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# Analytic Behaviour of Competition among Three Species

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**Abstract**

We analyse the classical model of competition between three species studied by May and Leonard (*SIAM J Appl Math* **29** (1975) 243-256) with the approaches of singularity analysis and symmetry analysis to identify values of the parameters for which the system is integrable. We observe some striking relations between critical values arising from the approach of dynamical systems and the singularity and symmetry analyses.

## 1 Introduction

In a classic study of a model of competition among three species May and Leonard [16] demonstrated the dramatic change in the qualitative behaviour of the model in simply going from two species to three species. The Gause-Lotka-Volterra [7, 13, 24] model for competition among $n$ species is

$$\dot{N}_i = r_i N_i \left(1 - \sum_{j=1}^{n} a_{ij} N_j\right), \qquad i = 1, ..., n, \tag{1.1}$$

where $N_i\,(t)$ is the size of population $i$ at time $t$, $r_i$ is its intrinsic growth rate, $a_{ij}$ the coefficient representing the effect on its growth rate due to species $j$ and overdot denotes differentiation with respect to time. May and Leonard restrict the number of competing species to three and make some assumptions about the parameters in the system to reduce the system to one which is susceptible to analytic treatment in the main. The critical point in choosing $n = 3$ is not the smallness of the number, but the potential for dramatic change in the behaviour of the system in going from $n = 2$ to $n = 3$. When $n = 2$, the autonomous system, (1.1) with $n = 2$, can be reduced to a single first-order equation and is integrable. This is not automatically the case for $n = 3$. Indeed the potential, if not its realisation, for chaos exists. The parameters, $r_i,\ i = 1, n$, are taken to be equal and then set at unity by a rescaling of time. Rescaling of the independent variables enables the diagonal elements of the quadratic terms to be set at unity. Finally the interaction coefficients are limited



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to just two by the assumptions that species $i+1(\bmod 3)$ affects species $i$, $i=1,2,3$, and species $i+2(\bmod 3)$ affects species $i$, $i=1,2,3$, in the same way. The model system is then

$$\begin{aligned} \dot{x} &= x\left(1-x-\alpha y-\beta z\right), \\ \dot{y} &= y\left(1-\beta x-y-\alpha z\right), \\ \dot{z} &= z\left(1-\alpha x-\beta y-z\right). \end{aligned} \tag{1.2}$$

We remark that the simplifications made to the values of the parameters are not as restrictive as one would imagine. For example in grasslands the reproductive rates of different species of ungulants of similar size are expected to be similar and the coefficients of competition likewise. Indeed under good grazing conditions the $a_{ij}$ would be anticipated to be low and of comparable magnitude. The mathematical attraction of this model is that the community matrix, *videlicet*

$$A=\left[\begin{array}{ccc} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{array}\right], \tag{1.3}$$

is a circulant matrix for which an explicit formula for the eigenvalues exists [3]. With the entries of $A$ as indicated its eigenvalues are

$$\begin{aligned} \lambda_1 &= 1+\alpha+\beta, \\ \lambda_{2\pm} &= \frac{1}{2}\left[2-\alpha-\beta\pm i\sqrt{3}\left(\alpha-\beta\right)\right]. \end{aligned}$$

May and Leonard give the equilibrium points of system (1.2) as $(0,0,0)$; $(1,0,0)$, $(0,1,0)$ and $(0,0,1)$; $\left(1-\alpha,1-\beta,0\right)/\gamma$, $\left(1-\beta,0,1-\alpha\right)/\gamma$ and $\left(0,1-\alpha,1-\beta\right)/\gamma$, where $\gamma = 1-\alpha\beta$; $(1,1,1)/\left(1+\alpha+\beta\right)$ for zero-, one-, two- and three-population equilibria. In this paper we investigate the properties of system (1.2) from the approaches of singularity analysis and symmetry analysis. We emphasise that the thrust of our investigations is the integrability of system (1.2) and not its qualitative behaviour for which the methods of dynamical systems are well-suited. The singularity analysis is directed towards the determination of the existence of solutions which are analytic. Symmetry analysis leads towards invariance of the system under infinitesimal transformation so that in the presence of a suitable number of symmetries the solution of the system may be reduced to a sequence of quadratures or the existence of three functionally independent invariants from which the solution follows by a process of elimination of variables. In the case of the latter the elimination may be only local through the use of the Implicit Function Theorem. Equally the performance of the quadratures may not be possible in closed form or lead to analytic solutions.

