reaction consisting of the steps

$$\mathrm{X} \underset{1}{\overset{1}{\rightleftarrows}} 2\mathrm{X} \quad \mathrm{Y} \underset{1}{\overset{1}{\rightleftarrows}} 2\mathrm{Y} \quad \mathrm{Z} \underset{1}{\overset{1}{\rightleftarrows}} 2\mathrm{Z} \tag{1.1}$$

$$\mathrm{X}+\mathrm{Y} \overset{\alpha_1}{\to} 0 \quad \mathrm{Y}+\mathrm{Z} \overset{\alpha_2}{\to} 0 \quad \mathrm{Y}+\mathrm{Z} \overset{\alpha_3}{\to} 0 \tag{1.2}$$

is an ordinary differential equation with a polynomial right hand side written down for the concentration vs. time functions as follows

$$\begin{aligned} \dot{x} &= x(1-x-\alpha_1 y-\alpha_3 z), \\ \dot{y} &= y(1-\alpha_1 x-y-\alpha_2 z), \\ \dot{z} &= z(1-\alpha_3 x-\alpha_2 y-z). \end{aligned} \tag{1.3}$$

A few remarks are in order. The positive numbers above and below the arrows (such as 1 or α_i) are *reaction rate coefficients*, characterizing the rate of the individual steps. A reaction step of the form $\mathrm{X} \underset{1}{\overset{1}{\rightleftarrows}} 2\mathrm{X}$ is a shorthand for $\mathrm{A}+\mathrm{X} \underset{1}{\overset{1}{\rightleftarrows}} 2\mathrm{X}$, where A is a species the concentration of which is supposed not to change during our investigation. A real (bio)chemical example described by this is the (simplified) description of the production of trypsin from trypsinogen, its precursor. On the other side, a reaction step $\mathrm{X} \underset{1}{\overset{1}{\rightleftarrows}} 2\mathrm{X}$ (or, $\mathrm{A}+\mathrm{X} \underset{1}{\overset{1}{\rightleftarrows}} 2\mathrm{X}$) expresses that the rate of formation of the species X is enhanced by its presence, this is usually called *autocatalysis*.

System (1.3) is a particular case of the system

$$\begin{aligned} \dot{x} &= x(1-x-\alpha_1 y-\beta_1 z), \\ \dot{y} &= y(1-\beta_2 x-y-\alpha_2 z), \\ \dot{z} &= z(1-\alpha_3 x-\beta_3 y-z) \end{aligned} \tag{1.4}$$

where $\alpha_i,\ \beta_i\ (1 \le i \le 3)$ are non-negative parameters.

In the literature system (1.4) is called the May-Leonard asymmetric model [3,10]. As this more general model can also be considered a kinetic differential equation [12], our results below can be interpreted in terms of mass action type kinetic models of a special class. One can write down reaction steps similar to (1.1)–(1.2) which have as their mass action type kinetic differential equation the equation (1.4), but they are not as easy to interpret as the special case (1.3) above. It is also true that the realizations of the system (1.4) are far from being unique, see [12,28].

Systems (1.3) and (1.4) are particular cases of the so-called Lotka-Volterra system

$$\dot{x}_i = x_i \left(\sum_{j=1}^{I} a_{ij} x_j + b_i \right) \quad (i = 1, 2, \ldots, I), \tag{1.5}$$

which, in turn, is a generalization of the simple models proposed by Lotka and Volterra in the beginning of the last century to describe the time evolution of fish populations [20]. Systems of the form (1.5) have wide range of applications in biochemistry. For instance, they can be used as a model to describe cold flames [11], to study enzyme kinetics [30], circadian clocks [23], or see also [16].

Generally speaking, systems (1.3)–(1.5) are so-called polynomial systems of ODEs, which are the systems written in the form

$$\dot{x}_i = P_i(x_1, \ldots, x_n) \quad (i = 1, \ldots, m), \tag{1.6}$$

where P_i are some polynomials, whose coefficients are parameters. Such systems arise frequently in the studies of chemical reactions since they appear naturally applying mass action law.

Solutions of systems (1.3)–(1.6) cannot, in general, be written in terms of elementary functions, so the study of qualitative properties of solutions should be performed. What are the usual questions raised in connection with such models? Existence and uniqueness of the solutions is obvious. However the other properties can be very difficult to determine. The really interesting and important question is how to ensure or exclude exotic phenomena, like multistationarity and oscillation. A good review of the first topic is [13].

As to oscillations, the fundamental theorems by Volpert on reactions with acyclic Volpert graphs [29], and the deficiency zero and the deficiency one theorems might be mentioned [15].

Among others, two important streams of the studies of polynomials systems appear: one is the search of first integrals of the system, since knowing an integral we can reduce the dimension of the system, and the other one is the search for periodic oscillations.

In this paper we discuss these two important questions using as the example the May-Leonard asymmetric system (1.4). A well-known and widely used approach for the search of oscillations in biochemical models is to find singular points of the system and then to determine periodic solutions arising as the result of the Hopf bifurcation in the reaction model, see, for instance, [14] and references therein.

