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AN ACCURATE SOLUTION TO THE MULTISPECIES LOTKA-VOLTERRA EQUATIONS*

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Abstract. The decomposition method is applied to the solution of the Lotka–Volterra equations modelling the dynamic behaviour of an arbitrary number of species. The analytical solution derived is an infinite power series for each species, where the n term is given by a recurrence relation. As particular examples, the cases of one, two, and three species are considered. For these cases, comparisons between the present semi-analytical solution and a fully numerical solution (or an exact one for one species) show exc ellent agreement.

Key words. Lotka–Volterra, decomposition, species dynamics

AMS subject classification. 92D25

1. Introduction. The Lotka–Volterra equations model the dynamic behaviour of an arbitrary number of competitors (Hofbauer and Sigmund (1988)). Though originally formulated to describe the time history of a biological system, these equations find their application in a number of engineering fields such as simultaneous chemical reactions and nonlinear control. In fact, the one predator one prey Lotka–Volterra model is one of the most popular ones to demonstrate a simple nonlinear control system.

The accurate solution of the Lotka–Volterra equations may become a difficult task either if the equations are stiff (even with a small number of species), or when the number of species is large.

The objective of this study is not a qualitative analysis of the rich dynamic behaviour of the noted equations, but to present an accurate solution to the Lotka–Volterra equations for an arbitrary number of competitors, using the "decomposition method."

The decomposition method yields analytical approximations to a rather wide class of nonlinear (and stochastic) equations without linearization, perturbation, closure approximations, or discretization methods.

The formal solution obtained by decomposition is generally an infinite series, where for computational purposes, usually a small number of terms is used to obtain accurate numerical results.

The advantage of the decomposition method relies on the fact that it provides an easily computable scheme and an efficient algorithm, as we shall see, for the continuous approximation of the dynamical response of the system equations.

As will be shown, the main achievement of this study is an accurate series solution by the decomposition method, which is very compact in form and easy to apply. It is a fortunate case here that the n term in the series can be written down immediately in terms of preceding ones, unlike a step by step procedure for its expression obtained by the decomposition method for other types of equations.

In §2 the decomposition method is introduced and in §3 it is applied to the solution of the Lotka–Volterra equations for an arbitrary number of species. In §4 we present results for either one, two, or three species. For one species, the results of the decomposition method are compared with both numerical and exact solutions. For two and three species the results of the solution by decomposition are compared with an accurate numerical solution, that uses the Runge–Kutta–Verner method. In all cases excellent agreement is obtained.

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2. The decomposition method. The presentation of the decomposition method in the sequel follows Adomian (1988). Consider an equation

$$Lu + Ru + Nu = g, \tag{1}$$

where L is an easily invertible linear differential operator (such as the highest-order derivative), R is the remainder of the linear differential operator, Nu represents the nonlinear terms, and g denotes the nonhomogeneous part. Solving for Lu yields

$$Lu = g - Ru - Nu. \tag{2}$$

Because L is invertible, an equivalent expression is

$$L^{-1}Lu = L^{-1}g - L^{-1}Ru - L^{-1}Nu. \tag{3}$$

In the case of an initial-value problem, the integral operator L^{-1} may be regarded as definite integrals from t_0 to t. If L is a second-order operator, L^{-1} is a two-fold integration operator and $L^{-1}Lu = u - u(t_0) - (t - t_0)u'(t_0)$. For boundary value problems (and, if desired, for initial-value problems as well), indefinite integrations are used and the constants are evaluated from the given conditions. Solving (3) for u yields

$$u = A + Bt + L^{-1}g - L^{-1}Ru - L^{-1}Nu. \tag{4}$$

The nonlinear term Nu will be equated to $\sum_{n=0}^{\infty} A_n$, where the A_n are special polynomials to be discussed, and u will be decomposed into $\sum_{n=0}^{\infty} u_n$, with u_0 identified as $A + Bt + L^{-1}g$, so that

$$\sum_{n=0}^{\infty} u_n = u_0 - L^{-1}R\sum_{n=0}^{\infty} u_n - L^{-1}\sum_{n=0}^{\infty} A_n. \tag{5}$$

Consequently, we can write

$$\begin{aligned} u_1 &= -L^{-1}Ru_0 - L^{-1}A_0 \\ u_2 &= -L^{-1}Ru_1 - L^{-1}A_1 \\ &\vdots \\ u_{n+1} &= -L^{-1}Ru_n - L^{-1}A_n. \end{aligned} \tag{6}$$

