Competing Species: Integrability and Stability

 $PGL\ LEACH\ ^\dagger$ and $J\ MIRITZIS\ ^\ddagger$

† School of Mathematical and Statistical Sciences, University of Natal, Durban 4041 Republic of South Africa E-mail: leachp@nu. ac. za

[‡] Department of Marine Sciences, University of the Aegean, Mytilene 81 100, Greece E-mail: john@env.aegean.qr

Received June 04, 2003; Accepted August 04, 2003

Abstract

We examine the classical model of two competing species for integrability in terms of analytic functions by means of the Painlevé analysis. We find that the governing equations are integrable for certain values of the essential parameters of the system. We find that, for all integrable cases with the nontrivial equilibrium point in the physically acceptable region, the nontrivial equilibrium point is stable.

1 Introduction

The simplest model for two competing species [13, 78 ff] is given by the quadratic system

$$\frac{dN_1}{d\tau} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right)
\frac{dN_2}{d\tau} = r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right)$$
(1.1)

in which N_1 and N_2 represent the populations of the two competing species, K_1 and K_2 the carrying capacities of each species, r_1 and r_2 the rates of reproduction of each species and b_{12} and b_{21} give the measure of the effects of competition between the two species. The system (1.1) has been analysed by Hsu *et al* [5] and Pianka [15] from the viewpoint of dynamical systems. The six parameters are excessive and may be reduced to only three by means of the rescalings and definitions

$$x = \frac{N_1}{K_1}, \quad y = \frac{N_2}{K_2}, \quad t = r_1 \tau, \quad \frac{r_2}{r_1} = \rho, \quad b_{12} \frac{K_2}{K_1} = \alpha \rho, \quad b_{21} \frac{K_1}{K_2} = \frac{\beta}{\rho}$$
 (1.2)

so that the dynamical system to be considered is simply

$$\dot{x} = x (1 - x - \alpha \rho y)
\dot{y} = \rho y (1 - y) - \beta x y.$$
(1.3)

Copyright © 2004 by PGL Leach and J Miritzis

(Note that in the standard presentation the parameters α and β are differently defined. The present definitions are adopted from the vantage point of hindsight.)

The equilibrium points of the system (1.3) are given by (0,0), (0,1), (1,0) and, if $1 - \alpha\beta \neq 0$, $x_4 = (1 - \alpha\rho)/(1 - \alpha\beta)$, $y_4 = (1 - \beta/\rho)/(1 - \alpha\beta)$. For the system (1.3) to describe the competition between two species it follows that $\alpha\rho < 1, \beta/\rho < 1, \alpha\beta < 1$ or $\alpha\rho > 1, \beta/\rho > 1$, $\alpha\beta > 1$. If $\alpha\beta = 1$, the isoclines are parallel and the possibility of a nontrivial equilibrium point vanishes.

We recall a well-known method for the determination of the nature of an equilibrium point. Let A be the Jacobian matrix evaluated at an equilibrium point \mathbf{q} . Let $d = \det A$ and $t = \operatorname{trace} A$. Since the eigenvalues of the matrix A are given by

$$\lambda_{1,2} = \frac{t \pm \sqrt{t^2 - 4d}}{2},$$

it is easy to see that,

- (i) if d < 0, then **q** is a saddle.
- (ii) if d > 0 and $t^2 4d \ge 0$, then ${\bf q}$ is a node $\left\{ \begin{array}{ll} \text{stable if} & t < 0 \\ \text{unstable if} & t > 0 \end{array} \right.$
- (iii) if d > 0 and t = 0, then **q** is a centre.
- (iv) if d > 0 and $t^2 4d < 0$ ($t \neq 0$), then **q** is a focus $\begin{cases} \text{stable if} & t < 0 \\ \text{unstable if} & t > 0 \end{cases}$.