In this paper we use another approach, which appears much less known to the community working on the investigation of biochemical models. An intrinsic feature of equations (1.6) arising from the mass action law is that it is easy to write down such systems, but already the determination of their singular points can be an extremely difficult and often unsolvable problem (if the system depends on many parameters). It is also difficult or impossible to determine systems with first integrals in a given family of systems (1.6) depending on parameters. However we will see below that there is an algorithmic way to find subfamilies admitting polynomial partial integrals, that is, having invariant algebraic surfaces. As it is shown below knowing such a surface in some cases we can find families of periodic solutions arising not due to a Hopf bifurcation, but provided by the so-called Lyapunov theorem on holomorphic integral. Below we will describe our approach for the May-Leonard asymmetric system (1.4), but it can be applied to any polynomial system (1.6).

System (1.4), which is the main object to study in our paper, was introduced in [27] as a generalization of the model proposed by May and Leonard [22], who studied the particular case of (1.4), where $\alpha_1 = \alpha_2 = \alpha_3 = \alpha$, $\beta_1 = \beta_2 = \beta_3 = \beta$. In [27] Schuster, Sigmund and Wolf studied system (1.4) under the assumptions

$$0 < \alpha_i < 1 < \beta_i, \quad \beta_i - 1 > 1 - \alpha_j \ (1 \le i, j \le 3). \tag{1.7}$$

Chi, Hsu and Wu [3] relaxed (1.7) to the assumptions

$$0 < \alpha_i < 1 < \beta_i \ (1 \le i \le 3). \tag{1.8}$$

Let

$$A_i = 1 - \alpha_i, \quad B_i = \beta_i - 1, \quad (1 \le i \le 3).$$

Chi, Hsu and Wu [3] showed that under assumptions (1.8) system (1.4) has a unique interior equilibrium P, which is locally asymptotically stable if $A_1A_2A_3 > B_1B_2B_3$, and if $A_1A_2A_3 < B_1B_2B_3$, then P is a saddle point with a one-dimensional stable manifold. They also have shown that if $A_1A_2A_3 \neq B_1B_2B_3$, then the system does not have periodic solutions, and if

$$A_1A_2A_3 = B_1B_2B_3, \tag{1.9}$$

then there is a family of periodic solutions.

In the present paper we study system (1.4) without assumption (1.8), that is, we assume only that $\alpha_i, \ \beta_i \ge 0$ $(1 \le i \le 3)$.

We first find all invariant planes of the system and then restrict our analysis to the study of some subfamilies of (1.4) with the invariant planes. We show that even if assumption (1.8) is dropped system (1.4) still can have a family of periodic solutions. Moreover, we show that the periodic solutions of the system do not arise as a result of Hopf bifurcations, but their existence is due to the Lyapunov theorem on holomorphic integral (see e.g. [2, 21]).

Our approach is different from the one of [3, 22, 27, 31], since it relies on making use of tools of computational algebra. Usually the analysis of biochemical, technical and other models described by systems of differential equations starts from finding singular points of the system and determining their types. However already the finding of singular points can be an extremely difficult problem even for polynomial systems of differential equations depending on parameters. Instead of looking for singular points in such systems we propose to look first for some surfaces invariant under the flow of the vector field. As we will see below it allows to "catch" in the space of the parameters some systems with an interesting behaviour (in particular, it is shown in Section 3 that condition (1.9) is one of conditions under which system (1.4) has an invariant plane passing through the origin and different from the planes $x = 0$, $y = 0$ and $z = 0$). An important good feature of the approach is that the search for the invariant surfaces can be performed algorithmically using routines of computer algebra systems (see also [1, 17]).

2 Preliminaries

One possible approach to find integrals of a polynomial system of ODEs is to find first integrals of some kind. The most natural choice is to look for first integrals in the class of polynomials, as, for instance, in [25]. A generalization of this approach is the method of Darboux, where a first integral is constructed from partial integrals (invariant surfaces) of the system (see e.g. [6, 18, 19]). To recall the method we first observe that a surface defined by the equation $H = 0$, with H being a polynomial, is an invariant surface of the system

$$\begin{cases} \dot{x} = P(x, y, z), \\ \dot{y} = Q(x, y, z), \\ \dot{z} = R(x, y, z), \end{cases} \tag{2.1}$$

where the maximal degree of polynomials P, Q, R is m, if and only if

$$D(H) := \frac{\partial H}{\partial x} P + \frac{\partial H}{\partial y} Q + \frac{\partial H}{\partial z} R = K\, H \tag{2.2}$$

with K being a polynomial of degree at most $m-1$. The polynomial H is called a Darboux polynomial [6] of system (2.1) and K is termed a cofactor. For system (1.4) the functions

$$H_1(x,y,z) = x, \quad H_2(x,y,z) = y, \quad H_3(x,y,z) = z \tag{2.3}$$

are Darboux polynomials with the cofactors

$$K_1(x,y,z) = 1-x-\alpha_1 y-\beta_1 z,\ K_2(x,y,z) = 1-\beta_2 x-y-\alpha_2 z,\ K_3(x,y,z) = 1-\alpha_3 x-\beta_3 y-z,$$

respectively.

Now, let n be an arbitrary natural number, H_i be arbitrary Darboux polynomials of system (2.1) and K_i the corresponding cofactors ($i = 1, 2, \dots, n$). A Darboux first integral of system (2.1) is a function of the form

$$\Psi(x,y,z) = \prod_{i=1}^{n} H_i(x,y,z)^{\lambda_i},$$

where H_i are Darboux polynomials with the cofactors satisfying

$$\sum_{i=1}^{n} \lambda_i K_i = 0 \tag{2.4}$$

and λ_i being some constants. We note that in the very special case of Eq. (2.3) such a $\lambda_1, \lambda_2, \lambda_3$ exists if and only if

$$\operatorname{rank} \begin{pmatrix} 1 & 1 & 1 \\ 1 & \beta_2 & \alpha_3 \\ \alpha_1 & 1 & \beta_3 \\ \beta_1 & \alpha_2 & 1 \end{pmatrix} \leq 2 \tag{2.5}$$

holds. In the original May-Leonard case this can only happen if $\alpha = \beta = 1$. We might find cases with rank 2 or less under the restrictions (1.7) or (1.8) on the parameters.