Before we begin any analysis we observe that under a constraint upon the parameters $\alpha$ and $\beta$ system (1.2) is an example of a decomposed system since, if we add the three equations, we have

$$(x+y+z)^{\cdot} = (x+y+z)-\left\{x^2+y^2+z^2+(\alpha+\beta)(xy+yz+zx)\right\}. \tag{1.4}$$

Clearly the constraint $\alpha+\beta=2$ enables us to write (1.4) as the composed system

$$\dot{u} = u-u^2, \tag{1.5}$$

where $x+y+z=u$, which is readily integrated to give the invariant

$$I_1 = \left[\frac{1}{x+y+z} - 1\right] e^t \tag{1.6}$$

and this can be rearranged as the analytic solution

$$x+y+z = \frac{\mathrm{e}^t}{I_1 + \mathrm{e}^t} \tag{1.7}$$

for the total population. (Recall that time was rescaled; this explains the simplicity of the time dependence in (1.7)). One of the attractive features of decomposible systems is that the composed equation, particularly in the case of systems of first-order differential equation of the type usually encountered in modelling, is usually integrable so that an invariant exists and the dimension of the system is effectively reduced by one [1, 9, 10].

## 2 Singularity analysis of system (1.2)

We follow the standard method of singularity analysis[2] and determine the leading-order behaviour by setting $x = A\tau^p$, $y = B\tau^q$ and $z = C\tau^r$, where $\tau = t - t_0$ and $t_0$ is the location of the putative movable pole, in system (1.2) to obtain

$$\begin{aligned}
pA\tau^{p-1} &= A\tau^p\left(1 - A\tau^p - \alpha B\tau^q - \beta C\tau^r\right),\\
qB\tau^{q-1} &= B\tau^q\left(1 - \beta A\tau^p - B\tau^q - \alpha C\tau^r\right),\\
rC\tau^{r-1} &= C\tau^r\left(1 - \alpha A\tau^p - \beta B\tau^q - C\tau^r\right),
\end{aligned}$$

from which it is evident that the linear terms of the right hand side are not to be considered for the determination of the leading-order behaviour or of the resonances. On the assumption that the leading-order behaviour assumed does in fact represent polelike behaviour in the three dependent variables the requirement of balance of the terms reduces to just $-1, p, q, r$ from which it is evident that $p = q = r = -1$. The possibility that one or other of the exponents differs from $-1$ cannot be entertained since the exponent would then be nonnegative and the singularity analysis does not admit such a possibility for integral leading-order behaviour. One could imagine the introduction of branch point singularities with fractional exponents, but this leads us away from the standard analysis.

With the common exponent of the leading-order behaviour being $-1$ the coefficients of the leading-order terms are found from the solution of the system

$$\begin{bmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{bmatrix} \begin{bmatrix} A \\ B \\ C \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix} \Rightarrow \begin{bmatrix} A \\ B \\ C \end{bmatrix} = \frac{1}{1+\alpha+\beta} \begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix}$$

and we note that the solution is the same as the location of the interior equilibrium point of the system (1.2).

[2] The reader is referred to Ramani *et al* [22] and Tabor [23] for an account of the details of the application of the Painlevé Test and implementation of the ARS algorithm.

The resonances are determined from system (1.2) (with the linear term omitted) by the substitutions

$$x = A\tau^{-1} + M\tau^{r-1}, \quad y = B\tau^{-1} + N\tau^{r-1}, \quad z = C\tau^{-1} + S\tau^{r-1},$$

where $r$ denotes, as usual, the resonance and should not been confused with the usage above as one of the exponents of the leading-order behaviour. The terms linear in $M$, $N$ and $S$ give the eigenvalue problem

$$\begin{bmatrix} r+A & \alpha A & \beta A \\ \beta B & r+B & \alpha B \\ \alpha C & \beta C & r+C \end{bmatrix} \begin{bmatrix} M \\ N \\ S \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} \tag{2.1}$$

from which it follows that

$$r_1 = -1 \quad \text{and } r_{2\pm} = \frac{1}{2}\left[\frac{\alpha+\beta-2 \pm i\sqrt{3}\,(\alpha-\beta)}{1+\alpha+\beta}\right]. \tag{2.2}$$

If we look at the eigenvalues of the Jacobian matrix of system (1.2) at the interior equilibrium, we find that

$$\lambda_i = -\left(1+\alpha+\beta\right) r_i, \quad i = 1, 2\pm .$$

May and Leonard have a stable equilibrium point with three species present if $\alpha+\beta<2$ $(\alpha,\beta>0)$. For the region $\alpha>1$ and $\beta>1$ the equilibrium points for all three single species are each stable. For the remaining points $(\alpha,\beta)$ of the parametric space asymptotically stable equilibrium points do not exist.

