

PAPER • OPEN ACCESS

## Linear Darboux polynomials for Lotka–Volterra systems, trees and superintegrable families

To cite this article: G R W Quispel *et al* 2023 *J. Phys. A: Math. Theor.* **56** 315201

View the [article online](#) for updates and enhancements.

You may also like

- [Passivity of Lotka–Volterra and quasi-polynomial systems](#)  
Lrinc Márton, Katalin M Hangos and Attila Magyar
- [Morphisms and automorphisms of skew-symmetric Lotka–Volterra systems](#)  
C A Evripidou, P Kassotakis and P Vanhaecke
- [A multiple scales approach to maximal superintegrability](#)  
G Gubbiotti and D Latini

# Linear Darboux polynomials for Lotka–Volterra systems, trees and superintegrable families

G R W Quispel<sup>1</sup> , Benjamin K Tapley<sup>2</sup> , D I McLaren<sup>1</sup>   
and Peter H van der Kamp<sup>1,\*</sup> 

<sup>1</sup> Department of Mathematical and Physical Sciences, La Trobe University, Bundoora, Victoria 3086, Australia

<sup>2</sup> Department of Mathematics and Cybernetics, SINTEF Digital, 0373 Oslo, Norway

E-mail: [P.vanderKamp@LaTrobe.edu.au](mailto:P.vanderKamp@LaTrobe.edu.au)

Received 28 February 2023; revised 13 June 2023

Accepted for publication 22 June 2023

Published 14 July 2023



CrossMark

## Abstract

We present a method to construct superintegrable  $n$ -component Lotka–Volterra (LV) systems with  $3n - 2$  parameters. We apply the method to LV systems with  $n$  components for  $1 < n < 6$ , and present several  $n$ -dimensional superintegrable families. The LV systems are in one-to-one correspondence with trees on  $n$  vertices.

Keywords: Darboux polynomials, Lotka–Volterra systems, superintegrability, trees

## 1. Introduction

The original 2-dimensional Lotka–Volterra (LV) system,

$$\dot{x} = x(a - by), \quad \dot{y} = y(-c + dx), \quad (1)$$

where  $\dot{x}$  denotes the derivative with respect to time, was derived as a model to describe the interaction between predator and prey fish [10, 18, 25]. Sternberg [22, chapter 11] gives a dynamical systems perspective and an explanation why fishing decreases the number of predators. The 2-dimensional system (1) has been generalised to  $n$ -dimensional systems of the form

\* Author to whom any correspondence should be addressed.



Original Content from this work may be used under the terms of the [Creative Commons Attribution 4.0 licence](https://creativecommons.org/licenses/by/4.0/). Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.

$$\dot{x}_i = x_i \left( b_i + \sum_j A_{i,j} x_j \right), \tag{2}$$

where  $\mathbf{b}$  is a real vector, and  $\mathbf{A}$  is a real matrix, and these have been studied extensively. For references on various aspects of LV systems, including integrability as well as their history, see [1–4, 6–8, 10, 12, 14, 16, 17, 19]. Prolle and Singer wrote a very influential paper [20] proving that if a polynomial ODE has an elementary integral, then it has a logarithmic integral. Note that in the mathematical physics literature the matrix  $\mathbf{A}$  is often assumed to be skew symmetric. This is not assumed here.

A vector field on an  $n$ -dimensional manifold is called superintegrable if it admits  $n - 1$  functionally independent constants of motion (i.e. first integrals), see [24]. In this paper we construct superintegrable  $n$ -component LV systems with  $3n - 2$  parameters.

Darboux polynomials (DPs) are building blocks of rational integrals and their generalisations [11, 13]. Given an ordinary differential equation (ODE)

$$\frac{d\mathbf{x}}{dt} = \mathbf{f}(\mathbf{x}),$$

where  $\mathbf{x}(t)$  and  $\mathbf{f}$  are  $n$ -dimensional vectors, a DP  $P(\mathbf{x})$  is defined by the existence of a polynomial  $C(\mathbf{x})$  s.t.

$$\frac{dP(\mathbf{x})}{dt} = C(\mathbf{x})P(\mathbf{x}). \tag{3}$$

Note that (3) implies that if  $P(\mathbf{x}(0)) = 0$ , then  $P(\mathbf{x}(t)) = 0, \forall t$ . For this reason DPs are also called second integrals.

In section 2, we provide a method to obtain  $m$  integrals for an  $n$ -dimensional homogeneous quadratic ODE, from  $m + n$  DPs. In section 3, we give conditions on  $\mathbf{b}$  and  $\mathbf{A}$  which are equivalent to

$$P_{i,k} = \alpha x_i + \beta x_k$$

being a DP for (2). In section 4, we look at the intersection of the above two classes, i.e. at homogeneous LV systems, and use the described method and mentioned DPs to construct some superintegrable systems in dimensions 2, 3, and 4. In section 5, we explain how these superintegrable  $n$ -dimensional LV systems are in one-to-one correspondence with trees on  $n$  vertices. Such a tree has  $n - 1$  edges, and each of these edges corresponds to an integral. If an edge exists between vertices  $i$  and  $k$ , the corresponding integral can be written as a product of  $P_{i,k}$  and powers of the variables  $x_j, j = 1 \dots n$ . In section 6, we cover the superintegrable LV-systems which relate to the three non-isomorphic trees on five vertices. We also describe the factorisation of the exponents of the variables in terms of minors of the matrix  $\mathbf{A}$ . In our final section we give some details for the superintegrable  $n$ -dimensional LV systems that relate to tall trees. In the appendix we explain how the Euler top relates to a special case of our superintegrable 3-dimensional LV system.

## 2. A rather general method

Let

$$\frac{dP_1}{dt} = C_1 P_1, \quad \frac{dP_2}{dt} = C_2 P_2$$

then

$$\frac{d}{dt}(P_1^{\alpha_1} P_2^{\alpha_2}) = (\alpha_1 C_1 + \alpha_2 C_2) P_1^{\alpha_1} P_2^{\alpha_2}.$$

Hence cofactors  $C_i$  form a linear space. Note that  $C_1 = C_2$  if and only if  $\frac{P_1}{P_2}$  is an integral. We also have

$$P_1^{\alpha_1} P_2^{\alpha_2} \text{ is a first integral} \Leftrightarrow \alpha_1 C_1 + \alpha_2 C_2 = 0, \tag{4}$$

and more generally

$$\prod_i P_i^{\alpha_i} \text{ is a first integral} \Leftrightarrow \sum_i \alpha_i C_i = 0. \tag{5}$$

It follows that integrals that arise in this way are factorisable.

If there are more functionally independent DPs than the dimension of this linear space, then there must be one or more integrals. The method we introduce here, produces  $m$  integrals for an  $n$ -dimensional homogeneous quadratic ODE, from  $n + m$  DPs.