3 Invariant planes of system (1.4)

To find invariant planes of system (1.4) we need a result from computational commutative algebra called the Elimination Theorem. We recall it here.

Let I be an ideal in $k[x_1, \dots, x_n]$ and ℓ be a fixed number from the set $\{0, 1, \dots, n-1\}$. The *ℓth elimination ideal* of I is the ideal $I^{(\ell)} = I \cap k[x_{\ell+1}, \dots, x_n]$. According to the Elimination Theorem (see, for example, [5,26]) in order to compute (for any $0 \leqslant \ell \leqslant n-1$) the ℓth elimination ideal $I^{(\ell)}$ of an ideal I of $k[x_1, \dots, x_n]$ one can choose the lexicographic term order on the ring $k[x_1,\dots,x_n]$ with $x_1 > x_2 > \cdots > x_n$ and compute a Gröbner basis G for the ideal I with respect to this order. Then, by the Elimination theorem, the set $G_\ell := G \cap k[x_{\ell+1},\dots,x_n]$ is a Gröbner basis for the ℓth elimination ideal $I^{(\ell)}$.

We look for an invariant plane in the form

$$H(x,y,z) = h_0 + h_{100}x + h_{010}y + h_{001}z. \tag{3.1}$$

with the corresponding cofactor

$$K(x,y,z) = c_0 + c_1x + c_2y + c_3z. \tag{3.2}$$

Substituting these $H(x,y,z)$ and $K(x,y,z)$ into the equation

$$D(H) = KH \tag{3.3}$$

and comparing the coefficients of similar terms, we obtain the polynomial system

$$g_1 = g_2 = \cdots = g_{10} = 0$$

where

$$\begin{aligned}
g_1 &= -\, c_0h_0,\\
g_2 &= -\, c_3h_0 + h_{001} - c_0h_{001},\\
g_3 &= -\, h_{001} - c_3h_{001},\\
g_4 &= -\, c_2h_0 + h_{010} - c_0h_{010},\\
g_5 &= -\, h_{010} - c_2h_{010},\\
g_6 &= -\, \beta_3h_{001} - c_2h_{001} - \alpha_2h_{010} - c_3h_{010},\\
g_7 &= -\, c_1h_0 + h_{100} - c_0h_{100},\\
g_8 &= -\, h_{100} - c_1h_{100},\\
g_9 &= -\, \beta_2h_{010} - c_1h_{010} - \alpha_1h_{100} - c_2h_{100},\\
g_{10} &= -\, \alpha_3h_{001} - c_1h_{001} - \beta_1h_{100} - c_3h_{100}.
\end{aligned} \tag{3.4}$$

To simplify computations we look separately for invariant planes of system (1.4) passing through the origin and not passing through the origin.

Theorem 1. *System* (1.4) *has an invariant plane passing through the origin and different from the planes* $x=0,\ y=0,$ *and* $z=0$ *if one of the following conditions holds:*

1) $\alpha_2 = \beta_1,\ \beta_2 \neq 1,$

2) $\alpha_1 = \beta_3,\ \ \alpha_3 \neq 1,$

3) $\alpha_3 = \beta_2,\ \ \beta_3 \neq 1,$

4) $\beta_3 = \frac{2-\alpha_1-\alpha_2+\alpha_1\alpha_2-\alpha_3+\alpha_1\alpha_3+\alpha_2\alpha_3-\alpha_1\alpha_2\alpha_3-\beta_1-\beta_2+\beta_1\beta_2}{(\beta_1-1)(\beta_2-1)},$

5) $\beta_1 = \alpha_3 = 1,\ (-1+\alpha_1)(-1+\beta_3) \neq 0,$

6) $\beta_2 = 1, \alpha_1\ (-1+\alpha_2)(-1+\beta_1) \neq 0.$

Proof. We denote by $J = \langle g_1, g_2, \ldots, g_{10} \rangle$ the ideal generated by polynomials of system (3.4). To obtain the conditions for existence of invariant planes we have to eliminate from system (3.4) the variables h_i and c_i, that is, to compute the 8-th elimination ideal of J in the ring

$$\mathbb{Q}[h, c, \alpha, \beta] := \mathbb{Q}[h_0, h_{100}, h_{010}, h_{001}, c_0, c_1, c_2, c_3, \alpha_1, \alpha_2, \alpha_3, \beta_1, \beta_2, \beta_3].$$

However we observe, that (3.3) always has the solution $H = h_0$, $K = 0$ and the solutions H_1, H_2, H_3. Thus, the 8-th elimination ideal of the ideal J is the zero polynomial. To overcome this difficulty we impose the condition that polynomial (3.1) is not a constant and it is different from H_1, H_2 and H_3.