In (2.2) the singularity analysis demonstrates that there is no possibility of an analytic solution unless $\alpha=\beta$ for otherwise $r_{2\pm}$ are complex. When $\alpha=\beta$, $r_{2\pm}$ coalesce into

$$r_2 = \frac{\alpha-1}{1+2\alpha},$$

with $r_2$ a positive integer, $n$, if

$$\alpha = -\frac{n+1}{2n-1},$$

which is necessarily negative and so beyond the acceptable parameter range of the model. Only in the case that $\alpha\,(=\beta)=1$, for which $r_2 = 0\,(2)$ can we expect an analytic solution. Then (2.1) is

$$\begin{bmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{bmatrix} \begin{bmatrix} M \\ N \\ S \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix} \Rightarrow \begin{bmatrix} M \\ N \\ S \end{bmatrix} = k_1 \begin{bmatrix} 1 \\ 0 \\ -1 \end{bmatrix} + k_2 \begin{bmatrix} 0 \\ 1 \\ -1 \end{bmatrix}, \tag{2.3}$$

where $k_1$ and $k_2$ are arbitrary parameters, and we have the two constants of integration entering at the leading-order behaviour. The linear terms omitted in the analysis of the dominant terms do not cause an inconsistency since they do not affect the leading order term of $\tau^{-2}$.

That the solution is analytic may be demonstrated by the explicit integration of system (1.2) with $\alpha = \beta = 1$. When the composed system is integrated and this is substituted into the equations for $x$ and $y$, say, *ie* $z$ is eliminated using the invariant, the equations for $x$ and $y$ decouple and one obtains the solution by simple quadratures to be

$$x = \frac{k_1 e^t}{C + e^t}, \quad y = \frac{k_2 e^t}{C + e^t}, \quad z = \frac{1 + (1 - k_1 - k_2)\, e^t}{C + e^t},$$

as is suggested by the solutions given in (2.3).

In terms of the singularity analysis system (1.2) is integrable in terms of analytic functions at the specific point $(1, 1)$ in the $(\alpha, \beta)$ plane. This is the point of contact between the two regions of stable equilibria reported by May and Leonard [16] [Fig 1]. We observe that the only pattern of leading-order behaviour compatible with the standard method of singularity analysis as found in, say, [22, 23] is that the exponents of the leading-order terms be at $-1$. However, we may depart[3] from that standard analysis and investigate the consequences. If we suppose that $p = q = -1$ and $r = 0$, the dominant terms of system (1.2) become

$$\begin{aligned} -A\tau^{-2} &= A\tau^{-1}\left(-A\tau^{-1} - \alpha B\tau^{-1}\right), \\ -B\tau^{-2} &= B\tau^{-1}\left(\beta A\tau^{-1} - B\tau^{-1}\right), \\ 0 &= C\left(-\alpha A\tau^{-1} - \beta B\tau^{-1}\right). \end{aligned} \tag{2.4}$$

The first two of (2.4) give

$$\begin{bmatrix} 1 & \alpha \\ \beta & 1 \end{bmatrix} \begin{bmatrix} A \\ B \end{bmatrix} = \begin{bmatrix} 1 \\ 1 \end{bmatrix} \Rightarrow \begin{bmatrix} A \\ B \end{bmatrix} = \frac{1}{1 - \alpha\beta} \begin{bmatrix} 1 - \alpha \\ 1 - \beta \end{bmatrix}.$$

The third of (2.4) gives either $C = 0$ or $\alpha A + \beta B = 0$. This second condition, coupled with the first and second of (2.4) demands either that $\alpha\beta = 1 \Rightarrow \alpha = 1, \beta = 1$, or places $\alpha$ and $\beta$ on the circle

$$\left(\alpha - \frac{1}{2}\right)^2 + \left(\beta - \frac{1}{2}\right)^2 = \frac{1}{2}$$

in the $(\alpha, \beta)$ plane. The former condition, $C = 0$, coincides with one of the equilibrium points with just two species, $x$ and $y$, present. The other two possibilities, *videlicet* $p = 0$, $q = r = -1$ and $p = -1$, $q = 0$ and $r = -1$, correspond to the equilibrium points with two solutions given by $(0, 1 - \alpha, 1 - \beta) / (1 - \alpha\beta)$ and $(1 - \beta, 1 - \alpha, 0) / (1 - \alpha\beta)$ respectively.