In our case the determinant and the trace of A at the four equilibrium points are

$$(0,0): d = \rho, \ t = 1 + \rho$$

$$(0,1): d = -\rho (1 - \alpha \rho), \ t = -\rho + (1 - \alpha \rho)$$

$$(1,0): d = -\rho (1 - \beta/\rho), \ t = -1 + \rho (1 - \beta/\rho)$$

$$(x_4, y_4): d = \frac{(1 - \beta/\rho)(1 - \alpha\rho)}{1 - \alpha\beta}, \ t = -\frac{(1 - \alpha\rho) + \rho(1 - \beta/\rho)}{1 - \alpha\beta}.$$

The isoclines $\dot{x} = 0$ and $\dot{y} = 0$ are given by the straight lines $1 - x - \alpha \rho y = 0$ and $\rho - \rho y - \beta x = 0$ respectively. There are four possibilities according to as these lines intersect each other or not.

- I $\alpha \rho < 1$ and $\beta/\rho > 1$ (0,1) is unstable and (1,0) is stable
- II $\alpha \rho > 1$ and $\beta/\rho < 1$ (0, 1) is stable and (1, 0) is unstable
- III $\alpha \rho < 1$ and $\beta/\rho < 1$ (0,1) is unstable and (1,0) is stable (x_4, y_4) is stable
- IV $\alpha \rho > 1$ and $\beta/\rho > 1$ (0, 1) is stable and (1, 0) is stable (x_4, y_4) is unstable

In all cases the origin is unstable. It can be shown [4] that the ω -limit point of every trajectory of the system is one of the equilibria, ie the populations of two competing species always tend to one of a finite number of limiting populations.

The interpretation of these results in biological terms can be found in [5] and [15]. Only case III leads to an equilibrium state where both species survive. In particular in case IV there exists a separatrix such that every trajectory starting above this curve asymptotically approaches the equilibrium point (0,1), ie species y reaches its carrying capacity while species x becomes extinct. Analogous results hold for trajectories starting below the separatrix with the roles of x and y interchanged.

The final quarter of the nineteenth century was a period in which three different approaches to the study of differential equations were developed. One that was based upon

the concept of invariance under infinitesimal transformations was due to Lie. A second involved the analysis of the equations for movable singularities and is largely due to the School of Painlevé in France, but was already presaged in the pioneering work of Kowalevskaya [8]. The third was the study of the phase space of the system of equations with particular emphasis on the nature of the equilibrium points and the asymptotic behaviour of the system due to Poincaré. For some curious reason these three approaches to the study of systems of differential equations have tended to be separate. Thus one finds a system analysed for its symmetries without any regard to its singularities or the nature of any equilibrium points or some permutation of these three. In the case of systems of nonlinear first order ordinary differential equations the dynamical systems approach initiated by Poincaré has been dominant. There are good reasons for this. Generically systems of nonlinear first order ordinary differential equations are nonintegrable. The strengths of Lie and Painlevé are with integrable systems. The strength of the dynamical systems approach pioneered by Poincaré is in its ability to extract information from nonintegrable systems.

As it has happened, systems of first order nonlinear ordinary differential equations characteristically arise in areas of study such as ecology, economics, medicine and chemistry. In the so-called exact sciences the underlying equations are generically of the second order – even Hamiltonian systems are of even order – due to their Newtonian basis. Consequently there has been a natural separation of the standard modes of investigation of the differential equations in these two different classes of discipline. This is unfortunate. Different approaches should not be regarded as competing but as complementary.

In this paper we analyse a simple problem, that of two competing species, described by the cosmetically modified system (1.3) from the point of view of the singularity analysis of Painlevé. We establish the conditions under which the solutions of this system are analytic functions. For those conditions – some, since the total is infinite – we examine the system to see if it can be reduced to an easily integrable system.