- Find  $n$  independent DPs for the ODE:

$$\dot{P}_i(\mathbf{x}) = P_i(\mathbf{x}) C_i(\mathbf{x}). \tag{6}$$

The  $C_i$  will be linear. Defining  $\mathbf{v}$  to be the vector with components  $v_i := \ln(P_i)$ ,  $i = 1, \dots, n$ , the equation (6) can be written as

$$\dot{\mathbf{v}} = \mathbf{A}\mathbf{x} \tag{7}$$

where  $\mathbf{A}$  is some constant invertible matrix.

- Find  $m$  additional DPs for the ODE ( $m \leq n - 1$  is a necessary condition for the integrals to be independent). Defining  $\mathbf{w}$  to be the vector with components  $w_i := \ln(P_i)$ ,  $i = n + 1, \dots, n + m$ , we get

$$\dot{\mathbf{w}} = \mathbf{B}\mathbf{x}. \tag{8}$$

Eliminating  $\mathbf{x}$ , we again get

$$\dot{\mathbf{w}} - \mathbf{B}\mathbf{A}^{-1}\dot{\mathbf{v}} = 0 \rightarrow \mathbf{w} - \mathbf{B}\mathbf{A}^{-1}\mathbf{v} = \mathbf{I}. \tag{9}$$

For  $n$ -component LV systems,  $n$  DPs are given by the components of the vector  $\mathbf{x}$ , and we set  $\mathbf{v} = \mathbf{x}$ . From (9), by exponentiation of the logarithmic integrals  $\mathbf{I}$ , we obtain  $m$  integrals of the form

$$P_{n+i}^{|\mathbf{A}|} \prod_{j=1}^n x_j^{Z_{i,j}}, \quad i = 1, \dots, m,$$

where

$$\mathbf{Z} := -\mathbf{B}\mathbf{A}^{-1}|\mathbf{A}| \tag{10}$$

and  $|\mathbf{A}|$  is the determinant of  $\mathbf{A}$ .

### 3. Additional DPs for LV systems

The complement of  $\{i, k\}$  is denoted  $\{i, k\}^c := \{1, 2, \dots, n\} \setminus \{i, k\}$ .

**Lemma 1.** Consider a system with

$$\dot{x}_i = x_i \left( b_i + \sum_{j=1}^n A_{i,j} x_j \right), \quad \dot{x}_k = x_k \left( b_k + \sum_{j=1}^n A_{k,j} x_j \right). \tag{11}$$

The expression, with  $\alpha\beta \neq 0$ ,

$$P_{i,k} = \alpha x_i + \beta x_k, \tag{12}$$

is a DP if and only if, for some constant  $b$  and all  $j \in \{i, k\}^c$ ,

$$A_{i,j} = A_{k,j} \tag{13}$$

$$b_i = b_k = b \tag{14}$$

$$\alpha(A_{k,k} - A_{i,k}) = \beta(A_{k,i} - A_{i,i}) \tag{15}$$

and  $(A_{k,k} - A_{i,k})(A_{k,i} - A_{i,i}) \neq 0$ .

**Proof.** We first show that the conditions (13)–(15) are sufficient, i.e. if they are satisfied, then  $P_{i,k}$  defined by (12) is a DP for the ODE defined by (11). Equation (12) implies with (11) that

$$\begin{aligned} \alpha \dot{x}_i + \beta \dot{x}_k &= \alpha x_i \left( b_i + \sum_{j=1}^n A_{i,j} x_j \right) + \beta x_k \left( b_k + \sum_{j=1}^n A_{k,j} x_j \right) \\ &= \alpha x_i (b_i + A_{i,i} x_i + A_{i,k} x_k + \Sigma') + \beta x_k (b_k + A_{k,i} x_i + A_{k,k} x_k + \Sigma') \\ &= (\alpha x_i + \beta x_k) b + \alpha A_{i,i} x_i^2 + (\alpha A_{i,k} + \beta A_{k,i}) x_i x_k + \beta A_{k,k} x_k^2 + (\alpha x_i + \beta x_k) \Sigma' \\ &\quad \text{using (14)} \\ &= (\alpha x_i + \beta x_k) (b + A_{i,i} x_i + A_{k,k} x_k + \Sigma') \text{ using (15),} \end{aligned}$$

and where (using (13))

$$\Sigma' := \sum_{j \in \{i,k\}^c} A_{i,j} x_j = \sum_{j \in \{i,k\}^c} A_{k,j} x_j. \tag{16}$$

Next we show the conditions are necessary, i.e. if  $P_{i,k}$  defined by (12) is a DP for the ODE defined by (11) then (13)–(15) hold. Equation (12) implies with (11) that

$$\alpha \dot{x}_i + \beta \dot{x}_k = \alpha x_i \left( b_i + \sum_{j=1}^n A_{i,j} x_j \right) + \beta x_k \left( b_k + \sum_{j=1}^n A_{k,j} x_j \right). \tag{17}$$

First consider all terms that contain  $x_j$  on the r.h.s., where  $j \in \{i, k\}^c$ :

$$\alpha x_i A_{i,j} x_j + \beta x_k A_{k,j} x_j. \tag{18}$$

This must vanish if we substitute

$$x_k = -\frac{\alpha}{\beta} x_i. \tag{19}$$

We find  $\alpha(A_{i,j} - A_{k,j})x_i x_j = 0$  and hence

$$A_{i,j} = A_{k,j} \tag{20}$$

for all  $j \in \{i, k\}^c$ .

Now consider all remaining terms that do not contain any  $x_j$ , with  $j \in \{i, k\}^c$ , i.e.

$$\alpha x_i (b_i + A_{i,i}x_i + A_{i,k}x_k) + \beta x_k (b_k + A_{k,i}x_i + A_{k,k}x_k). \tag{21}$$

Once again (21) must vanish if we substitute (19). Hence

$$x_i(b_i - b_k) + x_i^2 \left[ A_{i,i} - \left( \frac{\alpha}{\beta} A_{i,k} + A_{k,i} \right) + \frac{\alpha}{\beta} A_{k,k} \right] = 0,$$

which implies that

$$b_i = b_k = b, \text{ say,}$$

and

$$\frac{\alpha}{\beta} = \frac{A_{i,i} - A_{k,i}}{A_{i,k} - A_{k,k}}.$$

□

Of course several low-dimensional instances of lemma 1 have appeared in papers by various authors over the years, cf e.g. a 2D instance in equation (3.2) of [15], a 3D instance in proposition 1#(3) of [5], and a 4D instance in equation (12) of [10].

