

NON-ALGEBRAIC OSCILLATIONS FOR PREDATOR-PREY MODELS

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Abstract: We prove that the limit cycle oscillations of the celebrated Rosenzweig–MacArthur differential system and other predator-prey models are non-algebraic.

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1. Introduction and statement of the main results

It is easy to see that the periodic orbits of the celebrated Lotka–Volterra model

$$\dot{x} = \frac{dx}{dt} = x(\alpha - \beta y), \quad \dot{y} = \frac{dy}{dt} = y(-\delta + \gamma x),$$

where $x, y \geq 0$ and all the parameters are positive, are non-algebraic curves. This holds because it is an integrable system, and their solutions are contained into the level sets

$$H(x, y) = x^\gamma y^\alpha e^{-\delta x - \beta y} = h \geq 0,$$

which are clearly non-algebraic. The aim of this work is to prove that the attracting periodic orbits (limit cycles) of the Rosenzweig–MacArthur system, as well as the periodic orbits of other non-integrable predator-prey models, are neither given by algebraic curves. This shows that the limit oscillatory behavior of these models has transcendental nature. Let us introduce with more detail the systems that we will consider.

To study the predator-prey interaction when the prey exhibits group defense, Freedman and Wolkowicz [9], Mischaikow and Wolkowicz [17], and Wolkowicz [22] proposed the following model (see also [16]):

$$(1) \quad \dot{x} = X(x, y) = xg(x, K) - yp(x), \quad \dot{y} = Y(x, y) = y(-D + q(x)).$$

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Here, x and y are functions of time representing population densities of prey and predator, respectively, and are assumed to be non-negative; $K > 0$ is the carrying capacity of the prey and $D > 0$ is the death rate of the predator. The function $g(x, K)$ represents the specific growth rate of the prey in the absence of predator and is assumed to satisfy certain conditions. A prototype is the logistic growth

$$(2) \quad g(x, K) = r \left(1 - \frac{x}{K}\right),$$

with $r > 0$, which satisfies all those conditions. The function $p(x)$ denotes the predator response function and is assumed to satisfy $p(0) = 0$ and $p(x) > 0$ for $x > 0$. The rate of conversion of prey to predator is described by $q(x)$. In Gause's model, we have

$$(3) \quad \frac{q(x)}{p(x)} = \gamma \in \mathbb{R}^+.$$

The Rosenzweig–MacArthur differential system (see [19])

$$(4) \quad \begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{mxy}{a+x}, \\ \dot{y} &= y \left(-D + \gamma \frac{mx}{a+x}\right), \end{aligned}$$

where all the parameters are positive, is of type (1) with g as in (2) and p and q as in (3). The same happens with the three models that we introduce next. The first one is due to Ruan and Xiao, see [20]. It considers $p(x) = x/(a+x^2)$, a simplified Monod–Haldane or Holling type IV function; see [21]. The system can be written as

$$(5) \quad \begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{xy}{a+x^2}, \\ \dot{y} &= y \left(-D + \gamma \frac{x}{a+x^2}\right), \end{aligned}$$

where all the parameters are again positive.

The second additional family appears in [23]. In that paper the authors consider again a Holling type IV functional response, associated with a Monod–Haldane function (see [3]) $p(x) = mx/(ax^2 + bx + 1)$, where $a, m > 0$ and $b > -2\sqrt{a}$ (so that $ax^2 + bx + 1 > 0$ for all $x \geq 0$).

The model writes as

$$(6) \quad \begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{mxy}{ax^2 + bx + 1}, \\ \dot{y} &= y \left(-D + \gamma \frac{mx}{ax^2 + bx + 1}\right), \end{aligned}$$

where all the remainder parameters are also positive. The function $p(x)$ models the situation where the prey can better defend or disguise themselves when their population becomes large enough, a phenomenon called group defense. See [9, 20] for more information.