Since we are looking for planes passing through the origin we set in (3.1) $h_0 = 0$. Then the equation $H = 0$ (with H given by (3.1)) defines a plane different from the planes $x = 0,\ y = 0$, and $z = 0$ if at least two from the coefficients $h_{100}, h_{010}, h_{001}$ are different from zero. The latter condition can be written in the polynomial form as

$$1 - wh_{100}h_{010} = 0, \quad \text{or} \quad 1 - wh_{100}h_{001} = 0, \quad \text{or} \quad 1 - wh_{010}h_{001} = 0,$$

where w is a new variable. To find planes (3.1) with h_{100} and h_{010} different from zero we compute the 8-th elimination ideal of the ideal $I = \langle J, 1 - wh_{100}h_{010} \rangle$ in the ring $\mathbb{Q}[w, h, c, \alpha.\beta]$. Performing computations with the command `eliminate` of Singular we obtain the principal ideal

$$(\alpha_2 - \beta_1)((\alpha_1 - 1)(\alpha_2 - 1)(\alpha_3 - 1) + (\beta_1 - 1)(\beta_2 - 1)(\beta_3 - 1))$$

which gives the conditions

$$\alpha_2 = \beta_1 \tag{3.5}$$

and

$$(\alpha_1 - 1)(\alpha_2 - 1)(\alpha_3 - 1) + (\beta_1 - 1)(\beta_2 - 1)(\beta_3 - 1) = 0. \tag{3.6}$$

Similarly, computing the 8-th elimination ideals of the ideals $I = \langle J, 1 - wh_{100}h_{001}\rangle$ and $I = \langle J, 1 - wh_{010}h_{001}\rangle$ we again obtain condition (3.6) and, additionally, conditions

$$\alpha_1 = \beta_3 \tag{3.7}$$

and

$$\alpha_3 = \beta_2. \tag{3.8}$$

We now should check if under the fulfillment of each of conditions (3.5)–(3.8) the corresponding system (1.4) has an invariant plane not passing through the origin.

Straightforward computations show that when condition (3.5) is fulfilled system (1.4) admits the invariant plane

$$H_4(x, y, z) = -x + \beta_2 x + y - \alpha_1 y$$

with the cofactor $K_4(x, y, z) = 1 - x - y - \beta_1 z$ provided that $\beta_2 \neq 1$. If $\beta_2 = 1$, then the system does not have invariant planes different from $x = 0,\ y = 0,\ z = 0$.

Similarly, if (3.7) or (3.8) holds, the invariant planes are $H_4(x, y, z) = -x+\alpha_3 x+z-\beta_1 z$ (if $\alpha_3 \neq 1$) and $H_4(x, y, z) = -y + \beta_3 y + z - \alpha_2 z$ (if $\beta_3 \neq 1$), respectively.

Thus, system (1.4) has an invariant plane passing through the origin, if one of conditions 1), 2), 3) of the theorem is fulfilled.

If condition (3.6) holds and $(\beta_1 - 1)(\beta_2 - 1) \neq 0$ then

$$\beta_3 = \frac{2 - \alpha_1 - \alpha_2 + \alpha_1\alpha_2 - \alpha_3 + \alpha_1\alpha_3 + \alpha_2\alpha_3 - \alpha_1\alpha_2\alpha_3 - \beta_1 - \beta_2 + \beta_1\beta_2}{(\beta_1 - 1)(\beta_2 - 1)}. \tag{3.9}$$

Easy computations show that under this condition the plane

$$H_4 = -x + \alpha_3 x + \beta_2 x - \alpha_3\beta_2 x + y - \alpha_1 y - \alpha_3 y + \alpha_1\alpha_3 y + z - \beta_1 z - \beta_2 z + \beta_1\beta_2 z \tag{3.10}$$

is an invariant plane of (3.1) with the corresponding cofactor

$$K_4(x, y, z) = 1 - x - y - z.$$

If $\beta_1 = 1$ then condition (3.6) takes the form

$$(-1 + \alpha_1)(-1 + \alpha_2)(-1 + \alpha_3) = 0.$$

Computations show that if $\alpha_1 = 1$ then only planes (2.3) pass through the origin.

If $\beta_1 = \alpha_2 = 1$ then the system has the invariant plane

$$H_4(x, y, z) = -x + \beta_2 x + y - \alpha_1 y$$

provided that $\beta_2 \neq 1$, but this is a subcase of case 1) of the theorem.

If $\beta_1 = \alpha_3 = 1$ and $(-1+\alpha_1)(-1+\beta_3) \neq 0$ then (1.4) admits the invariant plane

$$H_4(x,y,z) = -x(1-\beta_2)(1-\beta_3) + y(1-\alpha_1)(1-\beta_3) - z(1-\alpha_1)(1-\alpha_2)$$

If $\beta_1 = \alpha_3 = \beta_3 = 1$ then only planes (2.3) pass through the origin.

In a similar way using (3.6) we find that if condition 6) holds, then the system has invariant plane

$$H_4(x,y,z) = -x(1-\alpha_2)(1-\alpha_3) - y(1-\beta_1)(1-\beta_3) + z(1-\alpha_2)(1-\beta_1).$$

■

It is easy to check that condition (3.6) is just the expanded form of condition (1.9).

Theorem 2. *System* (1.4) *has an invariant plane not passing through the origin if one of the following conditions holds:*

1) $\alpha_2 + \beta_3 - 2 = \beta_1 + \alpha_3 - 2 = \alpha_1 + \beta_2 - 2 = 0$,

2)$\beta_3 = \beta_1 + \alpha_3 - 2 = \alpha_1 = 0$,

3) $\alpha_2 = \beta_1 = \alpha_1 + \beta_2 - 2 = 0$,

4) $\beta_1 = \alpha_1 = 0$,

5) $\alpha_3 = \beta_2 = \alpha_2 + \beta_3 - 2 = 0$,

6) $\beta_2 = \alpha_2 = 0$,

7) $\beta_3 = \alpha_3 = 0$.