#### 4. Superintegrable $n$ -component LV systems, $n = 2, 3, 4$

##### 4.1. $n = 2$

The system

$$\begin{cases} \dot{x}_1 = x_1 (a_1 x_1 + b_1 x_2) \\ \dot{x}_2 = x_2 (c_1 x_1 + a_2 x_2) \end{cases} \tag{22}$$

admits the DPs  $x_1, x_2$ , with cofactors  $a_1 x_1 + b_1 x_2, a_2 x_2 + c_1 x_1$ , and the DP  $(c_1 - a_1)x_1 + (a_2 - b_1)x_2$ , with cofactor  $a_1 x_1 + a_2 x_2$ . They give rise to matrices

$$\mathbf{A} = \begin{pmatrix} a_1 & b_1 \\ c_1 & a_2 \end{pmatrix} \text{ and } \mathbf{B} = (a_1 \quad a_2), \tag{23}$$

and hence to the integral

$$I = ((c_1 - a_1)x_1 + (a_2 - b_1)x_2)^{a_1 a_2 - b_1 c_1} x_1^{-a_2(a_1 - c_1)} x_2^{-a_1(a_2 - b_1)}.$$

##### 4.2. $n = 3$

The system

$$\begin{cases} \dot{x}_1 = x_1 (a_1 x_1 + b_1 x_2 + b_2 x_3) \\ \dot{x}_2 = x_2 (a_2 x_2 + b_2 x_3 + c_1 x_1) \\ \dot{x}_3 = x_3 (a_3 x_3 + c_1 x_1 + c_2 x_2) \end{cases} \tag{24}$$

relates to matrix

$$\mathbf{A} = \begin{pmatrix} a_1 & b_1 & b_2 \\ c_1 & a_2 & b_2 \\ c_1 & c_2 & a_3 \end{pmatrix}. \tag{25}$$

The following are two additional DPs:

$$P_{1,2} = (c_1 - a_1)x_1 + (a_2 - b_1)x_2, \quad P_{2,3} = (c_2 - a_2)x_2 + (a_3 - b_2)x_3,$$

with cofactors

$$C_{1,2} = a_1x_1 + a_2x_2 + b_2x_3, \quad C_{2,3} = c_1x_1 + a_2x_2 + a_3x_3.$$

Thus we have

$$\mathbf{B} = \begin{pmatrix} a_1 & a_2 & b_2 \\ c_1 & a_2 & a_3 \end{pmatrix}$$

and we find  $2 = n - 1$  integrals

$$I_1 = ((c_1 - a_1)x_1 + (a_2 - b_1)x_2)^{|A|} x_1^{-(a_2a_3 - b_2c_2)(a_1 - c_1)} x_2^{-(a_2 - b_1)(a_1a_3 - b_2c_1)} x_3^{b_2(a_2 - b_1)(a_1 - c_1)},$$

$$I_2 = ((c_2 - a_2)x_2 + (a_3 - b_2)x_3)^{|A|} x_1^{c_1(a_3 - b_2)(a_2 - c_2)} x_2^{-(a_2 - c_2)(a_1a_3 - b_2c_1)} x_3^{-(a_3 - b_2)(a_1a_2 - b_1c_1)}.$$

A special case of (24), where  $a_1 = -c_1$ ,  $c_2 = -a_2 = b_1$  and  $a_3 = -b_2$ , is linearly equivalent to the Euler top, which has an extra integral, cf [appendix](#).

### 4.3. $n = 4$

#### 4.3.1

The matrix

$$\mathbf{A} = \begin{pmatrix} a_1 & b_1 & b_2 & b_3 \\ c_1 & a_2 & b_2 & b_3 \\ c_1 & c_2 & a_3 & b_3 \\ c_1 & c_2 & c_3 & a_4 \end{pmatrix} \tag{26}$$

has the property that  $A_{i,j} = A_{i+1,j}$  for all  $i \in \{1, 2, 3\}$  and  $j \in \{i, i + 1\}^c$ . The associated LV system is

$$\begin{cases} \dot{x}_1 = x_1(a_1x_1 + b_1x_2 + b_2x_3 + b_3x_4) \\ \dot{x}_2 = x_2(c_1x_1 + a_2x_2 + b_2x_3 + b_3x_4) \\ \dot{x}_3 = x_3(c_1x_1 + c_2x_2 + a_3x_3 + b_3x_4) \\ \dot{x}_4 = x_4(c_1x_1 + c_2x_2 + c_3x_3 + a_4x_4) \end{cases}. \tag{27}$$

The system (27) has seven DPs. The obvious ones are  $P_i = x_i$ ,  $i = 1, 2, 3, 4$ , with cofactors  $C_i = \sum_{j=1}^n A_{i,j}x_j$ . The other three, obtained from lemma 1, are:

$$P_{1,2} = (c_1 - a_1)x_1 + (a_2 - b_1)x_2,$$

$$P_{2,3} = (c_2 - a_2)x_2 + (a_3 - b_2)x_3,$$

$$P_{3,4} = (c_3 - a_3)x_3 + (a_4 - b_3)x_4,$$

with cofactors

$$C_{1,2} = a_1x_1 + a_2x_2 + b_2x_3 + b_3x_4,$$

$$C_{2,3} = c_1x_1 + a_2x_2 + a_3x_3 + b_3x_4,$$

$$C_{3,4} = c_1x_1 + c_2x_2 + a_3x_3 + a_4x_4.$$

The coefficient matrix from these cofactors is

$$\mathbf{B} = \begin{pmatrix} a_1 & a_2 & b_2 & b_3 \\ c_1 & a_2 & a_3 & b_3 \\ c_1 & c_2 & a_3 & a_4 \end{pmatrix}.$$

The rather general method, introduced in section 2, gives rise to the following  $3 = n - 1$  functionally independent integrals:

$$I_i = P_{i,i+1}^{|\mathbf{A}|} x_1^{Z_{i,1}} x_2^{Z_{i,2}} x_3^{Z_{i,3}} x_4^{Z_{i,4}}, \quad i = 1, 2, 3,$$

where  $I_1$  is determined by

$$\begin{aligned} Z_{1,1} &= -(a_2 a_3 a_4 - a_2 b_3 c_3 - a_3 b_3 c_2 - a_4 b_2 c_2 + b_2 b_3 c_2 + b_3 c_2 c_3) (a_1 - c_1), \\ Z_{1,2} &= -(a_2 - b_1) (a_1 a_3 a_4 - a_1 b_3 c_3 - a_3 b_3 c_1 - a_4 b_2 c_1 + b_2 b_3 c_1 + b_3 c_1 c_3), \\ Z_{1,3} &= (a_4 b_2 - b_3 c_3) (a_2 - b_1) (a_1 - c_1), \\ Z_{1,4} &= b_3 (a_3 - b_2) (a_2 - b_1) (a_1 - c_1), \end{aligned}$$

$I_2$  is determined by

$$\begin{aligned} Z_{2,1} &= c_1 (a_4 - b_3) (a_3 - b_2) (a_2 - c_2), \\ Z_{2,2} &= -(a_2 - c_2) (a_1 a_3 a_4 - a_1 b_3 c_3 - a_3 b_3 c_1 - a_4 b_2 c_1 + b_2 b_3 c_1 + b_3 c_1 c_3), \\ Z_{2,3} &= -(a_3 - b_2) (a_1 a_2 a_4 - a_1 b_3 c_2 - a_2 b_3 c_1 - a_4 b_1 c_1 + b_1 b_3 c_1 + b_3 c_1 c_2), \\ Z_{2,4} &= b_3 (a_3 - b_2) (a_2 - c_2) (a_1 - c_1), \end{aligned}$$

and  $I_3$  is determined by

$$\begin{aligned} Z_{3,1} &= c_1 (a_4 - b_3) (a_3 - c_3) (a_2 - c_2), \\ Z_{3,2} &= (a_4 - b_3) (a_3 - c_3) (c_2 a_1 - c_1 b_1), \\ Z_{3,3} &= -(a_3 - c_3) (a_1 a_2 a_4 - a_1 b_3 c_2 - a_2 b_3 c_1 - a_4 b_1 c_1 + b_1 b_3 c_1 + b_3 c_1 c_2), \\ Z_{3,4} &= -(a_4 - b_3) (a_1 a_2 a_3 - a_1 b_2 c_2 - a_2 b_2 c_1 - a_3 b_1 c_1 + b_1 b_2 c_1 + b_2 c_1 c_2). \end{aligned}$$