The third additional family that we consider appears in [14]. The model is described by the following differential system:

$$(7) \quad \begin{aligned} \dot{x} &= x \left(r \left(1 - \frac{x}{K}\right) (x + M) - \frac{my}{a + x} \right), \\ \dot{y} &= y \left(-D + \gamma \frac{mx}{a + x} \right), \end{aligned}$$

with all the parameters except M positive and $M \geq 0$. Here instead of considering $g(x, K)$ given by the logistic function, the authors take $g(x, K) = r(x - 1/K)(x + M)$. The existence of this parameter $M \geq 0$ introduces the so-called weak Allee effect, which is an important and interesting phenomenon for ecologists, because this effect increases the risk of population extinction, see [6, 7]. The case $M = 0$ implies the collapse of two singularities. If $M > 0$, then the equation represents a compensatory growth function, see [5, 15].

Let Γ be an orbit of any of the above systems. If Γ is contained in the zero set of a polynomial in two variables $F \in \mathbb{R}[x, y]$, that is $\Gamma \subset \{(x, y) \in \mathbb{R}^2 : F(x, y) = 0\}$, then it is said that $F(x, y) = 0$ is an invariant algebraic curve and by abuse of language that Γ is an invariant algebraic solution. When Γ is a limit cycle we will say that Γ is an algebraic limit cycle of the system.

It is well-known that for some values of the parameters the limiting behaviour of the orbits of all these predator-prey systems is a limit cycle. For instance, for the Rosenzweig–MacArthur system it is proved that system (4) has an attracting periodic orbit if and only if $\delta(a + K) + \gamma m(a - K) < 0$, see [2]. Our main result is the following theorem.

Theorem 1. *The only invariant algebraic curves of the Rosenzweig–MacArthur system (4) and of the predator-prey models (5), (6) and (7) are the axes $x = 0$ and $y = 0$. In particular, the limit cycles of all these models are non-algebraic.*

Notice that the above result is quite natural. In fact nobody expected that the limit oscillation appearing in realistic predator-prey models was given in an algebraic closed form and precisely this is what we have been able to prove in this paper. Despite during these last years there has been an increasing interest in knowing whether the limit cycles of some remarkable planar systems are algebraic or not, see for instance [10, 18], almost no attention has been paid to ecological models. The only result that we know in this direction is the proof, given in the recent paper [2], that the limit cycles of a family of predator-prey systems of the form (1), but not satisfying (2), are non-algebraic.

Theorem 1 is a straightforward consequence of a similar result for the family of polynomial differential systems of degree 4

$$(8) \quad \begin{aligned} \dot{x} &= X(x, y) = x(a_0 + a_1y + a_2y^2), \\ \dot{y} &= Y(x, y) = y(x + b_0 + b_1y + b_2y^2 + b_3y^3). \end{aligned}$$

Theorem 2. *If $a_0 \neq 0$ and $b_0/a_0 \notin \mathbb{Q}^+$ then the only invariant algebraic curves of system (8) are the coordinate axes $x = 0$ and $y = 0$. In particular its limit cycles are non-algebraic.*

Our proof of Theorem 2 is based on the fact that for system (8) the axis $y = 0$ is an invariant set. Then a systematic study writing all the involved functions $G(x, y)$ as $G(x, y) = \sum_{j \geq 0} g_j(x)y^j$ turns to be very useful, see Subection 2.1. An extension of this idea, when an analytic curve $y = \alpha(x)$ is invariant under the flow of the system, already appears in [12]. Other methods for studying the existence of invariant algebraic curves are given in [8, 11, 13].

Remark 1. The hypotheses $a_0 \neq 0$ and $b_0/a_0 \notin \mathbb{Q}^+$ are essential for proving the nonexistence of invariant algebraic curves different from the axes. See the two examples in Section 2.

Remark 2. Most predator-prey systems have a saddle at the origin, because no solution with positive initial conditions tends to the extinction equilibrium. Theorem 2 includes this case, because the saddle condition reads for system (8) as $a_0b_0 < 0$.

We end this introduction by giving a simple family of quadratic systems, extracted from [4], that has for some values of the parameters an algebraic limit cycle. The system

$$(9) \quad \begin{aligned} \dot{x} &= 2 + 4x - 4ax^2 + 12xy, \\ \dot{y} &= b - 14ax - 2axy - 8y^2, \end{aligned}$$

for $0 < a < 1/4$ and $b = 8 - 3a$, has an algebraic limit cycle contained in the quartic curve

$$1 + 4x - 4x^2 + 4ax^3 + 4xy + 4x^2y^2 = 0.$$

Although system (9) does not come from a predator-prey model it shows that the question of knowing whether a polynomial system has or has not algebraic periodic orbits can be quite delicate.