Proof. To find invariant planes of the form (3.1) not passing through the origin we set in (3.1) $h_0 = 1$. To find planes (3.1) with $h_{100} \neq 0$ we add to the ideal J the polynomial $1 - wh_{100}$ obtaining the ideal $I = \langle J, 1 - wh_{100}\rangle$. Computing the 8-th eliminating ideal of I we obtain the ideal

$$\begin{aligned} I_8 = \langle &\beta_1^2 + \beta_1\alpha_3 - 2\beta_1, \alpha_1^2 + \alpha_1\beta_2 - 2\alpha_1, \beta_1\alpha_2\beta_3 + \beta_1\beta_3^2 - 2\beta_1\beta_3, \\ &\alpha_1\beta_1\beta_3 + \beta_1\beta_2\beta_3 - 2\beta_1\beta_3, \alpha_1\alpha_2\alpha_3 + \beta_1\beta_2\beta_3 + 2\alpha_1\beta_1 - 2\alpha_1\alpha_2 - 2\beta_1\beta_3, \\ &\alpha_1\alpha_2^2 + \alpha_1\alpha_2\beta_3 - 2\alpha_1\alpha_2, \alpha_1\beta_1\alpha_2 - \beta_1\beta_2\beta_3 - 2\alpha_1\beta_1 + 2\beta_1\beta_3\rangle \end{aligned}$$

To find the set of common zeros of the polynomials of the ideal I_8, that is, the variety $\mathbf{V}(I_8)$, we use the routine `minAssGTZ` of the computer algebra SINGULAR which computes minimal associate primes of a polynomial ideal using the algorithm of [9]. Computing with `minAssGTZ` we find that

$$\sqrt{I_8} = P_1 \cap P_2 \cap P_3 \cap P_4,$$

where the prime ideals P_i are:

$$P_1 = \langle \alpha_2 + \beta_3 - 2, \beta_1 + \alpha_3 - 2, \alpha_1 + \beta_2 - 2 \rangle,$$

$$P_2 = \langle \beta_3, \beta_1 + \alpha_3 - 2, \alpha_1 \rangle, \quad P_3 = \langle \alpha_2, \beta_1, \alpha_1 + \beta_2 - 2 \rangle, \quad P_4 = \langle \beta_1, \alpha_1 \rangle.$$

That means, that $\mathbf{V}(I_8)$ consists of 4 components defined by conditions 1)–4) of the proposition.

Similarly we find conditions 5)–7), which correspond to H with $h_{010} \neq 0$ and $h_{010} \neq 0$.

Computing we find that invariant plane corresponding to systems (1.4) with condition 1) fulfilled is $H_4(x, y, z) = 1 - x - y - z$.

If condition 2) or 9) holds then the system has the invariant plane $H_4(x, y, z) = 1 - x - z$, if condition 3) or 5) is satisfied then the plane is $H_4(x, y, z) = 1 - x - y$, and in the cases of conditions 6) and 8) the equation of the plane is $H_4(x, y, z) = 1 - y - z$.

Finally, the planes corresponding to cases 4), 7) and 10) are $H_4(x, y, z) = 1 - x$, $H_4(x, y, z) = 1 - y$ and $H_4(x, y, z) = 1 - z$, respectively.

■

The approach for finding invariant surfaces presented above relies on the Elimination Theorem. Another possible approach utilized e.g. in [24] is based on making use of resultants for the elimination of variables. Comparing these two approaches it is easy to see that our approach is simpler and more efficient, since most of computations are performed algorithmically using powerful routines of computational algebra (eliminate and `minAssGTZ`).

Theorem 3. *System* (1.4) *admits a Darboux first integral if condition 4) of Theorem 1 holds.*

Proof. If condition 4) of Theorem 1 is fulfilled the system is written in the form (1.4) with β_3 given by (3.9). The cofactors of the Darboux functions (2.3) are

$$K_1(x, y, z) = 1 - x - \alpha_1 y - \beta_1 z, \quad K_2(x, y, z) = 1 - \beta_2 x - y - \alpha_2 z$$

and

$$K_3(x,y,z) = 1 - \alpha_3 x - y - z - \frac{y(1-\alpha_1)(1-\alpha_2)(1-\alpha_3)}{(-1+\beta_1)(-1+\beta_2)},$$

respectively. The system also has the invariant plane (3.10) with the cofactor

$$K_4(x,y,z) = 1 - x - y - z.$$

Equating in the equation

$$\alpha_1 K_1 + \alpha_2 K_2 + \alpha_3 K_3 + \alpha_4 K_4 = 0$$

the coefficients of similar monomials we find that

$$\alpha_2 = -\frac{\alpha_1(-1+\beta_1)}{\alpha_2 - 1}, \quad \alpha_3 = \frac{\alpha_1(-1+\beta_1)(-1+\beta_2)}{(-1+\alpha_2)(-1+\alpha_3)},$$

$$\alpha_4 = -\frac{\alpha_1(1-\alpha_2+\alpha_2\alpha_3-\alpha_3\beta_1-\beta_2+\beta_1\beta_2)}{(-1+\alpha_2)(-1+\alpha_3)}.$$