In a similar situation, if we take the leading-order exponents to be $p = -1$, $q = r = 0$, we obtain the leading-order behaviour,

$$\begin{aligned} -A\tau^{-2} &= A\tau^{-1}\left(-A\tau^{-1}\right), \\ 0 &= B\left(\beta A\tau^{-1}\right), \\ 0 &= C\left(-\alpha A\tau^{-1}\right), \end{aligned}$$

[3] We do not claim any originality in making a departure. Daniel *et al* [6] did the same in their study of the Heisenberg spin chain with anisotropy and transverse field. For a deep study from the viewpoint of cosmological interests see the more recent work by Cotsakis [5].

for which the solution is obviously $(1, 0, 0)$. The other two possibilities are $(0, 1, 0)$ and $(0, 0, 1)$, *ie* we recover the equilibrium points with just a single species present.

Moreover, if one makes a formal expansion

$$x = \sum_{i=0}^{\infty} a_i \tau^{i-1}, \quad y = \sum_{i=0}^{\infty} b_i \tau^{i-1}, \quad z = \sum_{i=0}^{\infty} c_i \tau^{i-1}$$

and substitutes this into (1.2), one obtains (courtesy of Mathematica) that $b_i = 0$, $c_i = 0$, $\forall i$, all odd coefficients, $a_{2i+1}$, are zero and that

$$a_0 = 1,\ a_1 = \frac{1}{2},\ a_2 = \frac{1}{12},\ a_4 = -\frac{1}{720},\ a_6 = \frac{1}{30240},\ a_8 = -\frac{1}{1209600},\ a_{10} = \frac{1}{47900160}$$

which is in accordance with the solution of one species present, *videlicet*

$$x = \frac{1}{1 - \exp[t - t_0]}, \quad y = 0, \quad z = 0.$$

Here we must emphasise again that we are not applying singularity analysis in the sense of the Painlevé Test. Nevertheless we see an interesting connection between the results of dynamical systems analysis and the simple series substitution. The solution obtained is consistent with the Painlevé analysis in that it leads to a subsidiary solution [21] although the route to its obtention is formally different. Nevertheless it cannot be regarded as a subset of the Painlevé analysis since a fundamental feature of the analysis is that the coefficients of the leading order terms be nonzero.

We emphasise that this last part of the analysis is not in accordance with the norms of singularity analysis as presented in the standard references. Once we admit the possibility of a zero as the exponent of the leading-order behaviour of one or more species, we depart from the criteria for the application of the Painlevé test. Nevertheless we see that results can be obtained which are very suggestive and which connect in a natural way with the analysis of system (1.2) via dynamical systems. For an investigation of the presence of two competing species we refer the reader to [11].

We conclude our singularity analysis of system (1.2) with the final observation that generically (1.2) is not integrable in terms of analytic functions. Nevertheless the analysis has revealed aspects of the properties of the system which perhaps would not be anticipated a priori.

## 3 Symmetry analysis

The system (1.2) is autonomous and so possesses the Lie point symmetry $\partial_t$. For integrability in the sense of Lie we require the knowledge of a three-dimensional solvable algebra. The knowledge that (1.2) is a system of first-order differential equations and so possesses an infinite number of Lie point symmetries does not help us to find the additional two symmetries. For the purposes of symmetry analysis we make a change of variables to convert system (1.2) to a quadratic system[4].

[4]For a system of the general form of (1.1) this is not possible, but the simplifying assumptions of May and Leonard that $r_i = r \to 1,\ i = 1, n$, under a rescaling of time does enable the transformation of system (1.2) to the simpler form. The change of variables used here is not beneficial for the singularity analysis the outcome of which is very much dependent upon the representation of the coordinates used, but, as it is a point transformation, has no effect upon the algebraic structure of the system.