2. Preliminary results

Let us see that our four differential systems can be treated simultaneously.

Lemma 3. *There exist linear changes of coordinates and corresponding scalings of the time, globally defined for systems (5) and (6) and well defined on $a + x \neq 0$ for systems (4) and (7), such that the corresponding differential systems are transformed into subcases of the polynomial system (8) with $a_0b_0 < 0$.*

Proof: The proof follows easily after changing time, swapping the variables and scaling. For instance for the Rosenzweig–MacArthur system, taking

$$\bar{x} = y, \quad \bar{y} = x, \quad \frac{ds}{dt} = \frac{1}{a+x},$$

system (4) becomes system (8) with $a_0 = -aD < 0$ and $b_0 = ar > 0$. \square

In case that the planar differential system $(\dot{x}, \dot{y}) = (X, Y)$ is polynomial, the fact that the system has an invariant algebraic curve can be detected algebraically. Let X and Y be coprime polynomials of maximum degree $d \in \mathbb{N}$. Then an irreducible algebraic curve $f(x, y) = 0$ of degree $m \in \mathbb{N}$ is invariant under the flow of this system if there exists a polynomial $k(x, y)$ of degree at most $d - 1$, called the *cofactor*, such that

$$(10) \quad X \frac{\partial f}{\partial x} + Y \frac{\partial f}{\partial y} = kf.$$

Remark 3. Notice that if a rational planar differential system $(\dot{x}, \dot{y}) = (X_1/Z, Y_1/Z)$, with $X_1, Y_1, Z \in \mathbb{R}[x, y]$ has an invariant algebraic curve, then the same holds for the polynomial planar planar differential system $(\dot{x}, \dot{y}) = (X_1, Y_1)$.

Next lemma will play a key role in the proof of our results.

Lemma 4. For $x \geq 0$, consider the function

$$(11) \quad G(x) = Cx^{n-B}e^x \Gamma(B, x) + De^x x^{n-B},$$

where

$$\Gamma(B, x) = \int_x^\infty e^{-t} t^{B-1} dt$$

is the gamma function, $n \in \mathbb{N}$ and $B, C, D > 0$. Then G is a polynomial if and only if $D = 0$ and either $C = 0$ or $B \in \{1, \dots, n\}$.

Proof: We know (see [1, formula 6.5.32]) the following asymptotic expansion at $x = \infty$:

$$e^x \Gamma(B, x) \sim x^{B-1} \sum_{i \geq 0} \frac{\prod_{j=1}^i (B-j)}{x^i}.$$

Hence at infinity

$$G(x) \sim Cx^{n-1} \sum_{i \geq 0} \frac{\prod_{j=1}^i (B-j)}{x^i} + De^x x^{n-B}.$$

Therefore, for G to be a polynomial, we must take $D = 0$ in order to cancel the exponential term. Now if $C = 0$ we are finished. If $C \neq 0$ then $G(x)$ is a series in x . We have to take $B \in \mathbb{N}$ to make it finite. Moreover as there is a factor x^{B-1} in the denominator after doing the sum and a factor x^{n-1} in the numerator, we must take $B \leq n$. Then the lemma follows. \square

Theorem 2 assumes that $a_0 \neq 0$ and that $b_0/a_0 \notin \mathbb{Q}^+$. Next two examples show that these two hypotheses are unavoidable for proving Theorem 2.