The polynomials A_n are generated for each nonlinearity so that A_0 depends only on u_0, A_1 depends only on u_0 and u_1, A_2 depends on u_0, u_1, u_2, etc. All of the u_n components are calculable, and $u = \sum_{n=0}^{\infty} u_n$. If the series converges, the n-term partial sum $\phi_n = \sum_{i=0}^{n-1} u_i$ will be the approximate solution since $\lim_{n\to\infty} \phi_n = \sum_{i=0}^{\infty} = u$ by definition. It is important to emphasize that the A_n can be calculated for complicated nonlinearities of the form $f(u, u', \ldots)$ or $f(g(u))$.

The A_n polynomials are defined by

$$\begin{aligned} A_0 &= f(u_0), \\ A_1 &= u_1(d/du_0)f(u_0), \\ A_2 &= u_2(d/du_0)f(u_0) + (u_1^2/2!)(d^2/du_0^2)f(u_0), \\ A_3 &= u_3(d/du_0)f(u_0) + u_1u_2(d^2/du_0^2)f(u_0) + (u_1^3/3!)(d^3/du_0^3)f(u_0) \end{aligned} \tag{7}$$

There are a number of ways to define A_n. One form is

$$A_n = (1/n!)\sum_{\nu=1}^{n} c(\nu, n) d^\nu f/du^\nu, \tag{8}$$

where the second index in the coefficient is the order of the derivative and the first index progresses from 1 to n along with the order of the derivative. In the linear case $f(u) = u$, and the A_n reduce to u_n. Otherwise $A_n = A_n(u_0, u_1, \ldots, u_n)$. For $f(u) = u^2$, for example, $A_0 = u_0^2$, $A_1 = 2u_0u_1$, $A_2 = u_1^2 + 2u_0u_2$, $A_3 = 2u_1u_2 + 2u_0u_3, \ldots$. It is to be noted that in this scheme the sum of the subscripts in each term of the A_n are equal to n. It is possible to find simple symmetry rules for writing the A_n quickly to high orders.

3. Analysis. Consider the Lotka–Volterra model for an m species system

$$\frac{dN_i}{dt} = N_i\left(b_i + \sum_{j=1}^{m} a_{ij}N_j\right), \qquad i = 1, 2, \ldots, m. \tag{9}$$

No mathematical constraints are posed on the various coefficients. These equations may represent either predator-prey or competition cases.

It can be realized that in the present case the nonlinear terms are of the rather simple u^2 form, so that very simple symmetry rules for the decomposition polynomials can be used.

If we denote $L \equiv d/dt$, the formal solution of (9) may be put in the form

$$N_i(t) = N_i(0) + L^{-1}\left(b_iN_i + \sum_{j=1}^{m} a_{ij}N_iN_j\right), \qquad i = 1, 2, \ldots, m, \tag{10}$$

where $L^{-1} \equiv \int_0^t [\cdot]dt$. According to the decomposition method an expansion of the following form is assumed:

$$N_i(t) = \sum_{n=0}^{\infty} \tilde{N}_{in}, \qquad i = 1, 2, \ldots, m. \tag{11}$$

Substituting (11) into (10) gives

$$N_i(t) = N_i(0) + L^{-1}\left(b_i\sum_{n=0}^{\infty}\tilde{N}_{in} + \sum_{j=1}^{m} a_{ij}\sum_{n=0}^{\infty}\tilde{N}_{in}\sum_{n=0}^{\infty}\tilde{N}_{jn}\right), \quad i = 1, 2, \ldots, m, \tag{12}$$

or after rearranging the products

$$N_i(t) = N_i(0) + L^{-1}\left(b_i\sum_{n=0}^{\infty}\tilde{N}_{in} + \sum_{j=1}^{m} a_{ij}\sum_{n=0}^{\infty}\sum_{k=0}^{n}\tilde{N}_{ik}\tilde{N}_{j(n-k)}\right), \quad i = 1, 2, \ldots, m. \tag{13}$$