We write

$$X = x\mathrm{e}^{-t},\ Y = y\mathrm{e}^{-t},\ Z = z\mathrm{e}^{-t},\ T = \mathrm{e}^{t}.$$

Then system (1.2) becomes

$$\begin{aligned} X' &= -X\left(X + \alpha Y + \beta Z\right), \\ Y' &= -Y\left(\beta X + Y + \alpha Z\right), \\ Z' &= -Z\left(\alpha X + \beta Y + Z\right), \end{aligned} \tag{3.1}$$

where we use the prime to denote differentiation with respect to the 'new time', $T$. If one assumes a solution of the form $X \propto T^p$, $Y \propto T^q$ and $Z \propto T^r$, one finds that

$$\begin{bmatrix} X(T) \\ Y(T) \\ Z(T) \end{bmatrix} = \frac{T^{-1}}{1+\alpha+\beta}\begin{bmatrix} 1 \\ 1 \\ 1 \end{bmatrix}, \tag{3.2}$$

is a solution. It is not the general solution because it does not depend upon three arbitrary constants. It is simply a peculiar solution. In fact, going back to the original variables

$$X = x\mathrm{e}^{-t},\ Y = y\mathrm{e}^{-t},\ Z = z\mathrm{e}^{-t},\ T = \mathrm{e}^{t},$$

solution (3.2) corresponds to the equilibrium solution

$$\frac{1}{1+\alpha+\beta}\left(1,1,1\right)^T$$

of the original system (1.2). Note also that to every equilibrium solution of the original system (1.2) there corresponds a peculiar solution of (3.2).

By inspection (3.1) possesses the two Lie point symmetries

$$\Gamma_1 = \partial_T,\ \Gamma_2 = -T\partial_T + X\partial_X + Y\partial_Y + Z\partial_Z \tag{3.3}$$

with the Lie bracket $[\Gamma_1, \Gamma_2]_{LB} = -\Gamma_1$.

In analogy with (1.4) we add the constituent equations of (3.1) to obtain

$$(X+Y+Z)' = -\left\{X^2 + (\alpha+\beta)XY + Y^2 + (\alpha+\beta)YZ + Z^2 + (\alpha+\beta)ZX\right\}. \tag{3.4}$$

In the particular case that $\alpha + \beta = 2$ a possible source of additional symmetry is from the decomposition of symmetries of the composed system of (3.1), *videlicet*

$$N' + N^2 = 0, \tag{3.5}$$

where $N = X + Y + Z$. We are unaware of this approach being used in the literature before now.

As a first-order differential equation (3.5) has the same problem of determination of symmetries as the composed system (3.1), but it can be written as the second-order differential equation

$$w'' = 0, \tag{3.6}$$

by means of the Riccati transformation

$$N = \frac{w'}{w} \Leftrightarrow w = \exp\left(\int N\mathrm{d}T\right), \; w' = N\exp\left(\int N\mathrm{d}T\right).$$

A symmetry $\Sigma = \Theta\partial_T + \Xi\partial_w$ of (3.6) can be written as a symmetry of (3.5), $\Lambda = \tau\partial_T + \eta\partial_N$, as follows. The first extension of $\Sigma$

$$\Sigma^{[1]} = \Theta\partial_T + \Xi\partial_w + \left(\Xi' - w'\Theta'\right)\partial_{w'} \rightarrow \Theta\partial_T + \left(\frac{d}{dT}\left(\frac{\Xi}{w}\right) - N\Theta'\right)\partial_N,$$

so that

$$\tau = \Theta, \quad \eta = \frac{d}{dT}\left(\frac{\Xi}{w}\right) - N\Theta'.$$

The Lie point symmetries of (3.6) transform as follows

$$\begin{array}{lll}
\Sigma_1 = \partial_w & \rightarrow & \Lambda_1 = N\exp\left(-\int N\mathrm{d}T\right)\partial_N \\
\Sigma_2 = \tau\partial_w & \rightarrow & \Lambda_2 = (1 - TN)\exp\left(-\int N\mathrm{d}T\right)\partial_N \\
\Sigma = w\partial_w & & \text{lost (The source of the Riccati transformation)} \\
\Sigma_4 = \partial_T & \rightarrow & \Lambda_4 = \partial_T \\
\Sigma_5 = 2T\partial_T + w\partial_w & \rightarrow & \Lambda_5 = T\partial_T - N\partial_N \\
\Sigma_6 = T^2\partial_T + Tw\partial_w & \rightarrow & \Lambda_6 = T^2\partial_T + (1 - 2TN)\partial_N \\
\Sigma_7 = w\partial_T & \rightarrow & \Lambda_7 = \exp\left(\int N\mathrm{d}T\right)\left(\partial_T - N^2\partial_N\right) \\
\Sigma_8 = Tw\partial_T + w^2\partial_w & \rightarrow & \Lambda_8 = \exp\left(\int N\mathrm{d}T\right)\left(T\partial_T - TN^2\partial_N\right).
\end{array}$$