Example 1. The curve $x - \phi(y) = 0$ is invariant under the flow of the differential system $\dot{x} = kxy\phi'(y)$, $\dot{y} = xy + (k-1)y\phi(y)$, with $k \in \mathbb{R}$. If $\phi(y)$ is a polynomial of degree at most 2 then this system is of the form (8) with $a_0 = 0$. \square

Example 2. The curve $x - \phi(y) = 0$, with $\phi(0) = 0$, is invariant under the flow of the differential system $\dot{x} = kx\phi'(y)$, $\dot{y} = xy + (k-y)\phi(y)$, with $k \in \mathbb{R}$. If $\phi(y)$ is a polynomial of degree at most 3 such that $\phi'(0) \neq 0$, then this system is of the form (8) with $b_0/a_0 = 1 \in \mathbb{Q}^+$. \square

2.1. A method for proving the non-existence of invariant algebraic curves. Let $f = 0$ be an invariant algebraic curve of the polynomial differential system $(\dot{x}, \dot{y}) = (X, Y)$ and assume that $y = 0$ is another invariant algebraic curve, i.e. $y|Y$. Set $d = \max\{\deg P, \deg Q\} \in \mathbb{N}$. Let k be the cofactor of f and suppose that $y \nmid f$. Since $y = 0$ is invariant under the flow of system (1), it is natural to write

$$X(x, y) = \sum_{i=0}^d X_i(x)y^i, \quad Y(x, y) = \sum_{i=0}^d Y_i(x)y^i, \quad k(x, y) = \sum_{i=0}^{d-1} k_i(x)y^i$$

and $f(x, y) = \sum_{i=0}^m f_i(x)y^i$, with X_i, Y_i, k_i and f_i polynomials of degree at most $d-i, d-i, d-1-i$ and $m-i$, respectively. Then equation (10) can be written as

$$\sum_{j=0}^{m+d-1} \left(\sum_{i=0}^j [X_{j-i}(x)f'_i(x) + (iY_{j-i+1}(x) - k_{j-i}(x))f_i(x)] \right) y^j = 0.$$

From the above relation the functions $f_j(x)$ can be obtained recurrently by solving the corresponding linear differential equation in $f_j(x)$ obtained vanishing the coefficient in y^j ; that is, solving, for each j , the equation

$$(12) \quad \sum_{i=0}^j [X_{j-i}(x)f'_i(x) + (iY_{j-i+1}(x) - k_{j-i}(x))f_i(x)] = 0.$$

The method consists in forcing these f_j to be polynomial. Then several successive conditions on the coefficients of k, X and Y appear during the process. As we already mentioned, this method was extended in [12] to systems having an invariant analytic curve $y = \alpha(x)$.

3. Proof of Theorems 1 and 2

It is clear that Theorem 1 is a straightforward consequence of Remark 3, Lemma 3 and Theorem 2. So we will proceed with the proof of Theorem 2.

Since $a_0 \neq 0$, by scaling the variable x and the time if necessary, we can assume without loss of generality that $a_0 = -1$. Then $b_0/a_0 \notin \mathbb{Q}^+$ writes as $b_0 \notin \mathbb{Q}^-$.

Let $k = \sum_{i+j=0}^3 k_{i,j}x^i y^j$ be the cofactor of an invariant algebraic curve $f = 0$ of degree $m \in \mathbb{N}$ of system (8). According to Subsection 2.1, we write

$$X(x, y) = \sum_{i=0}^4 X_i(x)y^i, \quad Y(x, y) = \sum_{i=0}^4 Y_i(x)y^i, \quad k(x, y) = \sum_{i=0}^3 k_i(x)y^i,$$

with

$$X_0 = -x, \quad X_1 = a_1x, \quad X_2 = a_2x, \quad X_3 = X_4 = 0;$$

$$Y_0 = 0, \quad Y_1 = b_0 + x, \quad Y_2 = b_1, \quad Y_3 = b_2, \quad Y_4 = b_3;$$

$$k_0 = k_{0,0} + k_{1,0}x + k_{2,0}x^2 + k_{3,0}x^3, \quad k_1 = k_{0,1} + k_{1,1}x + k_{2,1}x^2,$$

$$k_2 = k_{0,2} + k_{1,2}x, \quad k_3 = k_{0,3};$$

and $f = \sum_{i=0}^m f_i(x)y^i$. Equation (12) with $j = 0$ is

$$(k_{0,0} + k_{1,0}x + k_{2,0}x^2 + k_{3,0}x^3)f_0(x) + xf_0'(x) = 0.$$

Since $y \nmid f$, $f_0 \neq 0$. Imposing that f_0 has to be a polynomial and checking the degrees of all the summands of the above equation we must take $k_{1,0} = k_{2,0} = k_{3,0} = 0$. Solving the differential equation we get

$$|f_0(x)| = |x|^{-k_{0,0}},$$

where we have fixed the integration constant to 1. From now on we will only study the region $x \geq 0$. Then we have $f_0(x) = x^{-k_{0,0}}$. As $f_0(x)$ is to be a polynomial, we must take $-k_{0,0} = n \in \mathbb{N} \cup \{0\}$. Therefore $f_0(x) = x^n$.