#### 4.3.2.

Next we consider the matrix

$$\mathbf{A} = \begin{pmatrix} a_1 & b_1 & b_2 & b_3 \\ c_1 & a_2 & b_2 & b_3 \\ c_1 & c_2 & a_3 & b_3 \\ c_1 & c_3 & b_2 & a_4 \end{pmatrix}.$$

It has the property that  $A_{i,j} = A_{k,j}$  for all  $(i, k) \in \{(1, 2), (2, 3), (2, 4)\}$  and  $j \in \{i, k\}^c$ . The corresponding LV system reads

$$\begin{cases} \dot{x}_1 = x_1 (a_1 x_1 + b_1 x_2 + b_2 x_3 + b_3 x_4) \\ \dot{x}_2 = x_2 (c_1 x_1 + a_2 x_2 + b_2 x_3 + b_3 x_4) \\ \dot{x}_3 = x_3 (c_1 x_1 + c_2 x_2 + a_3 x_3 + b_3 x_4) \\ \dot{x}_4 = x_4 (c_1 x_1 + c_3 x_2 + b_2 x_3 + a_4 x_4) \end{cases}. \quad (28)$$

The additional DPs are

$$\begin{aligned} P_{1,2} &= (c_1 - a_1) x_1 + (a_2 - b_1) x_2, \\ P_{2,3} &= (c_2 - a_2) x_2 + (a_3 - b_2) x_3, \\ P_{2,4} &= (c_3 - a_2) x_2 + (a_4 - b_3) x_4, \end{aligned}$$



with cofactors

$$\begin{aligned} C_{1,2} &= a_1x_1 + a_2x_2 + b_2x_3 + b_3x_4, \\ C_{2,3} &= c_1x_1 + a_2x_2 + a_3x_3 + b_3x_4, \\ C_{3,4} &= c_1x_1 + a_2x_2 + b_2x_3 + a_4x_4. \end{aligned}$$

The coefficient matrix from these cofactors is

$$\mathbf{B} = \begin{pmatrix} a_1 & a_2 & b_2 & b_3 \\ c_1 & a_2 & a_3 & b_3 \\ c_1 & a_2 & b_2 & a_4 \end{pmatrix}.$$

We label the special pairs of indices of rows of  $\mathbf{A}$  as follows,

$$e_1 = (1, 2), \quad e_2 = (2, 3), \quad e_3 = (2, 4). \tag{29}$$

The same label can be used to enumerate the functionally independent integrals,

$$I_i = P_{e_i}^{|\mathbf{A}|} x_1^{Z_{i,1}} x_2^{Z_{i,2}} x_3^{Z_{i,3}} x_4^{Z_{i,4}}, \quad i = 1, 2, 3,$$

where

$$\begin{aligned} Z_{1,1} &= -(a_2a_3a_4 - a_2b_2b_3 - a_3b_3c_3 - a_4b_2c_2 + b_2b_3c_2 + b_2b_3c_3)(a_1 - c_1) \\ Z_{1,2} &= -(a_2 - b_1)(a_1a_3a_4 - a_1b_2b_3 - a_3b_3c_1 - a_4b_2c_1 + 2b_2b_3c_1) \\ Z_{1,3} &= b_2(a_4 - b_3)(a_2 - b_1)(a_1 - c_1) \\ Z_{1,4} &= b_3(a_3 - b_2)(a_2 - b_1)(a_1 - c_1), \\ Z_{2,1} &= c_1(a_4 - b_3)(a_3 - b_2)(a_2 - c_2) \\ Z_{2,2} &= -(a_2 - c_2)(a_1a_3a_4 - a_1b_2b_3 - a_3b_3c_1 - a_4b_2c_1 + 2b_2b_3c_1) \\ Z_{2,3} &= -(a_3 - b_2)(a_1a_2a_4 - a_1b_3c_3 - a_2b_3c_1 - a_4b_1c_1 + b_1b_3c_1 + b_3c_1c_3) \\ Z_{2,4} &= b_3(a_3 - b_2)(a_2 - c_2)(a_1 - c_1), \end{aligned}$$

and

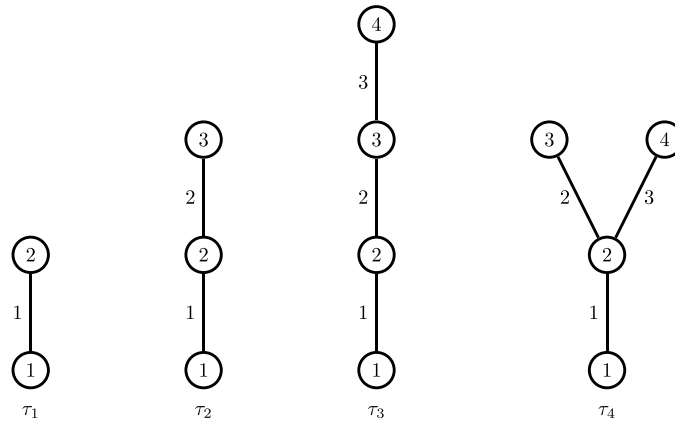
$$\begin{aligned} Z_{3,1} &= c_1(a_4 - b_3)(a_3 - b_2)(a_2 - c_3) \\ Z_{3,2} &= -(a_2 - c_3)(a_1a_3a_4 - a_1b_2b_3 - a_3b_3c_1 - a_4b_2c_1 + 2b_2b_3c_1) \\ Z_{3,3} &= b_2(a_4 - b_3)(a_2 - c_3)(a_1 - c_1) \\ Z_{3,4} &= -(a_4 - b_3)(a_1a_2a_3 - a_1b_2c_2 - a_2b_2c_1 - a_3b_1c_1 + b_1b_2c_1 + b_2c_1c_2). \end{aligned}$$

The special pairs of indices of rows of  $\mathbf{A}$  can be interpreted as edges of a tree, which we will do in the next section.

### 5. Connection to trees

To each of the above  $n$ -component LV systems we associate a free (unrooted) tree  $T$  on  $n$  vertices as follows. The tree has an edge between vertex  $i$  and vertex  $k$  if the condition that  $A_{i,j} = A_{k,j}$  for all  $j \in \{i, k\}^c$  is satisfied. Thus, the systems (23), (25), (26) and (28) relate to the trees depicted in figure 1.