The solution is ensured by requiring

$$\tilde{N}_{i0} = N_i(0), \qquad i = 1, 2, \ldots, m, \tag{14}$$

$$\tilde{N}_{i1} = L^{-1}\left(b_i\tilde{N}_{i0} + \sum_{j=1}^{m} a_{ij}\sum_{k=0}^{0}\tilde{N}_{ik}\tilde{N}_{j(0-k)}\right), \qquad i = 1, 2, \ldots, m, \tag{15}$$

$$\tilde{N}_{i2} = L^{-1}\left(b_i\tilde{N}_{i1} + \sum_{j=1}^{m} a_{ij}\sum_{k=0}^{1}\tilde{N}_{ik}\tilde{N}_{j(1-k)}\right), \qquad i = 1, 2, \ldots, m, \tag{16}$$

$$\vdots$$

$$\tilde{N}_{in} = L^{-1}\left(b_i\tilde{N}_{i(n-1)} + \sum_{j=1}^{m} a_{ij}\sum_{k=0}^{n-1}\tilde{N}_{ik}\tilde{N}_{j(n-k-1)}\right), \qquad i = 1, 2, \ldots, m. \tag{17}$$

After carrying out the integrations, the following solution is obtained:

$$N_i(t) = \sum_{n=0}^{\infty} c_{in}\frac{t^n}{n!}, \qquad i = 1, 2, \ldots, m, \tag{18}$$

where

$$c_{i0} = N_i(0), \qquad i = 1, 2, \ldots, m \tag{19}$$

and the general term is defined through the following recurrence relation:

$$c_{in} = b_i c_{i(n-1)} + (n-1)!\sum_{j=1}^{m}\sum_{k=0}^{n-1} a_{ij}\frac{c_{ik}}{k!}\,\frac{c_{j(n-k-1)}}{(n-k-1)!}, \qquad i = 1, 2, \ldots, m, \quad n \geq 1. \tag{20}$$

The decomposition method does not assure, on its own, existence and uniqueness of the solution. In fact, it can be safely applied when a fixed point theorem holds. A theorem proved in Répaci (1990) indicates that it is hopeless to look for solutions globally in time. On the other hand, the decomposition method can be used as an algorithm for the approximation of the dynamical response in a sequence of time intervals $[0, t_1)$, $[t_1, t_2)$, $\ldots$, $[t_{n-1}, T)$ such that the condition at t_p is taken as initial condition in the interval $[t_p, t_{p+1})$ which follows.

This method has the following advantages.

(1) In each time-interval one can apply a theorem proved in Répaci (1990), which states that the solution obtained by the decomposition method converges to a unique solution as the number of terms in the series becomes infinite.

(2) The approximation in each interval is continuous in time and can be obtained with the desired approximation corresponding to the desired number of terms.

The latter procedure is adopted in the numerical computations for the examples to be presented in the next section.

4. Results and discussion. In the following, a few numerical examples are presented for one, two, and three species.

4.1. One species. The Verhulst logistic equation for one species competing for a given, finite source of food is

$$\frac{dN}{dt} = N(b + aN), \qquad b > 0, \quad a < 0, \quad N(0) > 0, \tag{21}$$

where a and b are constants. This equation has an exact solution

$$N(t) = \frac{be^{bt}}{\dfrac{b + aN(0)}{N(0)} - ae^{bt}} \qquad \text{for } b \neq 0, \tag{22}$$

TABLE 1

One species competing over a common ecological niche—comparison between the decomposition solution with different time steps and number of terms in the series and numerical and exact solutions. $b = 1$, $a = -3$, $N(0) = 0.1$. The number of terms in the decomposition series solution is denoted by n and time steps are denoted by Δt.

t	Decomposition $\Delta t = 0.1$ $n = 3$	Decomposition $\Delta t = 0.001$ $n = 3$	Decomposition $\Delta t = 0.1$ $n = 16$	Numerical	Exact
0.0	0.1000000000	0.1000000000	0.1000000000	0.1000000000	0.1000000000
0.5	0.1380362959	0.1380126144	0.1380126120	0.1380126120	0.1380126120
1.0	0.1794249532	0.1793671813	0.1793671754	0.1793671754	0.1793671754
1.5	0.2192866937	0.2192063831	0.2192063750	0.2192063750	0.2192063750
2.0	0.2534123465	0.2533347169	0.2533347092	0.2533347092	0.2533347092
2.5	0.2798079939	0.2797519782	0.2797519727	0.2797519727	0.2797519727
3.0	0.2986706260	0.2986403402	0.2986403373	0.2986403373	0.2986403373

$$N(t) = \frac{N(0)}{1 - aN(0)t} \quad \text{for } b = 0. \tag{23}$$

The exact solution will serve to assess both the accuracy of the solution by the decomposition method and the numerical solution by the Runge–Kutta method. For one species, the solution by decomposition takes the following form:

$$N(t) = \sum_{n=0}^{\infty} c_n \frac{t^n}{n!}, \tag{24}$$

where

$$c_0 = N(0), \tag{25}$$

and the general term is defined as follows:

$$c_n = bc_{(n-1)} + (n-1)!a \sum_{k=0}^{n-1} \frac{c_k}{k!} \frac{c_{(n-k-1)}}{(n-k-1)!}, \qquad n \geq 1. \tag{26}$$