Thus, for any α_1 different from zero

$$\Psi = H_1^{\alpha_1} H_2^{\alpha_2} H_3^{\alpha_3} H_4^{\alpha_4} \tag{3.11}$$

is a first integral of the system. ■

4 Families of periodic solutions

We first recall the center manifold theorem, which we will use to prove the existence of a family of periodic solutions in system (1.4). Consider a $n+m$-dimensional system of ordinary differential equations of the form

$$\begin{aligned} \dot{x} &= A'x + u(x,y) \\ \dot{y} &= A''y + v(x,y), \end{aligned} \tag{4.1}$$

where $x \in \mathbb{R}^m$, $y \in \mathbb{R}^n$, Re $\sigma(A') = 0$, Re $\sigma(A'') \neq 0$, $\sigma(A')$ and $\sigma(A'')$ are spectra of A' and A'', respectively, and u, v are C^k-functions, $k \geq 1$ which vanish together with their first derivatives at the origin. By definition a C^k-manifold $W^c \equiv W^c(0,U)$ in a neighborhood U of 0 is said to be a *center manifold* of (4.1) if W^c is invariant under the flow as long as the solution remains in U and W^c is the graph of a C^k function $y = h(x)$ which is tangent at $(0,0) \in \mathbb{R}^m \times \mathbb{R}^n$ to the x-space.

The following fundamental theorem (see e.g. [4] for the proof) shows that for system (4.1) always there is a center manifold in a neighborhood of the origin.

Theorem 4. *There exists a neighborhood U of $0 \in \mathbb{R}^m \times \mathbb{R}^n$ such that there exists a local center manifold W^c of (4.1) which is the graph of a C^k-function $y = h(x)$.*

We now look for periodic solutions in system (1.4). By Theorem 3 if condition 4) of Theorem 1 holds, then system (1.4) has a first integral (3.11). The only singular point of the system, which can be located in the domain

$$x > 0, y > 0, z > 0 \tag{4.2}$$

is the point $P(x_0, y_0, z_0)$ with the coordinates

$$\begin{aligned}
x_0 =&((-1+\alpha_1)(-1+\alpha_2))/(1+(-1+\alpha_1)\alpha_2+\beta_1(-1+\beta_2)-\alpha_1\beta_2)\\
y_0 =&((-1+\beta_1)(-1+\beta_2))/(1+(-1+\alpha_1)\alpha_2+\beta_1(-1+\beta_2)-\alpha_1\beta_2)\\
z_0 =&(-1+\alpha_1+\beta_2-\alpha_1\beta_2)/(1+(-1+\alpha_1)\alpha_2+\beta_1(-1+\beta_2)-\alpha_1\beta_2)
\end{aligned}$$

The eigenvalues of the matrix of the linear approximation at P are

$$\lambda_1 = -1\,; \tag{4.3}$$

$$\lambda_{2,3} = \pm\frac{(-1+\alpha_1)\sqrt{-1+\alpha_2}\sqrt{-1+\beta_2}\sqrt{1+\alpha_2(-1+\alpha_3)-\alpha_3\beta_1-\beta_2+\beta_1\beta_2)}}{1+(-1+\alpha_1)\alpha_2+\beta_1(-1+\beta_2)-\alpha_1\beta_2} \tag{4.4}$$

An oscillatory behavior in a neighborhood of P is possible if λ_2 and λ_3 are complex conjugate, and it is obvious from (4.3)–(4.4) that in this case λ_2 and λ_3 are pure imaginary. To find systems with such λ_2 and λ_3 and P located in the domain (4.2) we have to find solutions to the following semialgebraic systems:

$$x_0, y_0, z_0 > 0,\ \beta_2, \alpha_2 > 1,\ \alpha_3, \beta_1, \alpha_1, \beta_3 > 0,\ 1+\alpha_2(-1+\alpha_3)-\alpha_3\beta_1-\beta_2+\beta_1\beta_2 < 0, \tag{4.5}$$

$$\begin{array}{ccc}
x_0 > 0, & y_0 > 0, & z_0 > 0,\\
0 < \alpha_1, & 0 < \alpha_2 < 1, & 0 < \alpha_3,\\
0 < \beta_1, & 0 < \beta_2 < 1, & 0 < \beta_3,
\end{array} \tag{4.6}$$
$$1+\alpha_2(-1+\alpha_3)-\alpha_3\beta_1-\beta_2+\beta_1\beta_2 < 0,$$

$$\begin{array}{ccc}
x_0 > 0, & y_0 > 0, & z_0 > 0,\\
0 < \alpha_1, & 0 < \alpha_2 < 1, & 0 < \alpha_3,\\
0 < \beta_1, & \beta_2 > 1, & 0 < \beta_3,
\end{array} \tag{4.7}$$
$$1+\alpha_2(-1+\alpha_3)-\alpha_3\beta_1-\beta_2+\beta_1\beta_2 > 0,$$

$$
\begin{aligned}
&x_0 > 0, && y_0 > 0, && z_0 > 0,\\
&0 < \alpha_1 && 1 < \alpha_2, && 0 < \alpha_3,\\
&0 < \beta_1, && 0 < \beta_2 < 1, && 0 < \beta_3,\\
&1 + \alpha_2(-1 + \alpha_3) - \alpha_3\beta_1 - \beta_2 + \beta_1\beta_2 > 0,
\end{aligned}
\tag{4.8}
$$