Vice versa, a tree  $T$  on  $n$  (ordered) vertices has  $n - 1$  (ordered) edges. We associated to  $T$  a matrix  $\mathbf{A}$  as follows. We start with an  $n \times n$  diagonal matrix  $\mathbf{A}$ , with  $A_{i,i} = a_i$ . Then for each edge of  $T$  we fix two off-diagonal entries of  $\mathbf{A}$  as follows. For the  $m$ th edge of the graph  $T$ ,  $e_m = (i, k)$  with  $i < k$ , we set  $A_{i,k} = b_m$  and  $A_{k,i} = c_m$ . In [23] we show that the remaining



**Figure 1.** The trees connected to the LV systems (23), (25), (26) and (28) (from left to right).

entries of the matrix  $A$  are uniquely determined by the condition that  $A_{i,j} = A_{k,j}$  when  $(i, k)$  is an edge of  $T$  and  $j \in \{i, k\}^c$ . The matrix  $\mathbf{A}$  has  $3n - 2$  free parameters and defines a LV system

$$\dot{x}_i = x_i \sum_{j=1}^n A_{i,j} x_j, \quad i = 1, 2, \dots, n, \tag{30}$$

with  $n - 1$  integrals. In [23], we prove their functional independence, theorem 2.

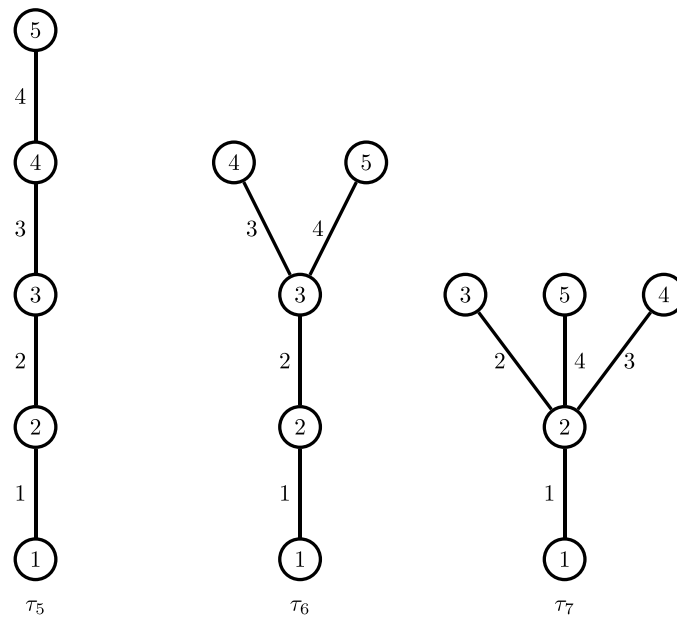
**Theorem 2.** *Each tree on  $n$  vertices gives rise to a LV system with  $3n - 2$  parameters, which admits  $n - 1$  functionally independent integrals.*

One can think of the parameters  $a_i, b_j, c_k$  as weights in a complete digraph  $D$  (allowing both loops and multiple edges) which is associated to  $T$ . The matrix  $A$  is then nothing but the adjacency matrix of  $D$ . The connection between LV systems and graphs, via the adjacency matrix of the graph, has been made before [2, 7, 9, 12], but in the context of undirected or directed graphs, and (mainly) anti-symmetric (and hence Hamiltonian) LV systems. The general setting of complete digraphs seems to be new. Note that the number of trees is given by the sequence [21, A000055].

### 6. Superintegrable five-component LV systems

There are three non-isomorphic trees on five vertices, see figure 2. Following the procedure in the previous subsection, the trees in figure 2 give rise to matrices  $(\mathbf{A})$

$$\begin{pmatrix} a_1 & b_1 & b_2 & b_3 & b_4 \\ c_1 & a_2 & b_2 & b_3 & b_4 \\ c_1 & c_2 & a_3 & b_3 & b_4 \\ c_1 & c_2 & c_3 & a_4 & b_4 \\ c_1 & c_2 & c_3 & c_4 & a_5 \end{pmatrix}, \begin{pmatrix} a_1 & b_1 & b_2 & b_3 & b_4 \\ c_1 & a_2 & b_2 & b_3 & b_4 \\ c_1 & c_2 & a_3 & b_3 & b_4 \\ c_1 & c_2 & c_3 & a_4 & b_4 \\ c_1 & c_2 & c_4 & b_3 & a_5 \end{pmatrix}, \begin{pmatrix} a_1 & b_1 & b_2 & b_3 & b_4 \\ c_1 & a_2 & b_2 & b_3 & b_4 \\ c_1 & c_2 & a_3 & b_3 & b_4 \\ c_1 & c_3 & b_2 & a_4 & b_4 \\ c_1 & c_4 & b_2 & b_3 & a_5 \end{pmatrix}, \tag{31}$$



**Figure 2.** These are the three non-isomorphic trees on five vertices.

and hence to LV systems, each with 13 free parameters,

$$\begin{cases} \dot{x}_1 = x_1 (a_1x_1 + b_1x_2 + b_2x_3 + b_3x_4 + b_4x_5) \\ \dot{x}_2 = x_2 (a_2x_2 + b_2x_3 + b_3x_4 + b_4x_5 + c_1x_1) \\ \dot{x}_3 = x_3 (a_3x_3 + b_3x_4 + b_4x_5 + c_1x_1 + c_2x_2) \\ \dot{x}_4 = x_4 (a_4x_4 + b_4x_5 + c_1x_1 + c_2x_2 + c_3x_3) \\ \dot{x}_5 = x_5 (a_5x_5 + c_1x_1 + c_2x_2 + c_3x_3 + c_4x_4), \end{cases} \tag{32}$$

$$\begin{cases} \dot{x}_1 = x_1 (a_1x_1 + b_1x_2 + b_2x_3 + b_3x_4 + b_4x_5) \\ \dot{x}_2 = x_2 (a_2x_2 + b_2x_3 + b_3x_4 + b_4x_5 + c_1x_1) \\ \dot{x}_3 = x_3 (a_3x_3 + b_3x_4 + b_4x_5 + c_1x_1 + c_2x_2) \\ \dot{x}_4 = x_4 (a_4x_4 + b_4x_5 + c_1x_1 + c_2x_2 + c_3x_3) \\ \dot{x}_5 = x_5 (a_5x_5 + b_3x_4 + c_1x_1 + c_2x_2 + c_4x_3) \end{cases} \tag{33}$$

and

$$\begin{cases} \dot{x}_1 = x_1 (a_1x_1 + b_1x_2 + b_2x_3 + b_3x_4 + b_4x_5) \\ \dot{x}_2 = x_2 (a_2x_2 + b_2x_3 + b_3x_4 + b_4x_5 + c_1x_1) \\ \dot{x}_3 = x_3 (a_3x_3 + b_3x_4 + b_4x_5 + c_1x_1 + c_2x_2) \\ \dot{x}_4 = x_4 (a_4x_4 + b_2x_3 + b_4x_5 + c_1x_1 + c_3x_2) \\ \dot{x}_5 = x_5 (a_5x_5 + b_2x_3 + b_3x_4 + c_1x_1 + c_4x_2). \end{cases} \tag{34}$$

Using the methods explained in sections 2 and 3, we can construct four functionally independent integrals for each of these systems. As in section 4, the exponents in the integrals exhibit interesting factorisation properties. Below we provide the integrals for systems (32), (33) and (34), expressing each exponent as a product of differences of parameters and a minor of **A**. We let  $\mathbf{A}^{I:J}$  denote the matrix **A** with rows  $i \in I$  and columns  $j \in J$  deleted. Its determinant  $|\mathbf{A}^{I:J}|$  is called a minor of **A**.