In $\Lambda_4$ and $\Lambda_5$ we have the $\Gamma_1$ and $\Gamma_2$ of (3.3). If we examine the remaining symmetries, $\Lambda_2$ and $\Lambda_6$ do not decompose. The remaining symmetries decompose according to

$$\begin{array}{lll}
\Lambda_1 & \rightarrow & \Delta_1^{[1]} = \exp\left(-\int N\mathrm{d}T\right)\left\{X\partial_X + Y\partial_Y + Z\partial_Z + 2\left(X'\partial_{X'} + Y'\partial_{Y'} + Z'\partial_{Z'}\right)\right\} \\
\Lambda_7 & \rightarrow & \Delta_7^{[1]} = \exp\left(\int N\mathrm{d}T\right)\left\{\partial_T - N\left[X\partial_X + Y\partial_Y + Z\partial_Z\right.\right. \\
 & + & \left.\left. 2\left(X'\partial_{X'} + Y'\partial_{Y'} + Z'\partial_{Z'}\right)\right]\right\} \\
\Lambda_8 & \rightarrow & \Delta_8^{[1]} = \exp\left(\int N\mathrm{d}T\right)\left\{T\partial_T - TN\left[X\partial_X + Y\partial_Y + Z\partial_Z\right.\right. \\
 & + & \left.\left. 2\left(X'\partial_{X'} + Y'\partial_{Y'} + Z'\partial_{Z'}\right)\right]\right\},
\end{array}$$

where we have written the first extensions of the decomposed symmetries to highlight the discomforting point that these three symmetries bring no new information. The effects of $\Delta_1, \Delta_7$ and $\Delta_8$ are the same as that of $\Gamma_2$ ($\Leftrightarrow \Lambda_6$) on the autonomous system. We conclude that it is possible to decompose symmetries just as it is possible to decompose equations, but the results are not necessarily useful.

We already have an invariant derived from the composition of system (1.2) with $\alpha + \beta = 2$ in (1.6), *videlicet*

$$I_1 = \frac{1}{X + Y + Z} - T,$$

when written in the new coordinates. It is evident that $I_1$ is not an invariant associated with either $\Gamma_1$ or $\Gamma_2$ and so we may use $\Gamma_1$ and $\Gamma_2$ to seek a new invariant, in fact an integral if we require the function to vanish under the action of both symmetries[5].

[5] Although one usually looks for an integral/invariant associated with a a single symmetry – the only way possible for a two dimensional system – there are at times great benefit and simplification to imposing the requirement that the integral/invariant be associated with two (or more) symmetries [4].

In essence we use the method of reduction of order [17, 18] with the two symmetries $\Gamma_1$ and $\Gamma_2$. The former is a consequence of the autonomy of system (3.1) and we eliminate $T$ as the independent variable in favour of $Z$ by writing[6]

$$\frac{dX}{dZ} = \frac{X\,(X+\alpha Y+\beta Z)}{Z\,(\alpha X+\beta Y+Z)}, \qquad \frac{dY}{dZ} = \frac{Y\,(\beta X+Y+\alpha Z)}{Z\,(\alpha X+\beta Y+Z)}. \tag{3.7}$$

System (3.7) is homogeneous with the obvious symmetry $\tilde{\Gamma}_2 = X\partial_X + Y\partial_Y + Z\partial_Z$ following from $\Gamma_2$. Under the standard change of variables

$$X = uZ, \quad Y = vZ, \quad \tilde{\Gamma}_2 \to Z\partial_Z$$

we may eliminate the ignorable coordinate $Z$ (actually in the form $\exp(-Z)$) to obtain the single first-order differential equation

$$\frac{dv}{du} = \frac{v\,[(\beta-\alpha)\,u+(1-\beta)\,v+(\alpha-1)]}{u\,[(1-\alpha)\,u+(\alpha-\beta)\,v+(\beta-1)]}. \tag{3.8}$$

It is a trivial matter to integrate (3.8) in the case $\alpha = \beta$ which, we recall, is the condition for the singularity analysis to give real resonances. The integral is

$$I_2 = \frac{v\,(u-1)}{u\,(v-1)},$$

in which we note that the parameter $\alpha$ is absent.