Nowadays there are few algorithms and computer algebra routines to solve semialgebraic systems. We use the routine `Reduce` of the computer algebra system MATHEMATICA. Calculations yield that systems (4.5) and (4.6) do not have solutions, the solution to system (4.7) is

$$
\begin{gathered}
(\alpha_2 > 0 \wedge \alpha_3 > 0 \wedge \alpha_3 < A \wedge \beta_2 > 1 \wedge \\
\left((\alpha_1 > 0 \wedge \beta_1 > 1 \wedge \alpha_1 < 1 \wedge \alpha_2 < 1) \vee \left(\alpha_1 > 1 \wedge \beta_2 < \frac{1}{1-\beta_1} \wedge \alpha_2 + \beta_2 < \beta_1\beta_2 + 1\right)\right) \\
\vee (\alpha_1 > 1 \wedge \beta_1 > 0 \wedge \alpha_2 < 1 \wedge -B + \alpha_3 < 0 \wedge \\
\frac{\alpha_1 + \beta_1 - 1}{\alpha_1} < \alpha_2 \wedge A < \alpha_3 \wedge \left(\beta_2 > 1 \vee \frac{1}{\beta_1 - 1} + \beta_2 \geq 0\right)\Big)
\end{gathered}
\tag{4.9}
$$

and the solution to (4.8) is

$$
\begin{gathered}
0 < \beta_2 < 1 \wedge ((\beta_1 > 1 \wedge 0 < \alpha_1 < 1 \wedge ((0 < \alpha_3 < A \wedge 1 < \alpha_2 < (\beta_1 - 1)\beta_2 + 1) \vee \\
\left(\alpha_2 > \frac{\alpha_1 + \beta_1 - 1}{\alpha_1} \wedge A < \alpha_3 < B\right)\Big)\Big) \vee \\
(\alpha_1 > 1 \wedge \alpha_2 > 1 \wedge 0 < \beta_1 < 1 \wedge A < \alpha_3 < B)
\end{gathered}
\tag{4.10}
$$

with

$$
A = \frac{\alpha_2 - \beta_1\beta_2 + \beta_2 - 1}{\alpha_2 - \beta_1}, B = -\frac{\alpha_1(-\alpha_2) + \alpha_1 + \alpha_2 - \beta_1\beta_2 + \beta_1 + \beta_2 - 2}{(\alpha_1 - 1)(\alpha_2 - 1)}.
$$

We conjecture that when parameters of system (1.4) satisfy condition (4.9) or condition (4.10) the system has a family of periodic solutions. To prove this claim it is sufficient to show that in some local coordinates (X, Y, Z) in which the system of the linear approximation near the singular point A is written as

$$
\dot{X} = -X, \ \dot{Y} = \omega Z, \ \dot{Z} = -\omega Y
$$

(where ω is a real number), the first integral (3.11) has the form

$$\Psi = Y^2 + Z^2 + h.o.t. \tag{4.11}$$

Since conditions (4.9) and (4.10) are rather cumbersome it is difficult to verify these for all systems satisfying these condition, but we verify the claim for a system satisfying (4.9) with the parameters $\beta_1 = 1/4,\ \beta_2 = 11/10,\ \alpha_1 = 5/4,\ \alpha_2 = 4/5,\ \alpha_3 = 3/2, \beta_3 = 2/3$.

In this case system (1.4) takes the form

$$\dot{x} = x\left(-x - \frac{5y}{4} - \frac{z}{4} + 1\right), \dot{y} = y\left(-\frac{11x}{10} - y - \frac{4z}{5} + 1\right), \dot{z} = z\left(-\frac{3x}{2} - \frac{2y}{3} - z + 1\right). \tag{4.12}$$

and the singular point P has the coordinates

$$x_0 = 1/3,\ y_0 = 1/2,\ z_0 = 1/6.$$

Proposition 1. *System* (4.12) *has a family of periodic solutions in a neighborhood of the singular point* $P(1/3, 1/2, 1/6)$.

Proof. Moving the origin to the singular point by the substitution

$$u = x - x_0,\ v = y - y_0,\ w = z - z_0$$

and then performing the linear change of coordinates

$$u = 2X + 370Y/249,\ v = 3X - Y - 15\sqrt{10}Z/83,\ w = X + 1/249(-235Y + 77\sqrt{10}Z)$$

we obtain from (4.12) the system

$$\begin{aligned}
\dot{X} =& -6X^2 - X + \frac{10450Y^2}{268671} + \frac{38048\sqrt{10}YZ}{806013} - \frac{10450Z^2}{268671},\\
\dot{Y} =& -6XY + \sqrt{\frac{2}{5}}XZ - \frac{2090Y^2}{39923} + \frac{16979\sqrt{\frac{2}{5}}YZ}{39923} + \frac{2090Z^2}{39923} + \frac{Z}{3\sqrt{10}},\\
\dot{Z} =& -\sqrt{\frac{2}{5}}XY - 6XZ + \frac{19187\sqrt{10}Y^2}{119769} + \frac{7730YZ}{119769} - \frac{Y}{3\sqrt{10}} - \frac{19187\sqrt{10}Z^2}{119769}.
\end{aligned} \tag{4.13}$$

By Theorem 4 system (4.12) has an analytic center manifold $X = h(X, Y)$ passing through the origin $X = Y = Z = 0$. On the other hand expanding the first integral (3.11) into power series near $X = Y = Z = 0$ we see that it has the form

$$\Psi(X, Y, Z) = X^2 + Y^2 + h.o.t.$$

Thus, in a neighborhood of the origin system (4.12) has a family of closed (periodic) orbits formed by the intersection of the graphs of the function $X = h(Y, Z)$ and the family of two dimensional surfaces $\Psi = c$ $(0 < c < c_0)$. Thus, system (4.12) has a family of periodic solutions in a neighborhood of P. ■

In the following figure we plot few trajectories of system (4.12).