The LV system (32) admits the four functionally independent integrals

$$\begin{aligned}
 I_1 &= ((c_1 - a_1)x_1 + (a_2 - b_1)x_2) |A| x_1^{(c_1-a_1)} |A^{1;1}| x_2^{(b_1-a_2)} |A^{2;2}| x_3^{(a_2-b_1)(a_1-c_1)} |A^{2;3;1,2}| \\
 &\quad \times x_4^{(a_3-b_2)(a_2-b_1)(a_1-c_1)} |A^{2,3,4;1,2,3}| x_5^{(a_4-b_3)(a_3-b_2)(a_2-b_1)(a_1-c_1)b_4} \\
 I_2 &= ((c_2 - a_2)x_2 + (a_3 - b_2)x_3) |A| x_1^{(a_5-b_4)(a_4-b_3)(a_3-b_2)(a_2-c_2)c_1} x_2^{(c_2-a_2)} |A^{2;2}| x_3^{(b_2-a_3)} |A^{3;3}| \\
 &\quad \times x_4^{(a_3-b_2)(a_2-c_2)(a_1-c_1)} |A^{1,3,4;1,2,3}| x_5^{(a_4-b_3)(a_3-b_2)(a_2-c_2)(a_1-c_1)b_4} \\
 I_3 &= ((c_3 - a_3)x_3 + (a_4 - b_3)x_4) |A| x_1^{(a_5-b_4)(a_4-b_3)(a_3-c_3)(a_2-c_2)c_1} \\
 &\quad \times x_2^{(a_3-b_4)(a_4-b_3)(a_3-c_3)} |A^{2,4,5;3,4,5}| x_3^{(c_3-a_3)} |A^{3;3}| x_4^{(b_3-a_4)} |A^{4;4}| x_5^{(a_4-b_3)(a_3-c_3)(a_2-c_2)(a_1-c_1)b_4} \\
 I_4 &= ((c_4 - a_4)x_4 + (a_5 - b_4)x_5) |A| x_1^{(a_5-b_4)(a_4-c_4)(a_3-c_3)(a_2-c_2)c_1} \\
 &\quad \times x_2^{(a_3-b_4)(a_4-c_4)(a_3-c_3)} |A^{2,3,5;3,4,5}| x_3^{(a_5-b_4)(a_4-c_4)} |A^{3,5;4,5}| x_4^{(c_4-a_4)} |A^{4;4}| x_5^{(b_4-a_5)} |A^{5;5}|.
 \end{aligned}$$

The LV system (33) admits the four functionally independent integrals

$$\begin{aligned}
 I_1 &= ((c_1 - a_1)x_1 + (a_2 - b_1)x_2) |A| x_1^{(c_1-a_1)} |A^{1;1}| x_2^{(b_1-a_2)} |A^{2;2}| x_3^{(a_1-c_1)(a_2-b_1)} |A^{2;3;1,2}| \\
 &\quad \times x_4^{(a_1-c_1)(a_2-b_1)(a_3-b_2)(a_5-b_4)b_3} x_5^{(a_1-c_1)(a_2-b_1)(a_3-b_2)(a_4-b_3)b_4} \\
 I_2 &= ((c_2 - a_2)x_2 + (a_3 - b_2)x_3) |A| x_1^{(a_2-c_2)(a_3-b_2)(a_4-b_3)(a_5-b_4)c_1} x_2^{(c_2-a_2)} |A^{2;2}| x_3^{(b_2-a_3)} |A^{3;3}| \\
 &\quad \times x_4^{(a_1-c_1)(a_2-c_2)(a_3-b_2)(a_5-b_4)b_3} x_5^{(a_1-c_1)(a_2-c_2)(a_3-b_2)(a_4-b_3)b_4}, \\
 I_3 &= ((c_3 - a_3)x_3 + (a_4 - b_3)x_4) |A| x_1^{(a_2-c_2)(a_3-c_3)(a_4-b_3)(a_5-b_4)c_1} \\
 &\quad \times x_2^{(a_3-c_3)(a_4-b_3)(a_5-b_4)} |A^{2,4,5;3,4,5}| x_3^{(c_3-a_3)} |A^{3;3}| x_4^{(b_3-a_4)} |A^{4;4}| x_5^{(a_1-c_1)(a_2-c_2)(a_3-c_3)(a_4-b_3)b_4}, \\
 I_4 &= ((c_4 - a_3)x_3 + (a_5 - b_4)x_5) |A| x_1^{(a_2-c_2)(a_3-c_4)(a_4-b_3)(a_5-b_4)c_1} \\
 &\quad \times x_2^{(a_3-c_4)(a_4-b_3)(a_5-b_4)} |A^{2,4,5;3,4,5}| x_3^{(c_4-a_3)} |A^{3;3}| x_4^{(a_1-c_1)(a_2-c_2)(a_3-c_4)(a_5-b_4)b_3} x_5^{(b_4-a_5)} |A^{5;5}|.
 \end{aligned}$$

The LV system (34) admits the four functionally independent integrals

$$\begin{aligned}
 I_1 &= ((c_1 - a_1)x_1 + (a_2 - b_1)x_2) |A| x_1^{(c_1-a_1)} |A^{1;1}| x_2^{(b_1-a_2)} |A^{2;2}| x_3^{(a_1-c_1)(a_2-b_1)(a_4-b_3)(a_5-b_4)b_2} \\
 &\quad \times x_4^{(a_1-c_1)(a_2-b_1)(a_3-b_2)(a_5-b_4)b_3} x_5^{(a_1-c_1)(a_2-b_1)(a_3-b_2)(a_4-b_3)b_4}, \\
 I_2 &= ((c_2 - a_2)x_2 + (a_3 - b_2)x_3) |A| x_1^{(a_2-c_2)(a_3-b_2)(a_4-b_3)(a_5-b_4)c_1} x_2^{(c_2-a_2)} |A^{2;2}| x_3^{(b_2-a_3)} |A^{3;3}| \\
 &\quad \times x_4^{(a_1-c_1)(a_2-c_2)(a_3-b_2)(a_5-b_4)b_3} x_5^{(a_1-c_1)(a_2-c_2)(a_3-b_2)(a_4-b_3)b_4}, \\
 I_3 &= ((c_3 - a_2)x_2 + (a_4 - b_3)x_4) |A| x_1^{(a_2-c_3)(a_3-b_2)(a_4-b_3)(a_5-b_4)c_1} x_2^{(c_3-a_2)} |A^{2;2}| \\
 &\quad \times x_3^{(a_1-c_1)(a_2-c_3)(a_4-b_3)(a_5-b_4)b_2} x_4^{(b_3-a_4)} |A^{4;4}| x_5^{(a_1-c_1)(a_2-c_3)(a_3-b_2)(a_4-b_3)b_4}, \\
 I_4 &= ((c_4 - a_2)x_2 + (a_5 - b_4)x_5) |A| x_1^{(a_2-c_4)(a_3-b_2)(a_4-b_3)(a_5-b_4)c_1} x_2^{(c_4-a_2)} |A^{2;2}| \\
 &\quad \times x_3^{(a_1-c_1)(a_2-c_4)(a_4-b_3)(a_5-b_4)b_2} x_4^{(a_1-c_1)(a_2-c_4)(a_3-b_2)(a_5-b_4)b_3} x_5^{(b_4-a_5)} |A^{5;5}|.
 \end{aligned}$$

The factorisation for the general case will be described in more detail in [23].