Table 1 shows a comparison between the decomposition, numerical, and exact solutions for $b = 1$, $a = -3$, and $N(0) = 0.1$. From left to right, the first column shows time, the second and third columns represent the solution by the decomposition method with 3 terms in the series, and for time steps Δt of 0.1 and 0.001, respectively. The fourth column shows the solution by decomposition with 16 terms in the series and a time step of 0.1, in the fifth column there are the results of a numerical solution, and the last column shows the exact solution. The numerical solution is obtained by using the DIVPRK subroutine from the IMSL library. This high accuracy subroutine employs the Runge–Kutta–Verner method of the 5th and 6th order.

4.1.1. The accuracy of the solution by the decomposition method. From Table 1, it can be realized that the numerical solution and the one by decomposition with a time step of $\Delta t = 0.1$ and $n = 16$ terms in the series are identical to the exact solution for the 10 digits presented here. It can be seen that an increase in the accuracy by the decomposition method can be achieved by either decreasing the time step or by increasing the number of terms in the series. Note that the solution with 16 terms and a time step of 0.1 is more accurate than the one with 3 terms and time steps of 0.001. It may be realized that the decomposition solution is indeed very accurate.

In general, there is not known an exact solution for the Lotka–Volterra equations with more than one species. Thus, the accuracy of the decomposition method in the examples to be presented in the sequel will be assessed by its comparison to the numerical solution by the Runge–Kutta method.

4.2. Two species. The Lotka–Volterra equations for this case take the following form:

$$\frac{dN_1}{dt} = N_1(b_1 + a_{11}N_1 + a_{12}N_2), \tag{27}$$

$$\frac{dN_2}{dt} = N_2(b_2 + a_{21}N_1 + a_{22}N_2). \tag{28}$$

Equations (27) and (28) model two species competing for a common ecological niche.

According to the decomposition method, the consequent solution results

$$N_1(t) = \sum_{n=0}^{\infty} c_{1n}\frac{t^n}{n!}, \tag{29}$$

$$N_2(t) = \sum_{n=0}^{\infty} c_{2n}\frac{t^n}{n!}, \tag{30}$$

where

$$c_{10} = N_1(0), \tag{31}$$

$$c_{20} = N_2(0), \tag{32}$$

and the general terms are again given by the recurrence relation

$$c_{1n} = b_1 c_{1(n-1)} + \sum_{k=0}^{n-1}[a_{11}c_{1k}c_{1(n-k-1)} + a_{12}c_{1k}c_{2(n-k-1)}], \qquad n \geq 1, \tag{33}$$

$$c_{2n} = b_2 c_{2(n-1)} + \sum_{k=0}^{n-1}[a_{21}c_{1k}c_{2(n-k-1)} + a_{22}c_{2k}c_{2(n-k-1)}], \qquad n \geq 1. \tag{34}$$

The asymptotic behavior which results from the Lotka–Volterra equations for two species is convergence to one or other of the 4 possible equilibrium points: 1 and 2 coexisting; 1 alone; 2 alone; both vanishing, depending on the relative magnitudes of the competition coefficients.

Consider a numerical example which appears in Pielou (1969). The initial values are $N_1(0) = 4$ and $N_2(0) = 10$, and the various constants are $a_{11} = -0.0014$, $a_{12} = -0.0012$, $a_{21} = -0.0009$, $a_{22} = -0.001$, $b_1 = 0.1$, and $b_2 = 0.08$. It turns out that in this case the species coexist.

Table 2 shows a comparison between an analytical solution and a numerical solution obtained using subroutine DIVPRK from the IMSL library. The analytical solution is obtained with three terms in the series, and time steps of 0.001, in a procedure explained before. It may be realized that an excellent agreement between the two solutions is obtained, suggesting that both the decomposition and Runge–Kutta solutions for this case are accurate to at least 9 significant digits.