In the naive theory of integrable systems from the standpoint of Lie a differential equation is integrable if it possesses a sufficient number of Lie point (contact) symmetries. There has been a number of examples over the last century of differential equations which are integrable and vet somewhat lacking in point (contact) symmetries. The six Painlevé equations provide the most notable examples [7] [Chapter XIV], but there are more recent examples [1, 14]. The advantage of the more recent examples is that the symmetry analysis is complete whereas the six Painlevé equations have yet to be analysed successfully for their symmetries. In these examples there has been an obvious lack of symmetry in terms of the traditional understanding of symmetry. The obvious lack of symmetry has been due to a failure to understand the meaning of the symmetry in its fullest context. It was perfectly natural for Lie to think in terms of infinitesimal transformations which were functions of the independent, dependent and – eventually – the derivatives of the dependent variables. Lie had a very geometric sense of his transformations. This was a great strength, but also contained the seeds of constraint. When one is involved in the business of the solution of differential equations, the only constraint should be the constraint of mathematical correctness. However, the determination of Lie symmetries of differential equations is not easy when one moves beyond the determination of point (contact for the third and higher order) symmetries. In this respect the Painlevé analysis is easier. One can determine the integrability or not of a system easily. The price to pay is that the precise form of the

solution is not generally available, unless one is content with infinite Laurent expansions.

The approach which we adopt in this paper is that of Painlevé. However, once we have identified the values of the parameters for which the Painlevé analysis indicates integrability, a further step in the analysis of the system would be to look at the possibility of integrability in terms of Lie, *ie* a reduction of the system to an equation which is obviously reducible to quadratures.

2 Singularity analysis: poles and resonances

To determine the leading order behaviour of the system (1.3) we set $x = a\tau^p$ and $y = b\tau^q$, where a, b, p and q are constants to be determined and $\tau = t - t_0$, t_0 being the location of the presumed movable pole. The system (1.3) becomes

$$ap\tau^{p-1} = a\tau^{p} - a^{2}\tau^{2p} - \alpha\rho ab\tau^{p+q} bq\tau^{q-1} = \rho b\tau^{q} - \rho b^{2}\tau^{2q} - \beta ab\tau^{p+q}$$
(2.1)

from which it is evident that balance occurs with the derivatives and the quadratic terms provided p = q = -1. Balance also occurs for p = -1, $q \ge 0$, alternatively $p \ge 0$, q = -1, but this is not singular in the sense of the Painlevé Test and lies without the singularity analysis to determine integrability¹.

With p = q = -1 the dominant terms – the derivatives and the quadratic terms – balance if, as we see from (2.1),

$$-a = -a^{2} - \alpha \rho a b$$

$$-b = -\rho b^{2} - \beta a b$$

$$\Leftrightarrow \begin{pmatrix} a \\ \rho b \end{pmatrix} = \frac{1}{1 - \alpha \beta} \begin{pmatrix} 1 - \alpha \\ -\beta + 1 \end{pmatrix}$$
(2.2)

provided $1 - \alpha\beta \neq 0$. If $1 - \alpha\beta = 0$, $ie \beta = 1/\alpha$, (2.2a) is consistent if $\alpha = 1$, which gives also $\beta = 1$. Then $\rho b = 1 - a$, where a is arbitrary.

In general, $ie \ 1-\alpha\beta \neq 0$, the second arbitrary constant required for the general solution of (1.3) enters at the so-called resonance. To determine when this occurs we set

$$x = a\tau^{-1} + \mu\tau^{r-1} \quad y = b\tau^{-1} + \nu\tau^{r-1}, \tag{2.3}$$

where a and b are given by the (2.2), in the dominant terms of (2.1), ie (2.1) excluding the linear terms of the right-hand side. The terms linear in μ and ν give the system

$$\begin{pmatrix} r - 1 + 2a + \alpha \rho b & \alpha \rho a \\ \beta b & r - 1 + \beta a + 2\rho b \end{pmatrix} \begin{pmatrix} \mu \\ \nu \end{pmatrix} = 0$$
 (2.4)

for which a nontrivial solution exists if

$$r^{2} + \frac{r}{1 - \alpha \beta} (2 - \alpha - \beta) + \frac{1}{1 - \alpha \beta} (1 - \alpha)(1 - \beta) = 0,$$

 1 The reader is referred to Ramani et al [16] or Tabor [17] for an account of the details of the application of the test.

ie

$$r = -1, -\frac{1}{1 - \alpha \beta} (1 - \alpha)(1 - \beta),$$
 (2.5)

where the first root is generic.