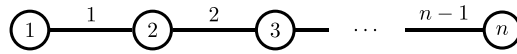


Figure 3. Tall tree on  $n$  vertices.

### 7. A hierarchy of superintegrable LV systems

Consider the tall tree on  $n$  vertices depicted in figure 3.

It gives rise to the  $n \times n$  matrix:

$$\mathbf{A} = \begin{pmatrix} a_1 & b_1 & b_2 & b_3 & \cdots & b_{n-1} \\ c_1 & a_2 & b_2 & b_3 & \cdots & b_{n-1} \\ c_1 & c_2 & a_3 & b_3 & \cdots & b_{n-1} \\ c_1 & c_2 & c_3 & a_4 & \cdots & b_{n-1} \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ c_1 & c_2 & c_3 & c_4 & \cdots & a_n \end{pmatrix}, \tag{35}$$

of which matrices (23), (25), (26), and the left matrix in (31), are special cases taking  $n = 2, 3, 4$  and 5 respectively.

For arbitrary  $n$ , the tall tree provides us with the LV system:

$$\begin{cases} \dot{x}_1 = x_1 (a_1 x_1 + b_1 x_2 + b_2 x_3 + \cdots + b_{n-1} x_n) \\ \dot{x}_2 = x_2 (c_1 x_1 + a_2 x_2 + b_2 x_3 + \cdots + b_{n-1} x_n) \\ \dot{x}_3 = x_3 (c_1 x_1 + c_2 x_2 + a_3 x_3 + \cdots + b_{n-1} x_n) \\ \vdots \\ \dot{x}_{n-1} = x_{n-1} (c_1 x_1 + c_2 x_2 + \cdots + a_{n-1} x_{n-1} + b_{n-1} x_n) \\ \dot{x}_n = x_n (c_1 x_1 + c_2 x_2 + \cdots + c_{n-1} x_{n-1} + a_n x_n), \end{cases} \tag{36}$$

The  $n$  coordinates  $x_i, i = 1, \dots, n$ , are DPs. The system (36) admits  $n - 1$  additional DPs of the form

$$P_{i,i+1} = (c_i - a_i)x_i + (a_{i+1} - b_i)x_{i+1}, \quad i = 1, \dots, n - 1,$$

with cofactors

$$C_{i,i+1} = c_1 x_1 + \cdots + c_{i-1} x_{i-1} + a_i x_i + a_{i+1} x_{i+1} + b_{i+1} x_{i+2} + \cdots + b_{n-1} x_n.$$

Their coefficients can be organised into the following  $(n - 1) \times n$  matrix:

$$\mathbf{B} = \begin{pmatrix} a_1 & a_2 & b_2 & b_3 & \cdots & b_{n-2} & b_{n-1} \\ c_1 & a_2 & a_3 & b_3 & \cdots & b_{n-2} & b_{n-1} \\ c_1 & c_2 & a_3 & a_4 & \cdots & b_{n-2} & b_{n-1} \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ c_1 & c_2 & c_3 & c_4 & \cdots & a_{n-1} & b_{n-1} \\ c_1 & c_2 & c_3 & c_4 & \cdots & a_{n-1} & a_n \end{pmatrix}. \tag{37}$$

Using the matrices  $\mathbf{A}$  and  $\mathbf{B}$ , and defining  $\mathbf{Z} = -\mathbf{B}\mathbf{A}^{-1}|\mathbf{A}|$ , we obtain  $n - 1$  integrals of the form

$$I_i = P_{i,i+1}^{|\mathbf{A}|} \prod_{j=1}^n x_j^{Z_{i,j}}, \quad i = 1, \dots, n - 1.$$

One can show, see [23], that the exponents factorise and that the integrals  $K_i$  are functionally independent (which implies superintegrability). Introducing the notation

$$\mathbb{N}_j^n = \{k \in \mathbb{N} : j \leq k \leq n\},$$

we find, for all  $i \in \mathbb{N}_1^{n-1}, j \in \mathbb{N}_1^n$ ,

$$Z_{i,j} = \begin{cases} (a_i - c_i) \prod_{j < k < i} (a_k - c_k) \prod_{i < k \leq n} (a_k - b_{k-1}) |\mathbf{A}^{\mathbb{N}_j^{i-1} \cap \mathbb{N}_{i+1}^n; \mathbb{N}_{j+1}^n}| & j < i, \\ (c_i - a_i) |\mathbf{A}^{i;i}| & j = i, \\ (b_i - a_{i+1}) |\mathbf{A}^{i+1;i+1}| & j = i + 1, \\ (a_i - c_i) \prod_{1 < k < i} (a_k - c_k) \prod_{i < k < j} (a_k - b_{k-1}) |\mathbf{A}^{\mathbb{N}_1^{i-1} \cap \mathbb{N}_{i+1}^j; \mathbb{N}_1^{j-1}}| & j > i + 1. \end{cases}$$

This formula provides a more efficient way to calculate the exponents in the integrals  $I_i$  than using the definition of  $\mathbf{Z}$ , which involves matrix multiplication, inversion and taking the determinant of an  $n \times n$  matrix.

The special case  $a_i = 0$  ( $i = 1, \dots, n$ ),  $b_i = -c_{i+1}$  ( $i = 1, \dots, n - 1$ ) was studied in [17].

### 8. Concluding remark

In this paper we have studied superintegrable LV systems without imposing any additional structure. We intend to investigate the role of measure-preservation and symplectic structure on LV equations in future work.

### Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

### Acknowledgments

G R W Q is grateful to Silvia Perez Cruz for alleviating the plague years and to Sydney Mathematical Research Institute (SMRI) for travel support.

### Appendix. The Euler top

The Euler top, in the form

$$\begin{cases} \dot{x}_1 = a^2 x_2 x_3 \\ \dot{x}_2 = b^2 x_1 x_3 \\ \dot{x}_3 = c^2 x_1 x_2, \end{cases} \tag{38}$$

admits the six DPs

$$cx_1 \pm ax_3, \quad cx_2 \pm bx_3, \quad bx_1 \pm ax_2.$$

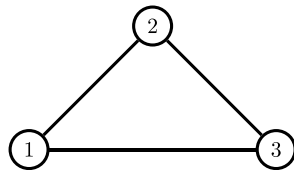


Figure 4. Complete graph on three vertices.