TABLE 2

Two species competing over a common ecological niche—a comparison between decomposition and numerical solutions. The model parameters are: $b_1 = 0.1$, $a_{11} = -0.0014$, $a_{12} = -0.0012$, $b_2 = 0.08$, $a_{21} = -0.0009$, $a_{22} = -0.001$, $N_1(0) = 4$, $N_2(0) = 10$.

	Decomposition solution		Numerical solution	
t	N_1	N_2	N_1	N_2
0	4.00000000	10.00000000	4.00000000	10.00000000
10	8.45764164	18.34438086	8.45764162	18.34438085
20	14.73840948	29.06458094	14.73840945	29.06458097
30	20.68367509	39.10222921	20.68367507	39.10222921
40	24.42920273	46.16594844	24.42920270	46.16594844
50	26.02503288	50.36508268	26.02503285	50.36508268
60	26.34551108	52.78271552	26.34551106	52.78271553
70	26.07375943	54.28149923	26.07375941	54.28149924
80	25.56693235	55.33333017	25.56693234	55.33333018
90	24.98478037	56.16294739	24.98478036	56.16294740
100	24.39370745	56.87231129	24.39370749	56.87231131

TABLE 3

Two species competing over a common ecological niche—long time variation of populations. A comparison between decomposition and numerical solutions. The model parameters are: $b_1 = 0.1$, $a_{11} = -0.0014$, $a_{12} = -0.0012$, $b_2 = 0.08$, $a_{21} = -0.0009$, $a_{22} = -0.001$, $N_1(0) = 4$, $N_2(0) = 10$.

	Decomposition solution		Numerical solution	
t	N_1	N_2	N_1	N_2
0	4.00000000	10.00000000	4.00000000	10.00000000
500	14.66140862	66.68801736	14.66140865	66.68801734
1000	12.87224339	68.39746922	12.87224339	68.39746921
1500	12.56961791	68.68415010	12.56961791	68.68415010
2000	12.51321778	68.73750049	12.51321778	68.73750050
2500	12.50251671	68.74762016	12.50251671	68.74762016
3000	12.50047945	68.74954663	12.50047945	68.74954663
3500	12.50009135	68.74991362	12.50009135	68.74991362
4000	12.50001741	68.74998354	12.50001740	68.74998354
4500	12.50000332	68.74999686	12.50000332	68.74999686
5000	12.50000063	68.74999940	12.50000063	68.74999940

Table 3 shows the population variation for long times, for the same model parameters as in Table 1. This case is of special interest since the steady state may easily be determined analytically by setting to zero the left-hand side of equations (21) and (22) and solving for N_1 and N_2. The values which result are $N_1 = 12.500$ and $N_2 = 68.750$. Again, comparing the solutions by decomposition and Runge–Kutta suggests that for this case both are accurate to at least 9 significant digits. One may also realize that the analytically determined steady state values are approached by the two solutions.

4.3. Three species. The case of two species is described by May and Leonard (1975) to be rather dull as compared to the case of three species. For in the latter case, there are 8 possible equilibrium points: all three coexisting; 3 combinations of two coexisting; 3 single populations; and all three vanishing. But, unlike the two-species case, there remain combinations of the competition coefficients such that the system does not converge to any one of the 8 equilibrium points. As stated in the introduction, this paper does not intend to analyze the case of three species in a qualitative way but rather to show that the decomposition method may be used to yield accurate predictions of the multispecies dynamics.

TABLE 4
Three species competing over a common ecological niche—a comparison between decomposition and numerical solutions. The model parameters are: $c = 0.1$, $\beta = 0.1$, $N_1(0) = 0.2$, $N_2(0) = 0.3$, $N_3 = 0.5$.

	Decomposition solution			Numerical solution		
t	N_1	N_2	N_3	N_1	N_2	N_3
0	0.200000	0.300000	0.500000	0.200000	0.300000	0.500000
2	0.554110	0.667837	0.799034	0.554111	0.667836	0.799031
4	0.766028	0.806442	0.841979	0.766027	0.806440	0.841978
6	0.819938	0.829794	0.837851	0.819939	0.829792	0.837849
8	0.830674	0.832908	0.834704	0.830675	0.832907	0.834704
10	0.832789	0.833289	0.833689	0.832788	0.833288	0.833689
12	0.833219	0.833330	0.833420	0.833217	0.833329	0.833420
14	0.833309	0.833334	0.833353	0.833308	0.833334	0.833354
16	0.833328	0.833334	0.833338	0.833328	0.833334	0.833334
18	0.833332	0.833333	0.833334	0.833332	0.833334	0.833334
20	0.833333	0.833333	0.833334	0.833333	0.833333	0.833334