Equation (12) with $j = 1$ is

$$x^n(a_1n - k_{0,1} - k_{1,1}x - k_{2,1}x^2) + (b_0 + n + x)f_1(x) - xf_1'(x) = 0.$$

We write their solutions as $f_1(x) = x^n \bar{f}_1(x)$. Then we have

$$a_1n - k_{0,1} - k_{1,1}x - k_{2,1}x^2 + (b_0 + x)\bar{f}_1(x) - x\bar{f}_1'(x) = 0.$$

Applying the method of variation of the constants we write $\bar{f}_1(x) = W(x)e^x x^{b_0}$, where $W(x)$ is a solution of

$$a_1n - k_{0,1} - k_{1,1}x - k_{2,1}x^2 - e^x x^{b_0+1}W'(x) = 0.$$

Then

$$W(x) = \int e^{-x} x^{-b_0-1} (a_1n - k_{0,1} - k_{1,1}x - k_{2,1}x^2) dx.$$

We note that this integral can be separated into a sum of three integrals, all of which are gamma functions. The property

$$\Gamma(s, x) = (s-1)\Gamma(s-1, x) + x^{s-1}e^{-x}$$

of the gamma function allows to write $W(x)$ as

$$\begin{aligned} W(x) = & \Gamma(-b_0, x)(-a_1n + k_{0,1} - b_0k_{1,1} + b_0(b_0 - 1)k_{2,1}) \\ & + e^{-x} x^{-b_0}(k_{1,1} + k_{2,1} - b_0k_{2,1} + k_{2,1}x) + C_1, \end{aligned}$$

where C_1 is a constant. Therefore

$$\begin{aligned} f_1(x) &= W(x)e^x x^{b_0+n} \\ &= e^x x^{b_0+n} \Gamma(-b_0, x) (-a_1 n + k_{0,1} - cb_0 k_{1,1} + b_0(b_0 - 1)k_{2,1}) \\ &\quad + x^n (k_{1,1} + k_{2,1} - b_0 k_{2,1} + k_{2,1} x) + C_1 e^x x^{b_0+n}. \end{aligned}$$

Since $-b_0 \notin \mathbb{N}$, from Lemma 4 we have $C_1 = 0$ and $-a_1 n + k_{0,1} - b_0 k_{1,1} + b_0(b_0 - 1)k_{2,1} = 0$. Thus we can obtain an expression for $k_{0,1}$.

From equation (12) with $j = 2$ we proceed in a similar way and we have

$$\begin{aligned} f_2(x) &= \left[a_2 n - k_{0,2} + b_1 k_{1,1} + b_0 k_{1,2} - (-b_1 + a_1 b_0 + 2b_0 b_1) k_{2,1} \right] \\ &\quad \times x^n (2x)^{2b_0} e^{2x} \Gamma(-2b_0, 2x) + e^{2x} x^{n+2b_0} C_2 + \bar{f}_2(x) x^n, \end{aligned}$$

where C_2 is a constant and $\bar{f}_2(x)$ is a polynomial of degree 2. Since $-2b_0 \notin \mathbb{N}$, by Lemma 4 we must take $C_2 = 0$ and $k_{0,2} = a_2 n + b_1 k_{1,1} + b_0 k_{1,2} - (-b_1 + a_1 b_0 + 2b_0 b_1) k_{2,1}$ to get a polynomial.