Hence, it is linearly equivalent to an LV system with three additional DPs. In terms of  $\mathbf{y} = (cx_1 + ax_3, cx_2 + bx_3, bx_1 + ax_2)/2$ , we have

$$\dot{y}_i = y_i \sum_{j=1}^n A_{ij} y_j, \quad i = 1, 2, 3, \quad \mathbf{A} = \begin{pmatrix} -b & a & c \\ b & -a & c \\ b & a & -c \end{pmatrix}, \quad (39)$$

which is a special case of (24). We note that the corresponding graph, see figure 4, is not a tree.

The additional DPs are  $ay_2 - cy_3$ ,  $by_1 - cy_3$ , and  $ay_2 - by_1$ , and three integrals (not functionally independent) are given by

$$y_1(ay_2 - cy_3), \quad y_3(by_1 - ay_2), \quad y_2(by_1 - cy_3).$$

It is now easy to generalise system (39) whilst keeping the same number of DPs (six). Indeed, we would take

$$\mathbf{A} = \begin{pmatrix} d & a & c \\ b & e & c \\ b & a & f \end{pmatrix}.$$

The corresponding LV system has additional DPs

$$P_1 = (a - e)y_2 + (f - c)y_3, \quad P_2 = (b - d)y_1 + (e - a)y_2, \quad P_3 = (b - d)y_1 + (f - c)y_3,$$

cofactor coefficient matrix

$$\mathbf{B} = \begin{pmatrix} b & e & f \\ d & e & c \\ d & a & f \end{pmatrix},$$

and three integrals


$$\begin{aligned} P_1 |^{\mathbf{A}} y_1^{b(c-f)(a-e)} y_2^{-(bc-df)(a-e)} y_3^{-(c-f)(ab-de)}, \\ P_2 |^{\mathbf{A}} y_1^{-(b-d)(ac-ef)} y_2^{-(bc-df)(a-e)} y_3^{c(b-d)(a-e)}, \\ P_3 |^{\mathbf{A}} y_1^{-(b-d)(ac-ef)} y_2^{a(c-f)(b-d)} y_3^{-(c-f)(ab-de)}, \end{aligned}$$

of which two are functionally independent.

### ORCID iDs

G R W Quispel  <https://orcid.org/0000-0002-6433-1576>

Benjamin K Tapley  <https://orcid.org/0000-0002-5488-760X>

D I McLaren  <https://orcid.org/0000-0003-2559-5066>

Peter H van der Kamp  <https://orcid.org/0000-0002-2963-3528>

## References

- [1] Ballesteros A, Blasco A and Musso F 2011 Integrable deformations of Lotka–Volterra systems *Phys. Lett. A* **375** 3370–4
- [2] Bogoyavlenskij O I 2008 Integrable Lotka–Volterra systems *Regul. Chaotic Dyn.* **13** 543–56
- [3] Bountis T and Vanhaecke P 2016 Lotka–Volterra systems satisfying a strong Painlevé property *Phys. Lett. A* **380** 3977–82
- [4] Bountis T, Zhunussova Z, Dosmagulova K and Kanellopoulos G 2021 Integrable and non-integrable Lotka–Volterra systems *Phys. Lett. A* **402** 127360
- [5] Cairo L 2000 Darboux first integral conditions and integrability of the 3D Lotka–Volterra system *J. Nonlinear Math. Phys.* **7** 511–31
- [6] Christodoulides Y T and Damianou P A 2009 Darboux polynomials for Lotka–Volterra systems in three dimensions *J. Nonlinear Math. Phys.* **16** 339–54
- [7] Damianou P A 2013 Lotka–Volterra systems associated with graphs *Group Analysis of Differential Equations and Integrable Systems* (Department of Mathematics and Statistics, University of Cyprus) pp 30–44
- [8] Damianou P A, Evripidou C A, Kassotakis P and Vanhaecke P 2017 Integrable reductions of the Bogoyavlenskij–Itoh Lotka–Volterra systems *J. Math. Phys.* **58** 17
- [9] Duarte P, Fernandes R L and Oliva W M 1998 Dynamics of the attractor in the Lotka–Volterra equations *J. Differ. Equ.* **149** 143–89
- [10] Damianou P A and Petalidou F 2014 On the Liouville integrability of Lotka–Volterra systems *Front. Phys.* **2** 1–10
- [11] Darboux G 1878 Mémoire sur les équations différentielles algébriques du premier ordre et du premier degré *Bull. Sci. Math.* **1** 60–96, 123–44, 151–200
- [12] Evripidou C A, Kassotakis P and Vanhaecke P 2022 Morphisms and automorphisms of skew-symmetric Lotka–Volterra systems *J. Phys. A: Math. Theor.* **55** 325201
- [13] Goriely A 2001 *Integrability and Nonintegrability of Dynamical Systems* (World Scientific) section 2.5
- [14] Hernández-Bermejo B and Fairén V 1998 Hamiltonian structure and Darboux theorem for families of generalized Lotka–Volterra systems *J. Math. Phys.* **39** 6162–74
- [15] Hua D D, Cairó L, Feix M R, Govinder K S and Leach P G L 1996 Connection between the existence of first integrals and the Painlevé property in two-dimensional Lotka–Volterra and quadratic systems *Proc. R. Soc. A* **452** 859–80
- [16] Itoh Y 1987 Integrals of a Lotka–Volterra system of odd number of variables *Prog. Theor. Phys.* **78** 507–10
- [17] Kouloukas T E, Quispel G R W and Vanhaecke P 2016 Liouville integrability and superintegrability of a generalized Lotka–Volterra system and its Kahan discretization *J. Phys. A: Math. Theor.* **49** 13
- [18] Lotka A J 1998 *Analytical Theory of Biological Populations (The Plenum Series on Demographic Methods and Population Analysis)* (Plenum Press) (translated from the 1939 French edition and with an introduction by David P Smith and H el ene Rossert)
- [19] Plank M 1995 Hamiltonian structures for the n-dimensional Lotka–Volterra equations *J. Math. Phys.* **36** 3520–34
- [20] Prelle M J and Singer M F 1983 Elementary first integrals of differential equations *Trans. Am. Math. Soc.* **279** 215–29
- [21] Sloan N J A 1964 The online encyclopedia of integer sequences (available at: <https://oeis.org/A000055>)
- [22] Sternberg S 2010 *Dynamical Systems* (Dover)
- [23] van der Kamp P H, Quispel G R W and McLaren D I Trees and superintegrable Lotka–Volterra families (unpublished)
- [24] van der Kamp P H, Kouloukas T, Quispel G R W, Tran D and Vanhaecke P 2014 Integrable and superintegrable systems associated with multi-sums of products *Proc. R. Soc. A* **470** 201404
- [25] Volterra V 2000 *Leçons sur la Théorie Mathématique de la Lutte Pour la vie (Les Grands Classiques Gauthier-Villars)* (Editions Jacques Gabay) (reprint of the 1931 original)