In general the second root is not a positive integer. It is n(>0) if α and β satisfy the constraint

$$\beta = \frac{n+1-\alpha}{(n-1)\alpha+1}.\tag{2.6}$$

We note that the parameter ρ does not appear in this expression. This is a consequence of the parameterisation introduced in (1.2) and we recall that that parameterisation was introduced on hindsight². In the case of the zero resonance both α and β are of like sign. This must be positive to maintain the qualitative property that the model be one for competing species. Were they both negative, the situation being modelled would be a type of symbiosis.

One could also contemplate that the second, nongeneric, resonance be a negative integer say that the Laurent expansion take the form of a Left Painlevé Series [10, 3], ie an expansion commencing at the leading order power, -1, and with the exponents diminishing to $-\infty$. However, the presence of nondominant terms is incompatible with the existence of a Left Painlevé Series and so n must necessarily be nonnegative.

3 Compatibility

When $1 - \alpha\beta = 0$, the resonance is r = 0 and there is no need to consider the compatibility of the nonresonant terms, x and ρy in (1.3a) and (1.3b) respectively, since they, by definition, enter the expansion at a power higher than that at which the arbitrary constant enters. Elsewise, ie for r a positive integer, compatibility must be verified. For an unspecified r = n we substitute

$$x = \sum_{i=0}^{n} \tau^{i-1}, \quad y = \sum_{i=0}^{n} \tau^{i-1}$$
(3.1)

into (1.3) to obtain the recurrence relations

$$(i-1)a_{i} = a_{i-1} - \sum_{j=0}^{i} a_{i-j} (a_{j} + \alpha \rho b_{j}), \quad i = 1, \dots$$

$$(i-1)b_{i} = \rho b_{i-1} - \sum_{j=0}^{i} (\beta a_{j} + \rho b_{j}) b_{i-j}$$
(3.2)

which provides pairs of linear simultaneous equations for the unique determination of the pairs of coefficients (a_i, b_i) for i = 1, n - 1. At i = n the coefficient matrix of (a_n, b_n) and

²One notes that this also gives part of the result, videlicet $\beta = 1$ already obtained for n = 0. That case must be derived by the alternate analysis given above since there is also the requirement $1 - \alpha\beta = 0$ which is precluded here.

requirement for the consistency of the system imposes a second constraint on α , β and ρ additional to that in (2.6). Thus at i = n (3.2) gives

$$\begin{pmatrix} n + a_0 & \alpha \rho a_0 \\ \beta b_0 & n + \rho b_0 \end{pmatrix} \begin{pmatrix} a_n \\ b_n \end{pmatrix} = \begin{pmatrix} a_{n-1} - \sum_{j=1}^{n-1} a_{i-j} (a_j + \alpha \rho b_j) \\ b_{n-1} - \sum_{j=1}^{n-1} (\beta a_j + \rho b_j) b_{i-j} \end{pmatrix}$$
(3.3)

when the basic constraint (2.2) is taken into account. The condition for compatibility is that

$$(n+a_0)\left[b_{n-1} - \sum_{j=1}^{n-1} (\beta a_j + \rho b_j) b_{i-j}\right] - \beta b_0\left[a_{n-1} - \sum_{j=1}^{n-1} a_{i-j} (a_j + \alpha \rho b_j)\right] = 0 \quad (3.4)$$

which is not a particularly transparent expression for general values of n. However, it does provide a second constraint on the parameters α , β and ρ . Consequently for each value of n there is a curve in the three-dimensional parameter space for which (1.3), hence (1.1), passes the Painlevé Test and so is integrable in terms of analytic functions.

To determine the constraints on the values of the parameters for which (1.3) passes the Painlevé Test we adopt the algorithmic procedure proposed by Hua [6]. Instead of taking a particular value for the resonance we work our way through the recurrence conditions (3.2) for increasing values of i. For each new value of i we allow for branching of the algorithm by posing the question of whether the coefficient matrix be singular or not. If it be singular, the constraints are calculated. If it be not singular, the coefficients (a_i, b_i) are computed and we move to the next value of i. We summarise our results.