From equation (12) with $j = 3$ we get

$$\begin{aligned} f_3(x) &= \left[k_{0,3} - b_2 k_{1,1} - b_1 k_{1,2} + (a_2 b_0 + a_1 b_1 + b_1^2 - b_2 + 2b_0 b_2) k_{2,1} \right] \\ &\quad \times x^n (3x)^{3b_0} e^{3x} \Gamma(-3b_0, 3x) + e^{3x} x^{n+3b_0} C_3 + \bar{f}_3(x) x^n, \end{aligned}$$

where C_3 is a constant and $\bar{f}_3(x)$ is a polynomial of degree 3. As $-3b_0 \notin \mathbb{N}$, again from Lemma 4 we must take $C_3 = 0$ and

$$(13) \quad k_{0,3} - b_2 k_{1,1} - b_1 k_{1,2} + (a_2 b_0 + a_1 b_1 + b_1^2 - b_2 + 2b_0 b_2) k_{2,1} = 0$$

to get a polynomial.

We distinguish two cases depending on b_3 . If $b_3 = 0$ then the cofactor k of $f = 0$ is $n(-1 + a_1 y + a_2 y^2)$, which is n times the cofactor of $x = 0$. This happens because since $b_3 = 0$ the degree of system (8) is 3 and therefore the monomials of degree 3 in k must vanish. Hence the equality (13) reads as $b_2 k_{1,1} = 0$. If $b_2 = 0$ then equation (12) for $j > 3$ writes as

$$(14) \quad -\frac{k_{1,1}^j (b_0 + x)}{(j-1)!} x^n + (j b_0 + n + j x) f_j(x) - x f_j'(x) = 0.$$

This equation has the solution

$$f_j(x) = C_j e^{jx} x^{n+jb_0} + \frac{k_{1,1}^j}{j!} x^n,$$

where C_j is a constant that must be taken as zero. Hence $f_j(x) = k_{1,1}^j x^n / j!$ for $j > 3$. Therefore we have $f(x, y) = x^n e^{k_{1,1}y}$, which means that $k_{1,1} = 0$ and hence that f is a power of x . Therefore the only invariant algebraic curve of system (8) different from $y = 0$ is $x = 0$ and the theorem follows in the case $b_2 = b_3 = 0$. In the other case, which is $b_3 = 0$ and $b_2 \neq 0$, then $k_{1,1} = 0$ and thus equation (12) for $j > 3$ writes as

$$(jb_0 + n + jx)f_j(x) - xf_j'(x) = 0,$$

which is equation (14) with $k_{1,1} = 0$. Hence $f_j(x) \equiv 0$ for $j > 3$. Then we have again that $f(x, y) = x^n$. Therefore the only invariant algebraic curve of system (8) different from $y = 0$ is $x = 0$ and the theorem follows also in this case.

From now on we assume that $b_3 \neq 0$. Hence from (13) we can obtain an expression for $k_{0,3}$. We proceed for $j > 3$ in a similar way as above: on each step the function $\Gamma(-jb_0, jx)$ appears in the expression of $f_j(x)$. As $-jb_0 \notin \mathbb{N}$ because $-b_0 \notin \mathbb{Q}^+$, by Lemma 4 the integration constant of f_j must be taken as zero and the coefficient of $\Gamma(-jb_0, jx)$ must vanish. Hence we have a condition for each case. The conditions for $j = 4$ and $j = 5$ are, respectively,

$$k_{1,1} = -\frac{b_2}{b_3}k_{1,2} + \frac{a_2b_1 + a_1b_2 + 2b_1b_2 - b_3 + 2b_0b_3}{b_3}k_{2,1}$$

and

$$k_{1,2} = \frac{a_2b_2 + b_2^2 + a_1b_3 + 2b_1b_3}{b_3}k_{2,1}.$$

For $j = 6$ the condition reads $(a_2 + 2b_2)k_{2,1} = 0$. The case $a_2 + 2b_2 = 0$ for $j = 6$ leads to $k_{2,1} = 0$ for $j = 7$. We note that for $j > 6$ (for $j > 7$ in the case $a_2 + 2b_2 = 0$) equation (12) is

$$(jb_0 + n + jx)f_j(x) - xf_j'(x) = 0,$$

which has the only polynomial solution $f_j(x) \equiv 0$, as we showed above. We obtain $f(x, y) = x^n$ and $k = n(-1 + a_1y + a_2y^2)$. Then again the only invariant algebraic curve different from $y = 0$ is $x = 0$ and therefore the theorem follows also in the case $b_3 \neq 0$. \square

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