For demonstration purposes, a reduced number of parameters will be used in the three-species system, by making some symmetry assumptions, to yield the equations obtained by May and Leonard (1975). These equations take the following form:

$$\frac{dN_1}{dt} = N_1(1 - N_1 - cN_2 - \beta N_3), \tag{35}$$

$$\frac{dN_2}{dt} = N_2(1 - \beta N_1 - N_2 - cN_3), \tag{36}$$

$$\frac{dN_3}{dt} = N_3(1 - cN_1 - \beta N_2 - N_3), \tag{37}$$

where c and β are constants.

It can be shown (May and Leonard (1975)) that for $c > 0$ and $\beta > 0$ the sufficient condition for neighborhood stability is $c + \beta < 2$. Such a case is shown in Table 4, for $c = \beta = 0.1$, where the initial conditions are 0.2, 0.3, and 0.5. As before, three therms in the series were used with time steps of 0.001. A comparison between the analytical and numerical solutions shows an agreement of 5 significant digits at least.

An interesting case is depicted in Fig. 1, where the variation of one species, namely $N_1(t)$, is shown for $c = 0.8$, $\beta = 1.3$, and the initial conditions are 0.6, 0.6, and 0.1. In this case the system equations is very stiff, and the nonlinearities mathematically produce nonperiodic phenomena, though biologically it is nonsense (see discussion in May and Leonard (1975)). In this figure, a comparison is made between the analytical solution (solid line) with three terms in the series and time steps of 0.001 and the numerical one (dashed line) using again subroutine DIVPRK. The curves are seen to practically coincide. It should be noted that care must be taken in employing numerical methods. Using subroutine DIVPAG from the IMSL library, which is based on the Gear method, yielded unacceptable results in the present case. For example, for relatively short times the results were in good agreement with the analytical method (or the numerical method based on subroutine DIVPRK), but for long times it yielded results which are substantially outside the range (0, 1), e.g., large positive or negative values.

To summarize, the decomposition method was employed to solve the multispecies Lotka–Volterra equations. Formally, this approximate analytical solution is an infinite power series for each species, and has a very compact form due to the particular form of the equations. For

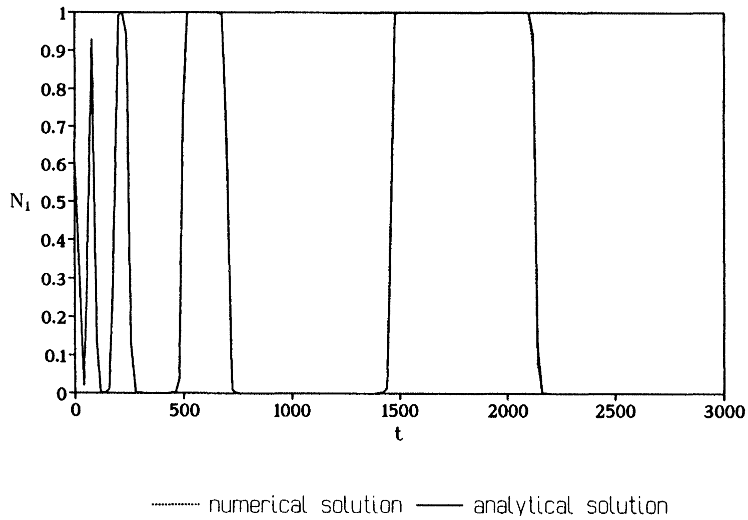

FIG. 1. *The behavior of one of the three species, namely $N_1(t)$, as a function of time for $c = 0.8$ and $\beta = 1.3$ and the initial conditions $N_1(0) = 0.6$, $N_2(0) = 0.6$, and $N_3(0) = 0.1$. A comparison between the analytical and numerical solutions shows that they practically coincide.*

practical computations, a finite number of terms in the series is used in a time step procedure outlined above.

The excellent accuracy of the present solution was demonstrated through comparisons between the present solution by decomposition and an exact analytical solution for one species (10 significant digits) or to fully numerical solutions for the cases of two (9 significant digits) and three species (5 significant digits).

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