The system

$$\dot{x} = x - x^2 - \alpha \rho xy$$

$$\dot{y} = \rho y - \rho y^2 - \beta xy$$

has a simple movable pole and may be written in terms of the Laurent expansion

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

in which the second arbitrary constant enters at, for example,

$$\tau^{-1} \quad \text{if} \quad 1 - \alpha \beta = 0 \quad \text{else} \left(\begin{array}{c} a_0 \\ \rho b_0 \end{array} \right) = \left(\begin{array}{c} (1 - \alpha)/(1 - \alpha \beta) \\ (1 - \beta)/(1 - \alpha \beta) \end{array} \right)$$

$$\tau^0 \quad \text{if} \quad \alpha + \beta = 2 \quad \text{else continue}$$

$$\tau^1 \quad \text{if} \quad \beta = \frac{3 - \alpha}{\alpha + 1} \quad \text{else continue}$$

$$\tau^2 \quad \text{if} \quad \beta = \frac{4 - \alpha}{2\alpha + 1} \quad \text{else continue}$$

$$\tau^3 \quad \text{if} \quad \beta = \frac{5 - \alpha}{3\alpha + 1} \quad \text{else continue}, \ etc.$$

$$(3.5)$$

One notes that the relationship between α and β which determines the Kowalevskaya exponent is independent of the value of ρ . The value of ρ does, however, enter into the relationship between the coefficients a_n and b_n and the resonance, n. Consequently the integrable cases of the system (1.3), hence (1.1), are found on that section of a curve in a two-dimensional space of parameters for which both α and β are positive.

4 Nontrivial equilibrium point, stability and integrability

The cases of (1.3) which are integrable in the sense of Painlevé are given when the parameters α and β satisfy the constraint (2.6). For r=0 the system is

$$\dot{x} = x - x^2 \rho xy
\dot{y} = \rho y - \rho y^2 - xy,$$
(4.1)

where the constraint $1 - \alpha \beta = 0$ is further constrainted to be $\alpha = \beta = 1$. When r = 1, we have

$$\dot{x} = x - x^2 - \alpha \rho xy
\dot{y} = \rho y - \rho y^2 - (2 - \alpha) xy,$$
(4.2)

where the additional constraint for consistency is $\rho^2 = 1$. Since $\rho = -1$ is not physical, we need consider only $\rho = 1$. In the case of r = 2 we find that

$$\dot{x} = x - x^2 - \alpha \rho xy
\dot{y} = \rho y - \rho y^2 - \frac{3 - \alpha}{\alpha + 1} xy,$$
(4.3)

for which they are two possible, physically acceptable, constraints on the value of ρ , videlicet $\rho = 1, \frac{1}{2}(1+\beta)$.

In general the system to be solved is

$$\dot{x} = x - x^2 - \alpha \rho xy$$

$$\dot{y} = \rho y - \rho y^2 - \frac{n+1-\alpha}{(n-1)\alpha+1} xy$$
(4.4)

subject to the constraint imposed by the requirements of consistency. For increasing values of r the possibilities become more complex and we do not list them.

The equilibrium points of (4.4) are (0,0), (1,0), (0,1) and (x_4,y_4) , where the first three are trivial, (x_4,y_4) is nontrivial and

$$(x_4, y_4) = \left(\frac{(1 - \alpha \rho)[(n - 1)\alpha + 1]}{(1 - \alpha)^2}, \frac{\alpha - n - 1 + \rho + (n - 1)\alpha \rho}{\rho (1 - \alpha)^2}\right). \tag{4.5}$$

To determine the nature of the nontrivial equilibrium point we examine the signs of the determinant and trace of the Jacobian matrix at that point. We have

$$d = \frac{(1 - \alpha \rho)[\alpha[1 + (n - 1)\rho] + \rho - 1 - n]}{(1 - \alpha)^2}$$

$$t = \frac{(1 - \alpha)[(1 - \alpha \rho)n + \alpha \rho - \rho]}{(1 - \alpha)^2}.$$
(4.6)

We recall that a nontrivial equilibrium point exists only for $n \ge 1$. For an equilibrium point in the first quadrant and $n \ge 1$ (4.5) requires that

$$1 - \alpha \rho > 0 \quad \text{and} \quad \alpha - n - 1 + \rho + (n - 1)\alpha \rho > 0 \tag{4.7}$$

so that d > 0 automatically.