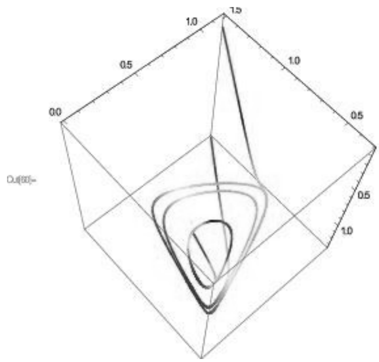

Figure 1: Trajectories of system (4.12) near P

The behavior of trajectories of system (4.12) near A (equivalently, of system (4.13) near the origin) can be also studied using the theory of normal form. In fact, it is the so-called case of "one pair of pure imaginary" eigenvalues, studied for the first type by Lyapunov [21] who showed that for an analytic system (4.1) with

$$A = \text{diag}(i\omega, -i\omega) \text{ and } B = \text{diag}(\kappa_3, \ldots, \kappa_n) \ (Re\, \kappa_i < 0 \text{ for } i = 3, \ldots, n) \qquad (4.14)$$

there are only two possibility:

(a) the case is "algebraic", in which case the origin is asymptotically stable or unstable and the question about stability is decided by a finite number of terms of the normal form;

(b) the case is "transcendental", in which case the origin is stable, but not asymptotically, the system (4.1) has a first integral of the form $\Phi = x_1^2 + x_2^2 + h.o.t.$ and a family of periodic solutions near the origin, and to determine this case from the normal form one has to compute the series for all orders.

Note that the center manifold of analytic system is not necessary analytic. The analyticity of the center manifold of system (4.1) under the assumption (4.14) was proved by Bibikov [2].

The following theorem shows that when condition 1) of Theorem 2 is satisfied we can not only prove the existence of the family of periodic solutions, but also determine its location.

Theorem 5. *When* $1 < \beta_1, \beta_2, \beta_3 < 2$ *and* $\alpha_2 + \beta_3 - 2 = \beta_1 + \alpha_3 - 2 = \alpha_1 + \beta_2 - 2 = 0$ *system* (1.4) *has a family of periodic solutions on the invariant plane*

$$H = 1 - x - y - z.$$

In the coordinates

$$u = 1 - x - y - z, \; v = y, \; w = z \tag{4.15}$$

the family is located on the invariant plane $u = 0$ *withing the triangle formed by the lines*

$$v = 0, \; w = 0, \; 1 - v - w = 0.$$

Proof. After substitution (4.15) we obtain from (1.4) the system

$$\begin{aligned} \dot{u} &= -\, u(1-u), \\ \dot{v} &= \;\; v(1 - \beta_2 + \beta_2 u - v + \beta_2 v - 2w + \beta_2 w + \beta_3 w) \\ \dot{w} &= -\, w(1 - \beta_1 - 2u + \beta_1 u - 2v + \beta_1 v + \beta_3 v - w + \beta_1 w) \end{aligned}$$

On the invariant plane $u = 0$ the system has the form

$$\begin{aligned} \dot{v} &= \;\; v(1 - \beta_2 - v + \beta_2 v - 2w + \beta_2 w + \beta_3 w) = V(v, w) \\ \dot{w} &= -\, w(1 - \beta_1 - 2v + \beta_1 v + \beta_3 v - w + \beta_1 w) = W(v, w). \end{aligned} \tag{4.16}$$

Obviously, it admits two invariant lines $l_1 = v, \; l_2 = w$ with cofactors $k_1 = V(v, w)/v$ and $k_2 = W(v, w)/w$, respectively, and additional search shows that there is one more invariant line $l_3 = 1 - v - w$ with the cofactor $k_3 = -v + \beta_2 v + w - \beta_1 w$ which allow to construct the Darboux first integral

$$\Psi = v^{-1+\beta_1}(1 - v - w)^{-1+\beta_3} w^{-1+\beta_2}.$$

By the Lyapunov theorem [2] the system has the infinite family of periodic solutions, surrounding the singular point P inside the triangle bounded by l_1, l_2 and l_3 and the trajectories from a neighborhood of the triangle fast tend to the periodic solutions. ■

5 Discussion and outlook

We have determined all systems with invariant planes of the May–Leonard model and have proved the existence of periodic solutions for some of these cases including a case, when condition (1.8) is not fulfilled. Note that conditions in our theorems relate the reaction rate coefficients. If they are required to be zero then it means that the corresponding reaction step does not occur.

One possible direction of further research might be to prove or disprove the existence of periodic solutions for sets of parameters satisfying conditions (4.9) and (4.10). As we have proven under these conditions the system has a first integral. If in local coordinates near the point P the integral has the form (4.11), then, similarly as above, by the Lyapunov theorem the system has a family of periodic solutions near the singular point P. However if the integral is of a form different from (4.11) then a further study would be necessary to determine if the system has periodic solutions.

Another interesting direction of the research is to determine subfamilies of (1.4) with quadratic invariant surfaces and look for first integrals of such subfamilies.

It appears it would be very hard to generalize our results for higher than three dimensional generalized Lotka–Volterra models. Similarly, the explicit polynomial form of the right hand sides was also of use, the Kolmogorov case would probably lead to much less explicit results.

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