When $\alpha \neq \beta$, the first-order differential equation is not integrable in closed form (as far as Mathematica is concerned). When $\alpha + \beta = 2$, the integration of (3.5) gives

$$J_1 = \frac{1}{N} - T \tag{3.9}$$

which corresponds to $I_1$.

May and Leonard note that the product $xyz$ (in our notation) has an interesting asymptotic behaviour.

From (3.1) we find that

$$(XYZ)' = -XYZ(1+\alpha+\beta)(X+Y+Z) \tag{3.10}$$

so that

$$\frac{(XYZ)'}{XYZ} = -kN$$

and in the case that $\alpha + \beta = 2$ so that (3.5) and (3.9) apply this is

$$\frac{(XYZ)'}{XYZ} = 3\frac{N'}{N}$$

whence

$$\frac{XYZ}{(X+Y+Z)^3} = I_2 \tag{3.11}$$

[6]There is no essential difference made by the particular choice of a new independent variable.

which also may be written as

$$XYZ = I_2 (J_1 + T)^3 . \tag{3.12}$$

The form (3.11) indicates that this integral corresponds to the symmetry $\partial_T$. The group theoretic origin of (3.11) is easily seen. The invariants of $\partial_T$ are $X$, $Y$ and $Z$. The requirement that $f(X, YZ)$ be an integral of (3.1) leads to the associated Lagrange's system

$$\frac{\mathrm{d}X}{X'} = \frac{\mathrm{d}Y}{Y'} = \frac{\mathrm{d}Z}{Z'}.$$

We may use the theory of first-order differential equations [8] [p 45] to combine the elements in a specific fashion to give, when (3.1) with $\alpha + \beta = 2$ is taken into account,

$$\frac{\mathrm{d}X}{X'} = \frac{\mathrm{d}Y}{Y'} = \frac{\mathrm{d}Z}{Z'} = \frac{\mathrm{d}(XYZ)}{-3XYZ(X+Y+Z)}.$$

Taking, say, the first with the fourth and using the equivalence of $\mathrm{d}X/X'$ to $\mathrm{d}T$ we have

$$\frac{\mathrm{d}(XYZ)}{XYZ} = -3N\mathrm{d}T$$

and (3.11) follows when the composed equation, (3.5), is used.

We may use (3.9) and (3.12) to eliminate $Y$ and $Z$ (say) from system (3.1) with $\alpha+\beta = 2$. To maintain a certain compactness of notation we write $X + Y + Z$ as $N(T)$ and $XYZ$ as $m(T)$. We obtain

$$Z = \frac{m}{XY} \quad \text{and} \quad Y^2 + (X - N)Y + \frac{m}{X} = 0 \tag{3.13}$$

so that

$$Y = \tfrac{1}{2}\left\{N - X \pm \sqrt{(N-X)^2 - \frac{4m}{X}}\right\}. \tag{3.14}$$

The first-order differential equation satisfied by $X$ is found to be

$$X' = -aX \mp \tfrac{1}{2}(\alpha - \beta)X\sqrt{(a-X)^2 - \frac{4b}{X}}. \tag{3.15}$$

The single first-order differential equation, (3.15), for $X(T)$ encapsulates the information already gleaned by our various analyses. The contents of the root ensure our inability to find a solution to (3.15) unless $\alpha = \beta$. When $\alpha = \beta = 1$, (3.15) is always integrable since then (3.15) is simply a linear first-order equation.

It would be evident to a reader with only a modest acquaintance with symmetry analysis that the procedure of this Section is not unique. We could look to replace the system (3.1) by either a single third-order differential equation or a second-order differential equation plus first-order differential equation which is a standard part of the method of reduction of order [17, 18].

For the system (3.1) the former option is not feasible as leads to a very awkward algebraic equation. The latter option is feasible and is found in the analysis of the Euler-Poinsot system [19]. Indeed it is a logical consequence of the case for which two equations are replaced by a single second-order ordinary differential equation [12, 14, 20]. In the papers cited the symmetries of the second-ordered differential equations sought were Lie point symmetries. In their study of the two-dimensional predator-prey system with malthusian growth Baumann and Freyberger [2] replace their two first-order differential equations with a polynomial second-order differential equation and then seek generalised symmetries with specific structure of the second-order equation. These give generalised – equally point since the two coalesce for systems of first-order equations – symmetries of the original Lotka-Volterra system. From the symmetries integrals and invariants follow easily.