We now consider the sign of the trace. Suppose that $\alpha > 1$. Then from (4.7a) $\rho < 1$ and the second term of the denominator of (4.7b) is

$$(1 - \alpha \rho)n + \alpha \rho - \rho > \alpha \rho - \rho = \rho(\alpha - 1) > 0$$

so that t < 0 and the nontrivial equilibrium point is stable.

Suppose now that $\alpha < 1$. Then from (4.7b)

$$-[(1 - \alpha \rho)n + \alpha \rho - \rho] + \alpha - 1 > 0$$

$$-[(1 - \alpha \rho)n + \alpha \rho - \rho] > 1 - \alpha$$

$$(1 - \alpha \rho)n + \alpha \rho - \rho < \alpha - 1 < 0,$$

$$(4.8)$$

ie t < 0 and the nontrivial equilibrium point is stable.

Thus we have the result that the existence of a stable nontrivial equilibrium point coincides with the possession of the Painlevé Property.

5 Comment

In this paper we have investigated a simple model for competing species in terms of the possession of the Painlevé Property, ie the existence of an analytic solution expressible as a Laurent expansion about a movable singular point. We found that for a constraint on the parameters in the model the system (1.3) possesses the Painlevé Property. Furthermore we saw that in those cases for which the system (1.3) possess the Painlevé Property and a nontrivial equilibrium point that nontrivial equilibrium point was stable for all values of the parameters permitted by the constraint. A nontrivial equilibrium point can exist for values of the parameters other than those imposed by the constraint of the possession of the Painlevé Property. This nontrivial equilibrium point can be stable, but need not be. Equally it could be a saddle point. It would appear that the possession of the Painlevé Property, apart from the case $1 - \alpha\beta = 0$, restricts the nontrivial equilibrium point to be stable. One finds it difficult to believe that this is a coincidence.

The Painlevé Analysis is based upon the existence of a polelike similarity in the complex time plane. This singularity could be for complex time or for real-time. In the case of the latter it must be in the past, $ie\ t_0 < 0$, since every trajectory starting in a bounded region of the first quadrant beyond that defined by the maximal ordinates of the isoclines and the axes remains bounded and ultimately approaches one of the equilibria. In the case of the conditions for the possession of the Painlevé Property all three equilibria are possible limit points.

To conclude with a slightly amusing point we note that the case $1 - \alpha\beta = 0$ for which the existence of a nontrivial equilibrium point is not possible since the isoclines are parallel does exhibit a feature often observed in the case of systems of first-order equations

possessing the Painlevé Property. We solve (4.1a) for y and substitute this into (4.1b) to obtain the scalar second-order equation

$$\frac{\ddot{x}}{x} - 2\frac{\dot{x}^2}{x^2} + (2 - \rho)\rho\dot{x}x + \rho - 1 + (1 - \rho)x = 0.$$
(5.1)

With the transformation w = 1/x, (5.1) becomes the linear nonhomogeneous second-order equation

$$\ddot{w} + (2 - \rho)\dot{w} + (1 - \rho)w = 1 - \rho. \tag{5.2}$$

Equation (5.2) is trivially solved to give

$$w = Ae^{-t} + Be^{(\rho - 1)t} + 1 \tag{5.3}$$

from which x and y follow easily.

Equation (5.2) is a second-order equation of maximal symmetry since it possesses eight Lie point symmetries [11] [p 405] with the Lie algebra sl(3,R). The two-dimensional system of first-order equations, (4.1), possesses the Painlevé Property and is linearisible as demonstrated above. Similar instances can be found in references [9, 14, 2].

In the case of (4.2), for which we consider only the physically admissible case $\rho = 1$ of the two given by $\rho^2 = 1$, we have a two-dimensional example of a class of three-dimensional models for three competing species which was treated by May and Leonard [12]. We remark that this is the only resonance for which the integrable cases take the form considered by May and Leonard. The addition of (4.2a) and (4.2b) gives the equation

$$\dot{\zeta} = \zeta - \zeta^2,\tag{5.4}$$

where $\zeta = x + y$, which is simultaneously a Riccati equation, a Bernoulli equation, a variables separable equation and the logistic equation. In the guise of either of the first two (5.4) is manifestly linearisible. The solution of (5.4) is

$$\zeta(t) = \frac{1}{1 + Ae^{-t}}. (5.5)$$

With this solution (4.2a) may be written as the linear first-order equation

$$\left(\frac{1}{x}\right)^{\cdot} + \left(1 - \alpha\zeta(t)\right)\left(\frac{1}{x}\right) = 1 - \alpha \tag{5.6}$$

which has the solution

$$x(t) = \frac{e^t}{\left(A + e^t\right)^\alpha - \left(A + e^t\right)},\tag{5.7}$$

where A and B by the two constants of integration. Again we see that the constraints imposed by the requirement of integrability in the sense of Painlevé leads through a linearisible equation to a straightforward quadrature.

Acknowledgements

PGLL expresses his deep appreciation of the generous hospitality of Dr and Mrs J Miritzis of Mytilene, Lesvos, Greece, during the period in which this work was undertaken and acknowledges the continued support of the National Research Foundation of South Africa and the University of Natal.

References

- [1] Abraham-Shrauner B, Govinder KS & Leach PGL, Integration of second order equations not possessing point symmetries, *Phys Lett A* **203** (1995), 169–174.
- [2] Andriopoulos K & Leach PGL, The Ladder Problem: Painlevé integrability and explicit solution (preprint: GEODYSYC, Department of Mathematics, University of the Aegean, Karlovassi 83 200, Greece), 2002.
- [3] Feix MR, Géronimi C, Cairó L, Leach PGL, Lemmer RL & Bouquet SÉ, On the singularity analysis of ordinary differential equations invariant under time translation and rescaling, J Phys A: Math Gen 30 (1997), 7437–7461.
- [4] Hirsh MW & Smale S, Differential Equations, Dynamical Systems and Linear Algebra, Academic Press, New York, 1974.
- [5] Hsu S-B, Hubbell SP & Waltman, A contribution to the theory of competing predators *Ecological Monographs* **48** (1979), 337–349.
- [6] Hua DD, Cairó L, Feix MR, Govinder KS & Leach PGL Connection between the existence of first integrals and the Painlevé Property in Lotka-Volterra and Quadratic Systems, Proc Roy Soc Lond 452 (1996), 859–880.
- [7] Ince EL, Ordinary Differential Equations, Longmans, Green & Co, London, 1927.
- [8] Kowalevski Sophie, Sur le problème de la rotation d'un corps solide autour d'un point fixe, *Acta Math* **12** (1888), 177–232.
- [9] Leach PGL, Flessas GP & Cotsakis S, Symmetry, singularities and integrability in complex dynamics I: The reduction problem, *J Nonlin Math Phys* **7** (2001), 445–479.
- [10] Lemmer RL & Leach PGL, The Painlevé test, hidden symmetries and the equation $y'' + yy' + ky^3 = 0$, J Phys A: Math Gen 26 (1993), 5017–5024.
- [11] Lie Sophus, Differentialgleichungen, BG Teubner, Stuttgart, 1967.
- [12] May Robert M & Leonard Warren J, Nonlinear aspects of competition between three species SIAM J Appl Math 29 (1975), 243–253.
- [13] Murray JD, Mathematical Biology, Biomathematics Texts 19, Springer-Verlag, Heidelberg, 1989.
- [14] Nucci MC & Leach PGL, An integrable S-I-S model, (preprint: Dipartimento di Matematica e Informatica, Università di Perugia, 06123 Perugia, Italy), 2002.
- [15] Pianka EL, Competition and niche theory in: Theoretical Ecology: Principles and Applications, May RM, Blackwells, Oxford, 167-196, 1981.

- [16] Ramani A, Grammaticos B & Bountis T, The Painlevé property and singularity analysis of integrable and nonintegrable systems *Phys Rep* **180** (1989), 159–245.
- [17] Tabor M, Chaos and Integrability in Nonlinear Dynamics, John Wiley & Sons, New York, 1989.