We have not follow the procedure of Baumann and Freyberger in this paper since our investigation is, as the title of the paper proclaims, of analytic solutions and the range of parameters is already set by the singularity analysis. Were our intentions otherwise, a symmetry analysis along the lines of those in the papers cited above would be appropriate. The problem with (systems of) first-order equations is that the number of Lie point symmetries (equivalent, as noted above, to generalised symmetries) is infinite and so there is no finite algorithm for their determination. The increase of order, which is an integral component of the method of reduction of order, makes it possible to implement a finite algorithm. However, if like Baumann and Freyberger one introduces generalised symmetries at the higher order, the finite algorithm is lost. One may as well substitute Ansätze of choice into the original system of first-order equations.

Our concern with the analytic behaviour of the system led us to use a rather restricted symmetry approach to the determination of appropriate symmetries. If one removes the requirement of analycity, a wider investigation, even as general as that of Baumann and Freyberger, would be appropriate.

# 4 Conclusion

Our investigation of the model for competition among three species presented by May and Leonard was motivated by the singularity and symmetry analyses which are appropriate to integrable systems. We found that the critical values of the parameters revealed in the analysis of the system using the methods of dynamical systems were echoed in subsequent analyses from the viewpoint of the singularity and symmetry approaches. That (1), *æq* (3.1), is a decomposed system when $\alpha+\beta=2$ made our analysis easier since the composed equation, (3.5), is trivially integrable. This provided one invariant for system (3.1). The second invariant was suggested by the analysis of May and Leonard who showed that $XYZ$ was expressible in terms of an invariant for all values of $\alpha$ and $\beta$ provided that the populations were small. When $\alpha=\beta=1$, the asymptotic invariant becomes a global invariant. The existence of these two invariants, corresponding to the two symmetries of invariance under time translation and similarity transformation (more evident in (3.1) than (1)), enabled the system of three autonomous first-order differential equations to be reduced to a single nonautonomous first-order differential equation. The consequence of a lack of further symmetry for general values of $\alpha$ and $\beta$ even with the constraint $\alpha+\beta=2$ is quite evident in the form of the equation with $\alpha+\beta=2$. The system (3.1) cannot exhibit chaos since the autonomous invariant (3.11) implies that the system can be reduced to an autonomous system of order two and is thereby formally integrable. However, this integrability is not in terms of an analytic function let alone in closed form[7]. This is quite evident from the form of (3.15). The improvement in the integrability of (3.15) as the parameters become more closely aligned to the values which give favorable results for the singularity analysis is clearly apparent. The simple removal of the imaginary part of the resonances when $\alpha=\beta$ enables (3.15) to be integrated trivially in terms of an analytic function. In this respect the system (3.1) is an excellent paradigm for the implications of the requirements of the singularity analysis.

May and Leonard rightly indicate the marked change in the behaviour of the system as the dimensionality is increased from two to three. The numerical results which they present for $\alpha+\beta>2$ are very suggestive of the behaviour in the solution which one would expect when the resonances are complex. Indeed one would expect similar behaviour for $\alpha+\beta\leq 2$, $\alpha\neq\beta$, but the change in sign of the real part of the exponent means that there is damping of the oscillations rather than growth. Indeed, if one considers the basis of the model, the values of the parameters $\alpha$ and $\beta$ should be such that $\alpha+\beta$ is likely to be an order of magnitude less than two.

The community matrix of system (1)/(3.1) is circulant and a general expression for the eigenvalues is available. When $\alpha=\beta$, the community matrix becomes symmetric. Although May and Leonard make the point that one could scarcely be interested at looking at the analysis of a system of dimension greater than five, there may be some merit in the consideration of systems of dimension greater than three. If all of the nondiagonal elements are equal, which is a fairly drastic extension of the $\alpha=\beta$ case discussed above, all submatrices containing the principal diagonal are circulant and the possibility of the existence of composed systems leading to invariants is real and integrability for competition among $n$ species is conceivable. The constraint on the interaction coefficients to make the community matrix circulant and so system (1) amenable to some analysis may be regarded as severe. However, as we observed in the Introduction, among species of similar habit as well as habitat the interaction coefficients are likely to be less dominant than the self-specific effects. This is not a small step from assuming equality.

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